

The deployment of visual attention during temporal integration: An electrophysiological investigation

ELKAN G. AKYÜREK AND STEVEN K. MEIJERINK

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

Abstract

The deployment of attention during temporal integration was investigated with event-related potentials. Attentional selection of an integrated percept and an actual singleton were examined. Integration performance was related to modulations of the N2pc, N2, and P3 components. Singleton localization performance was reflected in N2pc and P3 only. Of note, the singleton N2pc developed and subsided earlier than the integration N2pc. The singleton P3 seemed to develop in a single deflection, while the integration P3 showed two more distinct deflections. Physical stimulus differences could not explain these results. The N2pc and N2 modulations showed that attending to an integrated percept is not slower per se, but does differ from attending to a singleton. Integrated percepts furthermore have special correlates in late stages of perception (i.e., the P3). These differences are linked to the unique demand to combine and represent successive stimuli.

Descriptors: Temporal integration, Spatial attention, Visual event-related potential, N2pc, N2, P3

Temporal information is of vital importance to visual perception, because it affords the ability to not only perceive *what* was seen, but also *when* it was seen. An important aspect of temporal perception is deriving the correct order of events. Ordering perceptual input is essential for things like seeing motion or perceiving causality between the actions of two objects (Burr, Ross, & Morrone, 1986; Shallice, 1964). Before such order can be made, however, the underlying events themselves have to be perceptually interpreted and construed—a process referred to as integration.

Integration is a process that plays a role on very basic levels of perceptual processing (e.g., layers of visual cortex taking input from the optic nerve), as well as on more advanced ones. On the earliest levels of processing, successive stimulation of the neurons may be transformed into a single, stronger output signal, due to the physiology and input response functions of those neurons. Such processes play an important role when continuous light is perceived from sources that are in reality discontinuous, such as emitted by fluorescent light bulbs or cathode ray tube (CRT) monitors, and when stimuli produce visible persistence (e.g., Hecht & Shlaer, 1936; Hogben & Di Lollo, 1985). It has even been suggested that perception is not continuous altogether, and depends on a cyclic neuronal activity pattern (VanRullen, Carlson, & Cavanagh, 2007; VanRullen & Koch, 2003), which may call for integration across such a “travelling perceptual moment” (Allport, 1968).

More complex integration mechanisms than neuronal summation are needed to solve integration across larger time intervals, and it is likely that such intervals are common. A typical example of more complex integration is watching television at the standard frame rate of 24 frames per second. These sequential still images are interpreted by the brain as (more or less) fluid motion. In these circumstances, information is carried over between at least two frames of 42 ms each, at which point perceptual processing has advanced well beyond the early visual areas of the brain (e.g., Kirchner, Barbeau, Thorpe, Régis, & Liégeois-Chauvel, 2009).

The Span and Locus of Temporal Integration

A debate has risen in the literature with regard to the time span that can be covered by temporal integration. On one side are reports of integration across intervals of up to almost 3 s (Brockmole, Irwin, & Wang, 2003; Brockmole, Wang, & Irwin, 2002). On the other side are theories that attribute temporal integration to low-level mechanisms exclusively (Coltheart, 1980). Both these points of view have been challenged. For instance, evidence against late integration has been provided by Jiang and colleagues, who demonstrated that consolidation in visual working memory, rather than temporal integration, is a likely candidate to account for performance on integration tasks spanning longer intervals (Jiang, 2004; Jiang, Kumar, & Vickery, 2005; Kumar & Jiang, 2005). Visser and Enns (2001) have shown that attention can be implicated in integration even across the shortest of intervals (<40 ms), which argues against theories of integration based purely on low-level mechanisms. As these somewhat paradoxical results will illustrate, this debate is not yet settled.

The authors would like to thank Peter Albronda for technical support with the electrophysiological data acquisition, and Rolf Verleger for detailed and most helpful comments on a previous draft of this article.

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

This issue concerning the temporal range of integration is closely tied to the locus of temporal integration in the perceptual system. An early locus of integration would suggest it is a relatively quick, online process, which should also produce its output (i.e., integrated events) rather quickly. Some studies on the spatial counterpart of temporal integration (namely, feature integration; Treisman, 1996) suggest that such an early locus may be expected (for effects of spatial properties on temporal integration, see also Hermens, Scharnowski, & Herzog, 2009). Studies by Schoenfeld and colleagues (2003), Valdes-Sosa, Bobes, Rodriguez, and Pinilla (1998), and Zhang and Luck (2009) have shown that spatial integration can drive attentional selection with little delay.

Yet, this may also depend on what is being integrated. For instance, a color may be bound to an object or just a particular location in the visual field in early visual cortex (Zeki, 1978), but an abstract representation of “LEFT” that fits to both an object in the left visual field and the hand with which to execute a response later would involve wholly separate brain regions, and presumably more time to accomplish (Hommel, Müssele, Aschersleben, & Prinz, 2001). Furthermore, temporal integration of longer intervals would seem to require “stalling” subsequent perceptual processes until the extended integrated event was available—a scenario that may not often be feasible. Conversely, a late locus of temporal integration (e.g., at the time of memory consolidation) would predict that most perceptual processes finish before it. It is of importance to the present study that both predictions are testable: Depending on the locus of integration, the deployment of attention towards a stimulus should also differ. In particular, if integration has an early locus (i.e., within ~200 ms), attentional selection of an integrated percept should not be much delayed as compared to the selection of a simultaneous stimulus. If the locus of integration is in working memory, that is, late, the prediction would be that attention may be entirely unable to select integrated percepts until enough time has passed for consolidation to complete. The present study was designed to test these predictions.

Neurophysiological Evidence

In order to chart ongoing perception, and the deployment of attention during temporal integration in particular, the event-related potential (ERP) technique was used in the present study. Until recently, little was known with regard to the neural mechanisms underlying temporal integration. Two recent studies investigated the components of the ERP that are involved in temporal integration. The first of these was conducted by Akyürek, Riddell, Toffanin, and Hommel (2007), and measured the ERP elicited in a two-target, rapid serial visual presentation (RSVP) paradigm, which is known to elicit the attentional blink (Broadbent & Broadbent, 1987; Raymond, Shapiro, & Arnell, 1992). The attentional blink is the increased difficulty observers experience when trying to identify the second target when it follows the first target within an interval of 500 ms. In this study, the crucial condition was one in which the attentional blink was avoided despite the targets falling within the 500-ms interval: Lag 1 (see also Visser, Bischof, & Di Lollo, 1999). At Lag 1, the targets follow each other directly, without intervening distracters, and as such they may be integrated into the same event representation if the conditions are right (Akyürek et al., in press; Akyürek & Hommel, 2005; Akyürek, Toffanin, & Hommel, 2008; Hommel & Akyürek, 2005; Potter, Staub, & O'Connor, 2002). When this happens, the penalty involved in creating two events (one for each target) is avoided, which results in an escape from the attentional blink.

The study by Akyürek et al. (2007) showed that the N2 and P3 components of the ERP were implicated in temporal integration at Lag 1. The P3 component might be seen as a reflection of the last stage of perception, or even its end result, and it is commonly associated with consolidation in short-term memory and the transfer between perception and response initiation (Donchin & Coles, 1988; Polich, 2007; Verleger, Jaśkowski, & Wascher, 2005). The involvement of the N2, however, suggested that integration was indeed able to influence ongoing perceptual processes. The N2 component is a relatively early perceptual component, and has been associated with the detection and attentional selection of task-relevant singletons in visual search, spatial grouping, and context homogeneity processing (Heinze, Luck, Mangun, & Hillyard, 1990; Luck & Hillyard, 1994a; Schubö & Müller, 2009; Schubö, Schröger, & Meinecke, 2004; Schubö, Wykowska, & Müller, 2007).

The second study was carried out by Akyürek, Schubö, and Hommel (2010), who used a so-called missing element task (MET), a variant of which was employed in the present study as well. This task was developed on the basis of the classic paradigms used to study iconic memory and visible persistence, but which may also be viewed as most indicative of temporal coding (Di Lollo, 1977, 1980; Dixon & Di Lollo, 1994; Hogben & Di Lollo, 1974). It consisted of two successive stimulus displays, with a 10-ms interval in between. Together, the displays presented a square grid of 5 × 5 dots, but on each display only 12 dots were shown (i.e., 24 instead of 25 in total). The final missing dot then had to be detected and localized by the observers. The task can only be solved easily if the two displays are perceptually integrated, and the likelihood of integration depends on the duration of the displays. In particular, at 70-ms duration of the first display, and 10-ms for the second, success rate was around 50%. Akyürek et al. (2010) used this 50% level at 70-ms duration to compare the ERP elicited by trials on which integration succeeded with trials on which it did not (i.e., keeping physical stimulation identical).

It was shown that integration increased the amplitude of the N1 and N2 components, and modulated the P3 as well. Amplitude was decreased on an early (part of the) P3 component observed in this study, and increased on a late P3 component. The involvement of the N1 in this study was particularly salient. The N1 is one of the earliest components of the visual ERP at approximately 170 ms poststimulus at occipital electrode sites in the integration task, and has been associated with stimulus discrimination (Vogel & Luck, 2000). The N1 is also independently modulated by the deployment of spatial attention (Luck, Heinze, Mangun, & Hillyard, 1990; Mangun, 1995).

The Present Study

The ERP components implicated in the above-mentioned studies do not yet reveal the whole picture, however. An early modulation of the ERP, such as on the N1, does suggest that temporal integration starts relatively quickly, but the consequences of that start are unclear. It may well be that integration is not instantaneous but rather a process that takes some time to actually *finish*. Thus, even though initial integration steps may be traced back to the N1, the integrated percept may not yet be completed and thereby available to the perceptual system until more time has passed. That implies it may not be possible to attend to an integrated percept as quickly as to a veridical stimulus.

In order to tackle this issue, the present study measured a component that is able to track attentional deployment towards the integrated percept (as well as towards a singleton): the N2pc. The

N2pc is a sensitive measure of the deployment of attention to either side of the visual field (Eimer, 1996; Kiss, van Velzen, & Eimer, 2008; Luck & Hillyard, 1994b). There is some debate as to the precise function of the N2pc, for instance, whether it reflects attentional feature processing or attentional filtering functions, but its ability to reveal early lateral attentional deployment was of primary importance for the present study. Crucially, a lateralization of the missing element was introduced to the MET in the present study, which emerged only when the second stimulus display was shown; that is, when integration of the two displays produced the (lateralized) location of the missing element. In other words, the integrated percept was lateralized. At this same moment in time, on other trials, the missing element was replaced by an actual singleton (red square), which allowed the comparison of the N2pc towards the singleton with the N2pc towards the missing element.

The primary prediction of the present study was that any delay in completing integration should impair attentional processing, resulting in reduced N2pc amplitude. Furthermore, as hypothesized by Akyürek et al. (2010), increased N2 amplitude that is observed during integration may be related to spatial grouping across the two stimulus displays. Because localizing a singleton should not require such spatial processing, it was expected that increased N2 amplitude should be observed during successful integration, but not necessarily during successful singleton detection. Finally, if the dual P3 peaks observed previously by Akyürek et al. (2010) are indeed a result of integration (rather than being strictly stimulus induced), then it may be expected that a more singular P3 is observed in conditions that do not require (or achieve) integration.

Experiment 1

Experiment 1 was designed to measure the ERP to a missing element task, and to make the comparison between successful and unsuccessful integration (Akyürek et al., 2010). Furthermore, a condition was added in which the missing element was replaced by an actual singleton, whose detection did not depend on the integration of the two displays. Note that integration of the two displays was nonetheless possible in both conditions. However, even if the displays in the singleton condition were to be integrated, this would not be a prerequisite of correct localization, and would therefore by definition be less frequent. The two conditions thus allowed the comparison between the ERP of an integrated percept (i.e., the missing element) and that of an actual stimulus (i.e., the singleton), thereby charting potential differences in attentional selection (although perhaps underestimating the difference due to chance integration in the singleton condition). The relevant components of the ERP were, first, those previously investigated in the context of (temporal) integration (P1, N1, N2, and P3). Second, the paradigm was slightly adapted to allow the measurement of lateralized components, in particular, the N2pc.

Method

Participants. Twenty-five students (17 female, 8 male) at the University of Groningen participated for course credit. Informed consent was obtained in writing, and the study was approved by the Ethical Committee Psychology of the University of Groningen beforehand. Participants were unaware of the purpose of the experiment and reported normal or corrected-to-normal vision. Mean age was 20.4 years (range 18–28 years). The physiological data from two female participants were excluded from analysis because the combination of their task performance and the high

number of artifacts in the relevant segments of their electroencephalogram (EEG) resulted in fewer than 40 observations in one of the cells of the design (see below). The mean age of the remaining participants was 20.6 years (same range).

Apparatus and stimuli. Participants were individually seated in a dimly lit and sound attenuated testing chamber at a distance of approximately 50 cm from the screen (not fixed). Posture was monitored throughout the experiment by means of a video camera installed on the wall in front of the participant. An intercom system enabled two-way communication, in case of need. The 17" CRT screen was driven by a computer running Microsoft Windows XP, and refreshed at 100 Hz with a resolution of 800 × 600 pixels in 16-bit color. The experiment was programmed in E-Prime 2.0 Professional (Psychology Software Tools). Responses were recorded with a standard mouse. A white background was maintained throughout the experimental trials. The experimental stimuli consisted of black squares, arranged in a 5 × 5 grid centered on the screen. The grid was made up of 25 invisible fields of 20 × 20 pixels, within which the squares were centered in turn, each measuring 10 × 10 pixels. In the singleton condition, a single red (RGB 255, 0, 0) square appeared in place of the missing element on the second display.

Procedure and design. There were 896 experimental trials, which were preceded by 20 practice trials that were excluded from analysis. Trials continued without interruption within the 4 experimental blocks of 224 trials each. After each block, the participants were able to take a break. Participants initiated a block of trials by clicking the right mouse button. Each trial started with a variable blank interval of 600 to 800 ms. The experimental stimuli then followed, which were presented in two successive display frames, each containing a random selection of 12 out of 25 possible squares (without overlap). Thus, one square from the total of 25 was not drawn in either display. On half of the trials, this missing element was replaced by a red singleton in the second display. To optimize the calculation of the lateralized ERP (see below), the location of this missing element or singleton was evenly distributed across both sides of the visual field, and never fell on the central column of the displays. A blank interstimulus interval (ISI) of 10 ms was maintained between the two display frames. The duration of the first display frame varied between 40, 70, and 100 ms, while that of the second frame was set at 10 ms (a duration that also minimizes backward masking effects; see Enns & Di Lollo, 2000). All trial types were randomly intermixed.

Figure 1 shows a schematic representation of the trial structure. Trials were structured so that response input was delayed, minimizing associated effects on the ERP. After the offset of the last stimulus display, a 600-ms blank interval followed before the response screen appeared. The response screen consisted of an array of squares similar to the stimulus arrays, except that the stimuli were drawn as outlines with a line thickness of 1 pixel rather than as solid squares. The response screen stayed on screen for 1,200 ms or until a response was registered. Participants indicated the location of the missing element, or alternatively the red square, by moving a cross-shaped mouse cursor to the corresponding square outline and clicking it (using the left mouse button). Trials were counted as correct when the participant clicked within the 20-pixel virtual perimeter of the square outline that constituted the missing element or singleton. Finally, a brief display of 200 ms was added after the response screen at the end of each trial, which provided performance feedback to the participant (":)") for correct

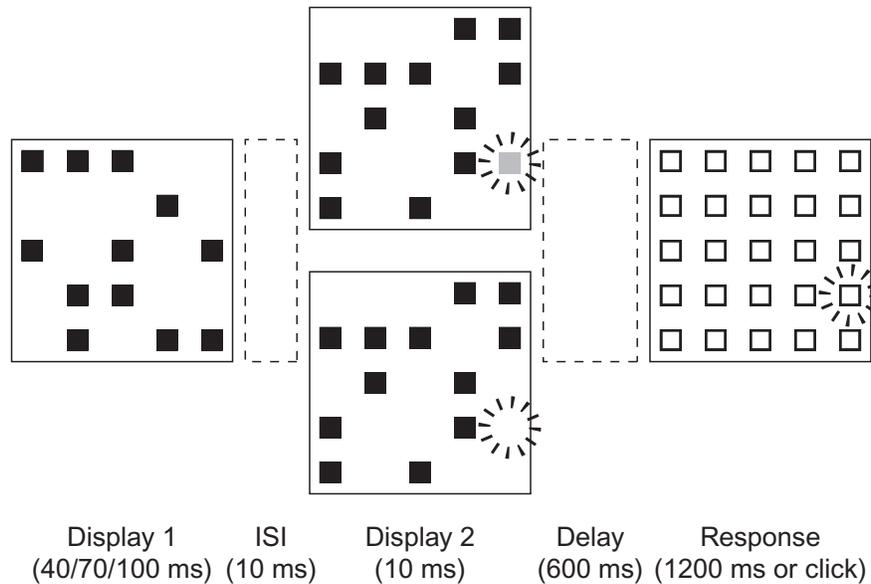


Figure 1. Schematic representation of the procedure in Experiment 1. Two brief stimulus displays presented 12 out of 25 black squares in an invisible 5×5 grid, with a 10-ms blank ISI. Depending on the condition, the one remaining square location remained white (integration condition; Display 2 bottom), or it was red (singleton condition; Display 2 top). In both cases, Display 2 is the first moment on which the perceptual information is available to solve the task. After another blank delay of 600 ms, the response screen appeared. The target location is indicated for illustration purposes only.

responses, and “:” for incorrect responses), and which served to send response information to the EEG acquisition computer.

To measure visual event integration, the ERP to the stimuli on trials on which the response was erroneous (and integration failed) was compared to those on which the response was correct (and integration succeeded). The same comparison was also made for the trials on which a singleton was shown, which then did not reflect integration but singleton detection and localization accuracy. The stimuli under comparison were physically identical (both in appearance and duration). To obtain an approximately equal distribution of correct and incorrect trials, the 70-ms duration condition was chosen as before (Akyürek et al., 2010). This condition was therefore also the most frequent by design (8/14), at the expense of the others (3/14 each).

Mean accuracy was analyzed in a 3×2 repeated measures analysis of variance (ANOVA) with one variable representing the duration of S1 (40, 70, or 100 ms), and one representing the task (integration or singleton). In case of significant tests of sphericity, the degrees of freedom were adjusted using the Greenhouse-Geisser epsilon correction when a variable contained more than two levels.

Electrophysiological recording and data analysis. EEG was recorded with tin electrodes from 64 positions (laid out according to the extended International 10–20 system). The electrodes were referenced to their common average and rereferenced offline to the average of both mastoids. An electrode affixed to the sternum served as ground. Horizontal electrooculogram (EOG) was recorded from the outer canthi of the eyes and the vertical EOG from above and below the left eye. Electrode impedance was kept below 5 k Ω . The REFA 8–72 amplifier used a 140 Hz cut-off filter, and recordings were made at a frequency of 500 Hz.

Using Brain Vision Analyzer 1.05 (Brain Products), EEG was averaged offline into 1,000-ms segments, starting 200 ms before the onset of S1 and ending 800 ms afterwards. Trials with amplitudes exceeding $\pm 80 \mu\text{V}$, voltage steps exceeding $\pm 50 \mu\text{V}$

between two sampling points, and trials with amplitude differences below $0.10 \mu\text{V}$ across a 100-ms interval were excluded from analysis. Ocular artifacts (blinks and eye movements) were corrected using the Gratton-Coles procedure (Gratton, Coles, & Donchin, 1983). Uncorrected horizontal EOG only showed deviations of less than $\pm 1.25 \mu\text{V}$ across the segments in all conditions. The data were filtered 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) to optimize power for early components and reduce low-frequency drifting, but a .1 Hz high-pass was chosen for the P3 analyses and the associated figures, to avoid amplitude attenuation (cf. Kappenman & Luck, 2010). A 200-ms prestimulus interval was used for baseline correction. Trials were categorized into correct, incorrect, and missing responses. The latter category was discarded from the analyses.

The lateral ERP as reflected by the N2pc was examined in an early (240–350 ms) and a late (350–460 ms) window. To compute the N2pc, ipsilateral waveforms (i.e., recorded from the left hemisphere electrode site when the missing element or singleton was in the left visual field, and the same for the right hemisphere site & right visual field) were subtracted from contralateral waveforms (i.e., left site & right visual field, and right site & left visual field). ANOVAs were furthermore performed for mean amplitude values obtained in time windows corresponding to the occipital P1 (90–130 ms after the onset of the first stimulus) and N1 (160–190 ms), the parietal-occipital N2 (230–280 ms), and the parietal P3 in both an early (280–440 ms) and a late (500–660 ms) time window. The following electrodes were chosen for analysis: PO7 and PO8 for the N2pc; PO7, PO8, and Oz for the P1 and N1; POz for the N2; and finally Pz for the P3.

The electrophysiological repeated measures ANOVAs were focused on the comparison of successful and unsuccessful trials at 70 ms S1 duration, which kept the physical appearance of the stimuli as constant as possible. As mentioned, the 70-ms condition was purposefully chosen because it was known to average close to 50% correct/error trials. Thus, S1 duration was *not* used as a

variable in these comparisons, and its place was taken by performance instead, yielding a 2×2 design of Task (integration, singleton) \times Performance (correct, incorrect). To give the reader at least an impression of the change in the ERP elicited by S1 duration, the Appendix figure shows the ERP of correct trials in both integration and singleton conditions, plotted separately for all durations of S1. Further follow-up one-way ANOVAs were conducted on the integration and singleton trials separately (i.e., without the task variable, contrasting only correct and incorrect trials), to investigate performance effects that might have remained hidden in the overall analysis. Finally, if a component was measured across multiple electrodes, this was fed into the analysis as an additional factor (e.g., a three-level electrode variable for the P1 & N1 analysis to test PO7, PO8, and Oz), and violations of sphericity were corrected as before.

Results and Discussion

Behavioral results. Figure 2 shows performance as a function of S1 duration. Behavioral performance was affected by S1 duration, $F(2,48) = 116.59$, $\epsilon = .58$, $MSE = .005$, $p < .001$, $\eta^2 = .83$. Performance peaked at 40 ms (62.6%), and dropped to 51.7% at 70 ms, and finally to 46% at 100-ms duration. There was no overall change in performance elicited by the two different tasks ($F < 1$), indicating that these were closely matched overall. Individual analyses of each condition (i.e., across duration only) confirmed this performance pattern; $F(2,48) = 115.12$, $\epsilon = .71$, $MSE = .004$, $p < .001$, $\eta^2 = .83$ in the integration condition, and $F(2,48) = 22.85$, $\epsilon = .58$, $MSE = .006$, $p < .001$, $\eta^2 = .49$ in the singleton condition.

However, in the overall analysis the task variable did interact with S1 duration, $F(2,48) = 13.39$, $\epsilon = .7$, $MSE = .005$, $p < .001$, $\eta^2 = .36$. The interaction reflected increased performance at 40-ms duration for the integration task compared to the singleton task (66.3% vs. 59%), while integration performance slightly lagged behind singleton performance at 70-ms (50.8% vs. 52.6%) and 100-ms duration (44.3% vs. 47.8%). The data thus demonstrated the expected increase in integration with shorter stimulus duration, which, importantly, was stronger than the effect observed in the singleton conditions. The fact that increased performance with shorter duration was also observed in the singleton condition need not be surprising: This effect likely reflected the diminishing ability of S1 to forward-mask S2 as the former's duration decreases. Note that this is not to say such masking cannot play a role in the integration condition, but that integration at least added further to this possible effect.

Electrophysiological results: N2pc. The top panel of Figure 3A shows the lateralized activity as a difference wave averaged over PO7 and PO8. The bottom panel shows the underlying ipsi- and contralateral waveforms for both task conditions. To also give an impression of activity across the scalp, topographic plots are additionally shown. The first set of analyses concerned lateral components of the ERP, which were split into two time windows. In the early window (240–350 ms), both the performance variable, $F(1,22) = 58.72$, $MSE = .243$, $p < .001$, $\eta^2 = .73$, and the task variable, $F(1,22) = 9.46$, $MSE = .749$, $p < .01$, $\eta^2 = .3$, had a reliable effect. Their interaction was not significant, however, $F < 1.9$. Mean amplitude was more negative on correct trials ($-.94 \mu\text{V}$) than on incorrect ones ($-.15 \mu\text{V}$), and more negative on singleton trials ($-.82 \mu\text{V}$) than on integration trials ($-.26 \mu\text{V}$). Despite the apparent weakness of the N2pc on integration trials in this time window, the performance effect was clearly present, $F(1,22) = 22.48$,

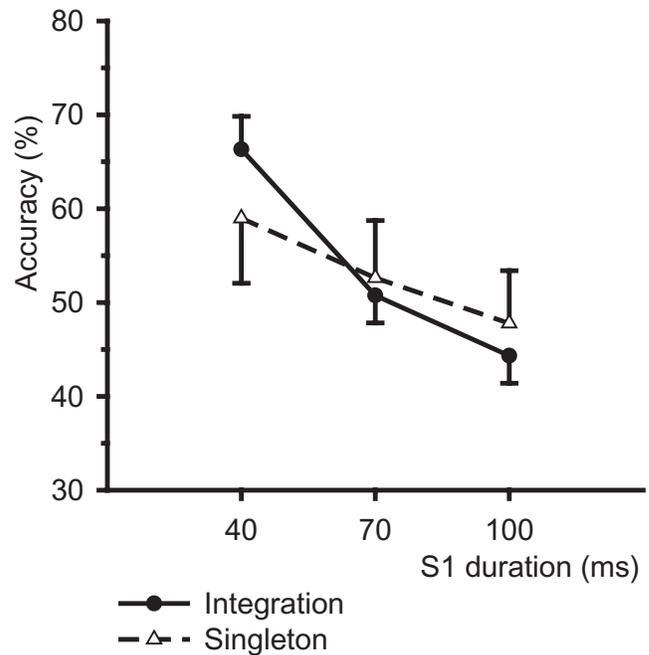


Figure 2. Response accuracy in percent correct in Experiment 1, plotted as a function of the duration of the first stimulus display. Solid lines represent the integration condition, and dashed lines represent the singleton condition. Error bars represent one standard error of the mean (plotted in a single arbitrary direction for visual clarity).

$MSE = .208$, $p < .001$, $\eta^2 = .51$. Amplitude was more negative on trials in which integration succeeded than on those in which it did not ($-.58 \mu\text{V}$ vs. $.06 \mu\text{V}$). Additionally, the correct integration trials differed reliably from zero when tested, $t = 4.23$, $p < .001$. On the singleton trials, performance similarly had an effect, $F(1,22) = 33.63$, $MSE = .3$, $p < .001$, $\eta^2 = .61$. Here, too, correct trials elicited a stronger N2pc (i.e., a more negative deflection) than incorrect ones ($-1.29 \mu\text{V}$ vs. $-.35 \mu\text{V}$).

In the late time window, both main effects of performance, $F(1,22) = 11.56$, $MSE = .335$, $p < .005$, $\eta^2 = .35$, and task, $F(1,22) = 4.58$, $MSE = .893$, $p < .05$, $\eta^2 = .17$, were again significant. The interaction between them was also reliable, $F(1,22) = 5.75$, $MSE = .302$, $p < .05$, $\eta^2 = .21$. The pattern of means was straightforward: Correct trials averaged more negative amplitude than incorrect trials ($-.57 \mu\text{V}$ vs. $-.16 \mu\text{V}$), and integration trials were more negative than singleton trials ($-.58 \mu\text{V}$ vs. $-.16 \mu\text{V}$). The interaction was manifested in a clear difference due to integration success ($.69 \mu\text{V}$ difference), which had no correlate in the singleton trials ($.14 \mu\text{V}$ difference). As expected, the analysis of the integration trials confirmed the performance effect, $F(1,22) = 29.33$, $MSE = .184$, $p < .001$, $\eta^2 = .57$. More negative amplitude was associated with successful integration ($-.92 \mu\text{V}$ vs. $-.24 \mu\text{V}$). In the analysis of the singleton trials, no such effect was present ($F < 1$).¹

1. To check whether the differences between singleton and integration N2pc might have been affected by increased intersubject variability, particularly in the latter condition, a subset of 15 participants was selected whose average integration and singleton performance were closest to each other. The resulting N2pc waveforms were virtually identical to those of the full group, suggesting that intersubject variability did not underlie the observed differences between integration and singleton trials.

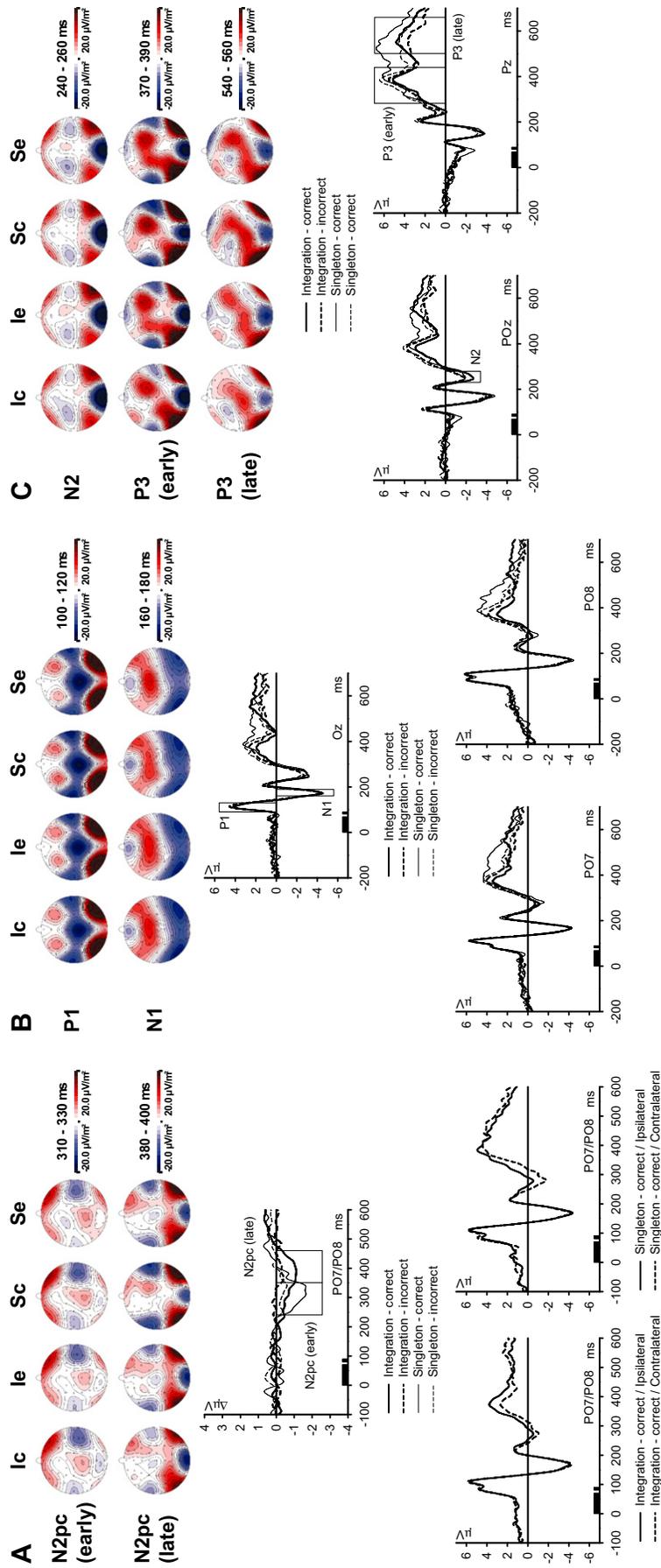


Figure 3. Mean ERP amplitude (μV) in Experiment 1 as a function of time in ms. Shown are the PO7/PO8 electrodes ($\Delta\mu\text{V}$; panel A), PO7, PO8, and Oz (panel B), and finally POz and Pz (panel C). The N2pc plot was low-pass filtered at 25 Hz for visual clarity. Stimulus on-/offset is denoted by the black rectangles on the abscissa. Thick lines represent the integration condition, and thin lines represent the singleton condition. Solid lines represent correct trials, and dashed lines represent incorrect trials. Box outlines delineate analysis windows. Topographical current source density maps were constructed using spherical spline interpolation and are shown for a 20-ms average of the relevant component peaks. From left to right, the maps represent correct integration trials (Ic), incorrect integration trials (Ie), correct singleton trials (Si), and incorrect singleton trials (Se).

Electrophysiological results: P1, N1, and N2. Figure 3B shows ERP amplitude as a function of time for both conditions on the Oz, PO7, and PO8 electrodes. The analysis of the P1 did not show reliable main effects of task ($F < 1$) or performance ($F < 1$). There was a significant main effect of electrode, $F(2,44) = 6.38$, $MSE = 13.592$, $p < .005$, $\eta^2 = .23$. Amplitude seemed to be lower at the Oz electrode ($3.04 \mu\text{V}$) than at PO7 ($4.28 \mu\text{V}$) and PO8 ($4.95 \mu\text{V}$). All of the interaction terms were unreliable ($F_s < 1$). This outcome was expected given that the P1 occurred at only 10–50 ms after S2, which is arguably too early for it to be affected by that stimulus. The absence of effects on the P1 nonetheless showed there were no differences in preparatory processes that might have affected the ERP at this stage.

There were no significant main effects on the N1 ($F_s < 2$). There were no reliable interaction terms either ($F < 1.6$). Neither the analysis of the integration trials ($F < 1$) nor that of the singleton trials ($F < 2.3$) provided evidence that the N1 was modulated as a result of integration or singleton detection.

The analysis of the N2 showed a different picture. Figure 3C (left panel) shows ERP amplitude as a function of time on the POz electrode. The performance variable had a main effect, $F(1,22) = 5.79$, $MSE = 1.445$, $p < .05$, $\eta^2 = .21$. The task variable remained unreliable ($F < 1$), and the interaction term was not significant either ($F < 1.3$). N2 amplitude on correct trials averaged $-1.95 \mu\text{V}$, while incorrect trials came to $-1.34 \mu\text{V}$. The analysis of integration trials showed a clear performance effect, $F(1,22) = 11.54$, $MSE = .784$, $p < .005$, $\eta^2 = .34$. Trials on which integration succeeded averaged $-2.22 \mu\text{V}$, while trials on which it failed averaged $-1.33 \mu\text{V}$. By contrast, the analysis of the singleton trials did not show an effect at all ($F < 1$), indicating that it was the integration trials alone that carried the effect in the overall analysis.

Electrophysiological results: P3. ERP amplitude on Pz as a function of time is shown in Figure 3C (right panel). Performance did not modulate the P3 in the early time window (280–440 ms; $F < 1$). The task variable was reliable, however, $F(1,22) = 8.03$, $MSE = 2.259$, $p < .01$, $\eta^2 = .27$. Less positive amplitude was elicited by integration trials than by singleton trials ($3.72 \mu\text{V}$ compared to $4.6 \mu\text{V}$). Further comparisons did not reveal reliable performance effects in either type of trial ($F_s < 1$).

In the late window (500–660 ms), reliable effects of performance, $F(1,22) = 8.09$, $MSE = 4.691$, $p < .01$, $\eta^2 = .27$, and of task were found, $F(1,22) = 5.71$, $MSE = 6.101$, $p < .05$, $\eta^2 = .21$. The interaction was not reliable ($F < 1$). Correct trials elicited more positive amplitude ($4.81 \mu\text{V}$) compared to incorrect trials ($3.52 \mu\text{V}$). The effect was present, but just shy of significance in the integration trials, $F(1,22) = 4.05$, $MSE = 2.673$, $p < .056$, $\eta^2 = .16$. Amplitude in singleton trials was similarly affected, $F(1,22) = 6.83$, $MSE = 4.301$, $p < .05$, $\eta^2 = .24$. Mean amplitude in correct integration trials averaged $4.04 \mu\text{V}$, compared to $3.06 \mu\text{V}$ for incorrect trials. In the correct singleton trials, amplitude averaged $5.58 \mu\text{V}$, compared to $3.98 \mu\text{V}$ in incorrect trials.

As can be seen from Figure 3C, there is one aspect of the data that is not captured by the analysis of the early and late time windows; the P3 in the singleton condition seemed to develop as more of a single deflection, while the integration condition showed two distinct peaks (early and late), as was also observed in the study of Akyürek et al. (2010). This rather salient difference was captured by an analysis of the interval between the previously used time windows (440–500), which confirmed that the task had a clear impact there, $F(1,22) = 10.94$, $MSE = 7.498$, $p < .005$, $\eta^2 = .33$.

The effect corresponded with higher amplitude in the singleton task ($4.93 \mu\text{V}$) than in the integration task ($3.04 \mu\text{V}$).

In summary, the results showed that integration was observed in modulations of the N2pc, N2, and, to a lesser extent, the P3. The detection and localization of the singleton followed a similar pattern but did not affect the N2. There was no evidence for modulation of the earlier P1 and N1 components. Differences between the integration and singleton trials were apparent across the N2pc, N2, and P3. On the N2pc, the component seemed to develop and disappear earlier on the singleton trials than on the integration trials. On the latter trials, the bulk of the lateral component seemed to be delayed until after 350 ms, but evidence for integration was nonetheless also obtained in the early time window. This suggested that the lateralization in the integration trials might be best characterized not by a late onset of this component, but by a more gradual and prolonged development. On the N2, the main difference seemed to be a lack of a performance effect on the singleton trials, while average amplitude remained quite comparable to that in the integration trials (and the task variable did not significantly affect the means). Finally, on the P3 component the most salient difference seemed to be the double peaks observed in the integration condition, compared to a more singular, sustained component in the singleton condition.

Experiment 2

One might argue that the results of Experiment 1 might also have reflected ERP differences elicited due to physical stimulus differences (i.e., the appearance of a red rather than a white/missing square in S2). The data provide evidence against this idea; the early P1 and N1 components of the ERP should then have reflected these supposed physical differences, but they clearly did not—they were identical for both integration and singleton trials. However, another experiment was designed to address the issue directly, and to further reduce the feasibility of a physical differences account. Experiment 2 was conducted to compare the differences found in Experiment 1 with the differences elicited by the physical properties of S2.

The task was identical to that of Experiment 1, with the exception that there was now only one stimulus display of 10 ms, similar to S2, which contained 24 black squares and either a “missing element” (white/missing square) or a “singleton” (red square). In other words, the two displays were physically integrated into one single display (of only 10 ms), and any differences between the ERPs of these two conditions can be attributed to physical differences between the missing element and the singleton. The implementation of this test was designed to be as close to the physical appearance of Experiment 1, in particular to mirror the time point at which the missing element or singleton appeared (i.e., both were only apparent at S2 in Experiment 1).

This implementation may elicit the concern that set size between experiments might have varied, with regard to the singleton detection task. In Experiment 1, it was theoretically possible to attend to only the second display to locate the singleton (though note that singletons occurred unpredictably amidst integration trials). In this case, set size, being the number of simultaneous squares, would come to 12, whereas in Experiment 2 the full grid of 24 squares was used. This may have facilitated detection of the red singleton in Experiment 1. However, the data showed virtually no evidence of an effect on actual task performance (50.8% vs. 52.6% accuracy in integration and singleton conditions), rendering this assumption unlikely.

Method

Participants. Seventeen new students (12 female, 5 male) participated for course credit. Participation conformed to the same criteria as before. Mean age was 20.4 years (range 18–26 years).

Apparatus, stimuli, design, and procedure. The experiment was identical to Experiment 1, except that S1 and the 10-ms ISI were omitted from the trial procedure. Accordingly, 24 rather than 12 black squares were shown on the remaining display “S2.” As a further consequence, there were no S1 duration conditions anymore either.

Electrophysiological recording and data analysis. Since integration performance played no role in this experiment, the analyses were focused on the task variable exclusively (white vs. red singleton). The same components as those examined in Experiment 1 were considered (N2pc, P1, N1, N2, and P3). Some small adjustments in the time windows (but not electrodes) were made to improve the fit to the observed waveforms. It was furthermore no longer sensible to consider both early and late windows for the N2pc and P3 components (see Figure 4). The time windows used in Experiment 2 were 140–340 ms for the N2pc, 100–140 ms for the P1, 170–200 ms for the N1, 240–290 ms for the N2, and 320–480 ms for the P3.

Results and Discussion

Behavioral results. Behavioral performance was reliably different between the two singleton conditions, $F(1,16) = 16.27$, $MSE = .019$, $p < .001$, $\eta^2 = .5$. The white singleton was clearly easier and averaged 94.3% correct, compared to 75% for the red singleton. The single display task was not particularly difficult, and the observed difference between the conditions was easily explained by the increased contrast ratio of the white singleton with the surrounding black squares, as compared to the contrast ratio of the red square.

Electrophysiological results: N2pc. Figure 4A shows mean lateralized amplitude as a difference wave averaged over PO7 and PO8. The N2pc was similarly affected by singleton type, $F(1,16) = 13.89$, $MSE = .497$, $p < .005$, $\eta^2 = .47$. Amplitude was increased in the white singleton condition ($-2.09 \mu\text{V}$ vs. $-1.19 \mu\text{V}$).

Electrophysiological results: P1, N1, and N2. Figure 4B shows mean amplitude on the Oz, PO7, and PO8 electrodes as a function of time. Singleton type affected the P1 component, $F(1,16) = 6.11$, $MSE = .804$, $p < .05$, $\eta^2 = .28$. The white singleton showed increased amplitude ($1.64 \mu\text{V}$), compared to the red singleton ($1.2 \mu\text{V}$). There was no main effect of electrode, and there was no interaction effect either ($F_s < 1$).

A similar effect of singleton type was observed on the N1 component, $F(1,16) = 39.16$, $MSE = 3.277$, $p < .001$, $\eta^2 = .71$. Increased amplitude was observed for the white singleton ($-6.15 \mu\text{V}$ vs. $-3.91 \mu\text{V}$). There was also a main effect of electrode, $F(2,32) = 6.62$, $MSE = 10.678$, $p < .005$, $\eta^2 = .29$, reflecting increasing amplitude from Oz ($-3.59 \mu\text{V}$) to PO7 ($-5.03 \mu\text{V}$) and PO8 ($-6.47 \mu\text{V}$). The interaction between singleton type and electrode was also reliable, $F(2,32) = 10.13$, $MSE = .54$, $p < .001$, $\eta^2 = .39$. The interaction seemed to reflect a larger amplitude difference due to singleton type at PO8 ($3.16 \mu\text{V}$ difference) than at PO7 ($1.9 \mu\text{V}$) and Oz ($1.67 \mu\text{V}$).

No reliable effect was observed on the N2 component ($F < 2.8$), despite the presence of a comparable trend in the means. Figure 4C (left panel) shows mean amplitude on the POz electrode as a function of time.

Electrophysiological results: P3. Figure 4C (right panel) shows mean amplitude on the Pz electrode as a function of time. The analysis of the P3 again showed a reliable effect of singleton type, $F(1,16) = 5.1$, $MSE = 3.176$, $p < .05$, $\eta^2 = .24$. P3 amplitude was higher in the white singleton condition ($5.93 \mu\text{V}$) than in the red singleton condition ($4.55 \mu\text{V}$).

The results of Experiment 2 clearly showed that the differences observed here between two different singletons in a singular display are not comparable to those observed in Experiment 1. Instead, they showed a rather diametrical pattern, which would have worked against the pattern observed in Experiment 1, not for it. In Experiment 2, the white singleton, in appearance identical to the missing element from Experiment 1, consistently elicited larger component amplitude. Of note, the differences observed in Experiment 1 on the N2pc and P3 component suggested that the missing element elicited lower, and partially delayed, component amplitude. Given the contrasting results of Experiment 2, the differences found in Experiment 1 can most likely be understood as a consequence of integration, rather than of physical stimulus differences.

General Discussion

The present study was designed to investigate the locus of temporal integration in visual perception. To that end, potential differences between the perception and attentional selection of an integrated percept and that of a singleton stimulus were examined. Some salient differences were indeed observed that reflect on the time-course of integration and attention.

N2pc

Primarily, the results of Experiment 1 showed that the N2pc elicited by a missing element in the integration task was different from the N2pc elicited by a singleton. Analysis of the lateralized ERP revealed that N2pc amplitude during integration was slower to develop, peaking close to 400 ms after the onset of the first stimulus. By contrast, at this late point in time there was no detectable lateral activity elicited by the singleton that still remained. Interestingly, even though the amplitude of the integration N2pc was reduced compared to that of the singleton N2pc, it was already present in the early analysis window as well, which covered an interval more commonly associated with the N2pc at around 300 ms post-S1, or 220 ms post-S2. Despite the apparent weakness of this component, it did dissociate between successfully integrated trials and trials on which integration failed. It therefore seemed untenable to propose that attentional selection as reflected by the N2pc was delayed (e.g., due to low perceptual strength), which might have seemed appropriate at first sight of the waveforms.

The key characteristics of the N2pc seemed to lie in component amplitude; the gradual development of the N2pc during integration, and its sustained presence at longer intervals (see also the discussion below). This pattern of amplitude modulation fits well with results from McDonald, Teder-Sälejärvi, Di Russo, and Hillyard (2005), who showed that even attention-induced shifts in the perception of stimulus order modulated the amplitude but not the

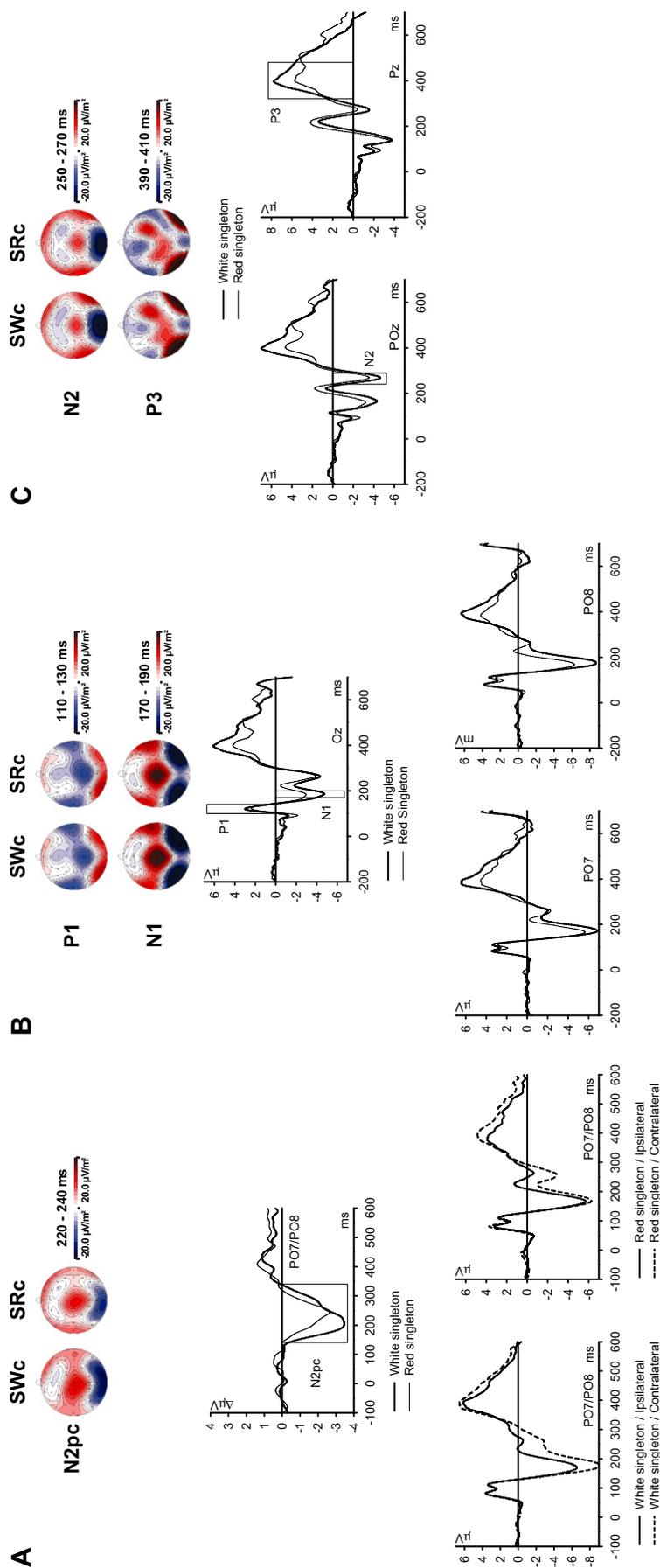


Figure 4. Mean ERP amplitude (μV) in Experiment 2 on correct trials as a function of time in ms. Shown are the PO7/PO8 electrodes ($\Delta\mu\text{V}$; panel A), PO7, PO8, and Oz (panel B), and finally POz and Pz (panel C). The onset of the only remaining stimulus array (“S2”) is set at time zero. Topographical plots represent correct white (SWC) and red singleton trials (SRC) from left to right. Figure conventions are otherwise identical to Figure 3.

latency of early ERP components. The features of the N2pc observed in the present study are furthermore unlikely to be a fluke of the present dataset, as they were also apparent from a reanalysis of the data from Akyürek et al. (2010), even though lateral appearance of the missing element was not strictly balanced in the latter study.

The N2pc elicited by a missing element (i.e., a white singleton) in a single 10-ms display was furthermore shown to differ from the N2pc elicited by a color singleton in Experiment 2. However, this difference was opposite in character to the one observed in Experiment 1. In Experiment 2, the missing element elicited an N2pc that peaked at 200 ms post-“S2,” while that of the color singleton was reliably smaller in amplitude, and, if anything, peaked slightly later. The task did not differ between these conditions, and the differences in the N2pc observed here must therefore reflect the physical properties of the stimuli. At least when no integration is required, the appearance of the missing element seemed to be perceived more easily, as it generally elicited increased amplitude. It is important to note that these physical differences were qualitatively different and (in several aspects) diametrical to the results of Experiment 1, and thus cannot provide an account for the differences observed in that experiment.

When the results of both experiments are taken together, it would thus seem fair to claim that attentional selection as reflected by the N2pc elicited by the critical element is indeed modulated by temporal integration, as described above. Previous behavioral work has suggested that attention can modulate temporal integration, and the range of ERP components previously implicated in integration would certainly allow for such modulation (Akyürek et al., 2010; Visser & Enns, 2001). The present results confirmed and extended this hypothesis, in that they demonstrated how attention as reflected by the N2pc is modulated by temporal integration. The sustained development of the N2pc that was observed during integration may be understood as evidence that the integrated percept gains potency over time. Speculatively, it might reflect ongoing neural synchronization of the two successive displays. This account interprets maximal N2pc amplitude as a reflection of the strongest deployment of lateral attention.

It may also be worthwhile to link these N2pc effects to studies on temporal discrimination, which have shown that the allocation of attention in the visual field may reduce temporal resolution and consequently the ability to detect stimulus on- and offset (Rolke, Dinkelsbach, Hein, & Ulrich, 2008; Rolke, Ulrich, & Bausenhardt, 2006; Yeshurun & Levy, 2003). In the study by Yeshurun and Levy (2003), the ability of observers to detect a temporal gap in the presentation of a probe stimulus was reduced when its location was (exogenously) precued. At the same time, however, spatial resolution was enhanced. The authors suggested that this tradeoff between spatial and temporal resolution may have come about due to attentional facilitation of parvocellular neurons in particular and accompanying inhibition of associated magnocellular neurons. Parvocellular neurons tend to sustain activity longer and show slower decay (Schiller & Logothetis, 1990). Although the association remains speculative, this fits perfectly to the pattern of N2pc activity observed here. Without implying a direct link between parvocellular activity and N2pc amplitude, the latter could be understood as an eventual consequence of the former. It seems clear that further experiments are necessary to investigate the links between temporal integration and the N2pc. The current results support the prediction that bidirectional links between integration and attention will thus emerge.

Sustained Lateral Activity

A noteworthy feature of the lateralized ERP (alluded to above), particularly in the integration condition, was the sustained negativity carrying over into the (early) P3 range. It is possible that this reflected the so-called sustained posterior contralateral negativity (SPCN) or contralateral delay activity (CDA). The SPCN/CDA component is clearly associated with visual short-term memory load (Jolicoeur, Brisson, Robitaille, 2008; Klaver, Talsma, Wijers, Heinze, & Mulder, 1999; Vogel & Machizawa, 2004). As such, it might be indicative of the storage of the missing element or singleton at its spatial location in the present task.

Even though the storage of this information might appear to be similar between both singleton and integration trials, at least from a load perspective, an explanation for the discrepancy between these trials might be that the representation of the integrated percept likely requires more effort to achieve, due to the need to combine information across both stimulus displays. This difficulty might in turn be expressed in suppressed component amplitude. Of course, this account remains post hoc, and necessarily speculative, until further targeted investigation of the relationship between sustained lateral activity and temporal integration.

Nonlateralized Components

Unlike the lateral ERP, which is evoked by the missing element or singleton (i.e., by S2) exclusively by definition, the “normal” ERP may be affected by both S1 and S2. Thus, before considering these components, it is useful to discuss the complexities of the ERP elicited by these two successive stimulus displays. In particular, one might expect the ERP to reflect the superposition of two series of components (i.e., twice P1, N1, N2, P3), elicited by the two displays. There is evidence to suggest that this is not the case, however.

First, as shown in the top panel of the Appendix figure, changing the duration of S1 does not affect the latency of the components until the P3 (see also below), which is inconsistent with a strict superposition view. Second, the inability of S2 to elicit an individual ERP is demonstrated by comparing the bottom panels of the Appendix figure. These plots superimpose the ERP of (red) singleton correct trials of Experiments 1 and 2. The ERP of this condition of Experiment 1 is plotted with the onset of S2 at time zero (i.e., shifted 80 ms; right panel) and with the onset of S1 at zero (left panel), the latter as in the other figures. As can be seen, a clear correspondence is apparent between the ERP elicited in Experiment 2 by its single “S2,” and that of Experiment 1, as elicited by S1. Comparison between S2 from Experiment 1 (i.e., the shifted plot) and “S2” from Experiment 2 reveals no such correspondence. Thus, it seems fair to assume that the ERP observed as a consequence of these two successive stimulus displays is one that largely originates from S1, and that the effects of S2 are expressed as (amplitude) modulations of that ERP—in essence, an expression of the joint, ongoing processing of the stimuli. Without seeking to strongly reject the superposition view, the interpretation of the present results will build on this assumption.²

2. It may be brought forward that a decisive test of this matter would require an experiment that allows for a proper statistical comparison of these ERPs. Because the present paper was focused on the interaction between attention and integration, and not meant to dissociate between alternative interpretations of the ERPs elicited by the two successive stimuli, this test is deferred to future experimentation.

With regard to the earliest components of the ERP, a point worth noting about the present results is that the integration effect on the N1 found previously was absent here. Akyürek et al. (2010) showed that integration success increased N1 amplitude, but no modulation of this component was observed at present. This may be attributed to the changed nature of the present task. Because half of the trials did not require integration, but rather singleton detection and localization, the participants may have been unable to tune their perceptual system to optimally accommodate for integration. This account gains credibility from previous results that demonstrated that integration is an adaptive process, which can be tuned to temporal windows sensitive to intervals of less than 100 ms (Akyürek et al., 2007, 2008). Speculatively, the key to this adaptive system might thus in part be attributed to the perceptual processes reflected by the N1.

The present analyses revealed a subtle difference between integration and singleton trials on the N2 component, although amplitude did not vary reliably between tasks. However, at the same time, amplitude in the integration trials was sensitive to task performance, while this was not the case on the singleton trials. Until now, it was not certain whether the modulation in this range could perhaps be explained as a form of selection negativity (Hillyard & Münte, 1984). The present comparisons provided some important clues to this issue. Since both the singleton and the missing element elicited a comparable N2 overall, the selection process for both of these stimuli must have been similar. What did differ, however, was the amplitude between successful and unsuccessful trials, but only during integration. During temporal integration, it was essential for successful detection of the missing element to solve the spatial puzzle across the two displays. By contrast, in the singleton trials, this was not necessary; it was sufficient to just find the one singleton stimulus, regardless of the appearance of the remaining black squares. The modulation of the N2 that was unique to integration trials thus fitted well with previous studies that have linked the component to spatial grouping and contour detection (Schubö & Müller, 2009; Schubö et al., 2004, 2007). In the present study, increased N2 amplitude was observed for trials in which the global stimulus patterns were processed successfully, which in turn resulted in successful localization of the missing element.

P3

A further difference between integration and singleton trials was observed on the P3. At an interval between the early and late peaks observed in the integration trials, the singleton (correct) trials showed much less of a return to baseline. On the integration trials that were successful, the early and late components were more clearly demarcated. The special correlate of integrated percepts in memory as reflected in the P3 may be related to “short-term visual memory” (Phillips, 1974), and provides the opportunity for access at a later stage. Such access after memory consolidation may account for previous studies that found improved performance in integration tasks after extended time delays beyond 1 s (Brockmole et al., 2002, 2003). If the information consolidated after perception does not exceed a certain complexity, it may be manipulated later in working memory to optimize retrieval as needed by the task.

This account is compatible with the findings of Jiang and colleagues (Jiang, 2004; Jiang et al., 2005; Kumar & Jiang, 2005) as well. The effect of integration on consolidation as reflected by the P3 may also account for the results from a study by Scharnowski et al. (2009), who showed that integration can be disturbed when transcranial magnetic stimulation (TMS) is applied to disturb per-

ceptual process at intervals beyond 100 ms. It may be that the disturbance caused by TMS altered the integrated and consolidated percept in memory, and thereby also distorted the special correlate established after integration. Subsequent responses that rely on this correlate would consequently have been affected as well. It has to be noted that, in the present study, the P3 effects were not found in isolation (i.e., other components were also modulated), which necessitates the important qualification that even though late memory-related effects may exist, these do not account for all aspects of temporal integration.

The dual P3 peaks that seemed to emerge most clearly in integration trials (but which were also visible when a singleton was missed) might also be interpreted as a reflection of individual P3 components to S1 and S2, respectively. As previously alluded to, the P3 did seem to show a latency shift as S1 duration changed (top panel of the Appendix figure). However, the shift was in the opposite direction; shorter S1 durations caused later P3 onsets. Furthermore, in the comparison of the singleton ERPs (bottom panel of the Appendix figure), the P3 elicited in Experiment 2 also seemed to consist of two peaks, albeit to a lesser degree. For these reasons, we hesitate to subscribe to the idea that these P3 peaks reflect strict S1- and S2-locked components. The weaker claim that these two peaks are related to processing certain aspects of the individual displays, as well as the emergent perception of the full array, could still be tenable, but would require further research to be substantiated.

Previous research has shown that P3 amplitude decreases as a consequence of multiple task demands, which has been interpreted as a correlate of the available amount of both attentional and memory-related processing resources (e.g., Kok, 2001). A resource-based account for the present modulation of the P3 observed in the late window does seem feasible. If integration is accomplished, the emerging percept is that of a single stimulus (event). Compared to the percept of two separate stimuli, as established when integration fails, successful integration may represent cognitive savings. The resources that are freed up by integration may be reflected in the increased amplitude of the P3. Similarly, successful selection of the singleton allows the observer to discard the information obtained from the spatial configuration across the two displays.

A functional interpretation of the P3 activity observed in the present paradigm might also be given in terms of P3a and P3b (Squires, Squires, & Hillyard, 1975). The P3a component typically peaks before the P3b and has a more frontocentral distribution. These features are at least globally compatible with the P3 waveform in the early window of the present study. The P3b typically peaks later, is more sustained, and has a more parietal distribution, compared to the P3a, which is also compatible with the waveform observed in the late window in the present study. It has been theorized that the P3a reflects attentional processing, resulting from stimulus evaluation, while the P3b is thought to reflect context updating in the service of working memory operations (Polich, 2007). The P3b has also been shown to reflect a link between perceptual analysis and response selection (Verleger et al., 2005).

From the present data, it might first be inferred that such attentional processing, as it might be observed from early P3 (i.e., P3a) amplitude, is comparable between successful and unsuccessful trials. However, there did seem to be a task difference, with singleton trials eliciting increased amplitude, perhaps indicative of the detection of the target. This pattern held true also when more frontal electrodes (Cz and FCz) were analyzed. Second, if the late P3 can indeed be interpreted as a P3b component, then it would seem that increased amplitude corresponds with successful storage

of the target location, which is eventually followed by correct response execution. In this time window, the dynamics of these mechanisms appear to be similar for the integration and singleton tasks.

Concluding Remarks

Although the discussion has mainly focused on the differences between successful integration and singleton perception, and on the differences between failures thereof, it should also be noted that, overall, the ERPs in both tasks were remarkably similar. For

instance, the ERPs to the two displays were not displaced by the different task requirements, something which did happen when the different durations of S1 were overlaid (Appendix figure, top panel). Thus, with the noted exceptions discussed above, the perception of a singleton does not differ greatly from that of an integrated percept. The perceptual system processes integrated representations as it does veridical ones to a considerable degree, at least in the paradigm employed in the present study. Overall, the conclusion seems justified that temporal integration is a natural process that fits rather easily into the ongoing course of attention and perception.

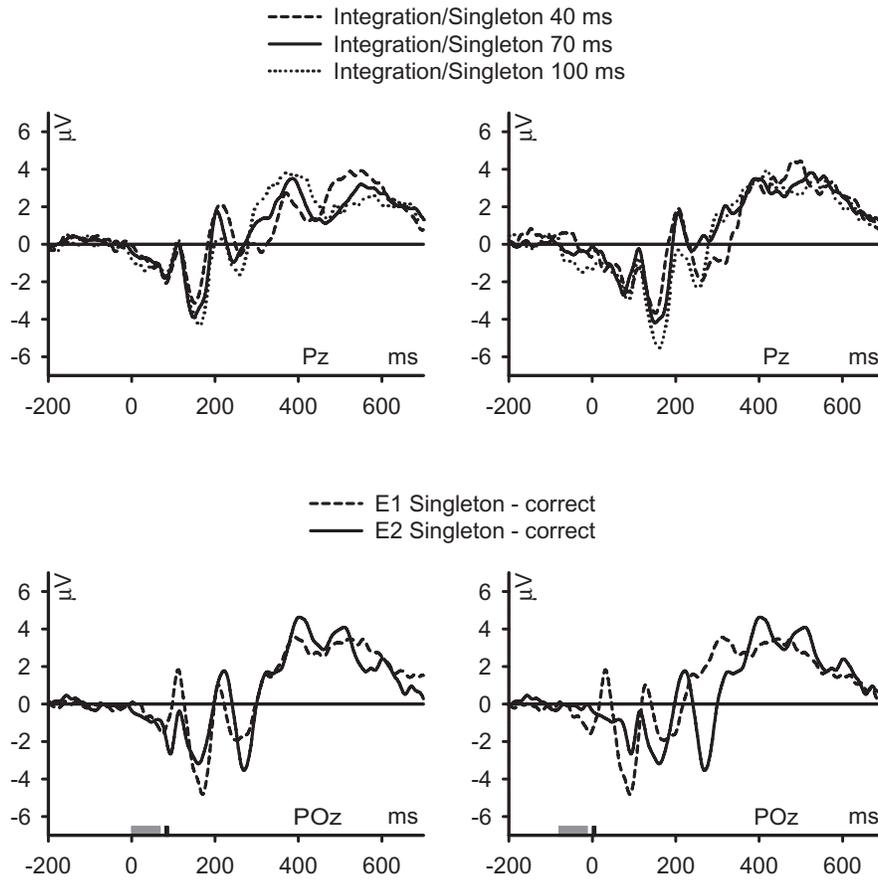
References

- Akyürek, E. G., Eshuis, S. A. H., Nieuwenstein, M. R., Saija, J. D., Başkent, D., & Hommel, B. (in press). Temporal target integration underlies performance at Lag 1 in the attentional blink. *Journal of Experimental Psychology: Human Perception and Performance*. doi: 10.1037/a0027610
- Akyürek, E. G., & Hommel, B. (2005). Target integration and the attentional blink. *Acta Psychologica*, *119*, 305–314. doi: 10.1016/j.actpsy.2005.02.006
- Akyürek, E. G., Riddell, P. M., Toffanin, P., & Hommel, B. (2007). Adaptive control of event integration: Evidence from event-related potentials. *Psychophysiology*, *44*, 383–391. doi: 10.1111/j.1469-8986.2007.00513.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
- Akyürek, E. G., Toffanin, P., & Hommel, B. (2008). Adaptive control of event integration. *Journal of Experimental Psychology: Human Perception and Performance*, *34*, 569–577. doi: 10.1037/0096-1523.34.3.569
- Allport, D. A. (1968). Phenomenal simultaneity and the perceptual moment hypothesis. *British Journal of Psychology*, *59*, 395–406. doi: 10.1111/j.2044-8295.1968.tb01154.x
- Broadbent, D. E., & Broadbent, M. H. P. (1987). From detection to identification: Response to multiple targets in rapid serial visual presentation. *Perception & Psychophysics*, *42*, 105–113. doi: 10.3758/BF03210498
- Brockmole, J. R., Irwin, D. E., & Wang, R. F. (2003). The locus of spatial attention during the temporal integration of visual memories and visual percepts. *Psychonomic Bulletin & Review*, *10*, 510–515. doi: 10.3758/BF03196514
- Brockmole, J. R., Wang, R. F., & Irwin, D. E. (2002). Temporal integration between visual images and visual percepts. *Journal of Experimental Psychology: Human Perception and Performance*, *28*, 315–334. doi: 10.1037/0096-1523.28.2.315
- Burr, D. C., Ross, J., & Morrone, M. C. (1986). Smooth and sampled motion. *Vision Research*, *26*, 643–652. doi: 10.1016/0042-6989(86)90012-X
- Coltheart, M. (1980). Iconic memory and visible persistence. *Perception & Psychophysics*, *27*, 183–228. doi: 10.3758/BF03204258
- Di Lollo, V. (1977). Temporal characteristics of iconic memory. *Nature*, *267*, 241–243. doi: 10.1038/267241a0
- Di Lollo, V. (1980). Temporal integration in visual memory. *Journal of Experimental Psychology: General*, *109*, 75–97. doi: 10.1037/0096-3445.109.1.75
- 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
- Donchin, E., & Coles, M. G. (1988). Is the P300 component a manifestation of context updating? *Behavioral & Brain Sciences*, *11*, 357–374. doi: 10.1017/S0140525X00058027
- Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity. *Electroencephalography and Clinical Neurophysiology*, *99*, 225–234. doi: 10.1016/S0921-884X(96)95711-2
- Enns, J. T., & Di Lollo, V. (2000). What's new in visual masking? *Trends in Cognitive Sciences*, *4*, 345–352. doi: 10.1016/S1364-6613(00)01520-5
- 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
- Hecht, S., & Shlaer, S. (1936). Intermittent stimulation by light: V. The relation between intensity and critical fusion frequency for different parts of the spectrum. *Journal of General Physiology*, *19*, 965–977. doi: 10.1085/jgp.19.6.965
- Heinze, H. J., Luck, S. J., Mangun, G. R., & Hillyard, S. A. (1990). Visual event-related potentials index focused attention within bilateral stimulus arrays. I. Evidence for early selection. *Electroencephalography and Clinical Neurophysiology*, *75*, 511–527. doi: 10.1016/0013-4694(90)90138-A
- Hermens, F., Scharnowski, F., & Herzog, M. H. (2009). Spatial grouping determines temporal integration. *Journal of Experimental Psychology: Human Perception and Performance*, *35*, 595–610. doi: 10.1037/a0013706
- Hillyard, S. A., & Münte, T. F. (1984). Selective attention to color and location: An analysis with event-related brain potentials. *Perception & Psychophysics*, *36*, 185–198. doi: 10.3758/BF03202679
- 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
- Hogben, J. H., & Di Lollo, V. (1985). Suppression of visible persistence in apparent motion. *Perception & Psychophysics*, *38*, 450–460. doi: 10.3758/BF03207176
- 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
- Hommel, B., Müssele, J., Aschersleben, G., & Prinz, W. (2001). The theory of event coding (TEC): A framework for perception and action planning. *Behavioral and Brain Sciences*, *24*, 849–937. doi: 10.1017/S0140525X01000103
- Jiang, Y. (2004). Time window from visual images to visual short-term memory: Consolidation or integration? *Experimental Psychology*, *51*, 45–51. doi: 10.1027/1618-3169.51.1.45
- Jiang, Y., Kumar, A., & Vickery, T. J. (2005). Integrating sequential arrays in visual short-term memory. *Experimental Psychology*, *52*, 39–46. doi: 10.1027/1618-3169.52.1.39
- Jolicœur, P., Brisson, B., & Robitaille, N. (2008). Dissociation of the N2pc and sustained posterior contralateral negativity in a choice response task. *Brain Research*, *1215*, 160–172. doi: 10.1016/j.brainres.2008.03.059
- Kappenman, E. S., & Luck, S. J. (2010). The effects of electrode impedance on data quality and statistical significance in ERP recordings. *Psychophysiology*, *47*, 888–904. doi: 10.1111/j.1469-8986.2010.01009.x
- Kirchner, H., Barbeau, E. J., Thorpe, S. J., Régis, J., & Liégeois-Chauvel, C. (2009). Ultra-rapid sensory responses in the human frontal eye field region. *Journal of Neuroscience*, *29*, 759–7606. doi: 10.1523/JNEUROSCI.1233-09.2009
- 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
- Klaver, P., Talsma, D., Wijers, A. A., Heinze, H.-J., & Mulder, G. (1999). An event-related brain potential correlate of visual short-term memory. *NeuroReport*, *10*, 2001–2005.

- Kok, A. (2001). On the utility of P3 amplitude as a measure of processing capacity. *Psychophysiology*, *38*, 557–577. doi: 10.1017/S0048577201990559
- Kumar, A., & Jiang, Y. (2005). Visual short-term memory for sequential arrays. *Memory & Cognition*, *33*, 488–498. doi: 10.3758/BF03193066
- 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. (1994a). Electrophysiological correlates of feature analysis during visual search. *Psychophysiology*, *31*, 291–308. doi: 10.1111/j.1469-8986.1994.tb02218.x
- Luck, S. J., & Hillyard, S. A. (1994b). 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
- McDonald, J. J., Teder-Sälejärvi, W. A., Di Russo, F., & Hillyard, S. A. (2005). Neural basis of auditory-induced shifts in visual time-order perception. *Nature Neuroscience*, *8*, 1197–1202. doi: 10.1038/nn1512
- Phillips, W. A. (1974). On the distinction between sensory storage and short-term visual memory. *Perception & Psychophysics*, *16*, 283–290. doi: 10.3758/BF03203943
- 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
- Potter, M. C., Staub, A., & O'Connor, D. H. (2002). The time course of competition for attention: Attention is initially labile. *Journal of Experimental Psychology: Human Perception and Performance*, *28*, 1149–1162. doi: 10.1037/0096-1523.28.5.1149
- 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
- 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., & Bausenhart, K. M. (2006). Attention delays perceived stimulus offset. *Vision Research*, *46*, 2926–2933. doi: 10.1016/j.visres.2006.02.022
- Scharnowski, F., Rüter, J., Jolij, J., Hermens, F., Kammer, T., & Herzog, M. J. (2009). Long-lasting modulation of feature integration by transcranial magnetic stimulation. *Journal of Vision*, *9*, 1–10. doi: 10.1167/9.6.1
- Schiller, P. H., & Logothetis, N. K. (1990). The color-opponent and broad-band channels of the primate visual system. *Trends in Neurosciences*, *13*, 392–398. doi: 10.1016/0166-2236(90)90117-S
- Schoenfeld, M. A., Tempelmann, C., Martinez, A., Hopf, J.-M., Sattler, C., Heinze, H.-J., & Hillyard, S. A. (2003). Dynamics of feature binding during object-selective attention. *Proceedings of the National Academy of Sciences of the USA*, *100*, 11806–11811. doi: 10.1073/pnas.1932820100
- Schubö, A., & Müller, H. J. (2009). Selecting and ignoring salient objects within and across dimensions in visual search. *Brain Research*, *1283*, 84–101. doi: 10.1016/j.brainres.2009.05.077
- Schubö, A., Schröger, E., & Meinecke, C. (2004). Texture segmentation and visual search for pop-out targets. An ERP study. *Cognitive Brain Research*, *21*, 317–334. doi: 10.1016/j.cogbrainres.2004.06.007
- Schubö, A., Wykowska, A., & Müller, H. J. (2007). Detecting pop-out targets in contexts of varying homogeneity: Investigating homogeneity coding with event-related brain potentials (ERPs). *Brain Research*, *1138*, 136–147. doi: 10.1016/j.brainres.2006.12.059
- Shallice, T. (1964). The detection of change and the perceptual moment hypothesis. *British Journal of Statistical Psychology*, *17*, 113–135. doi: 10.1111/j.2044-8317.1964.tb00254.x
- Squires, N. K., Squires, K. C., & Hillyard, S. A. (1975). Two varieties of long-latency positive waves evoked by unpredictable auditory stimuli in man. *Electroencephalography and Clinical Neurophysiology*, *38*, 387–401. doi: 10.1016/0013-4694(75)90263-1
- Treisman, A. (1996). The binding problem. *Current Opinion in Neurobiology*, *6*, 171–178. doi: 10.1016/S0959-4388(96)80070-5
- Valdes-Sosa, M., Bobes, M. A., Rodriguez, V., & Pinilla, T. (1998). Switching attention without shifting the spotlight: Object-based attentional modulation of brain potentials. *Journal of Cognitive Neuroscience*, *10*, 137–151. doi: 10.1162/089892998563743
- VanRullen, R., Carlson, T., & Cavanagh, P. (2007). The blinking spotlight of attention. *Proceedings of the National Academy of Sciences of the USA*, *104*, 19204–19209. doi: 10.1073/pnas.0707316104
- VanRullen, R., & Koch, C. (2003). Is perception discrete or continuous? *Trends in Cognitive Sciences*, *7*, 207–213. doi: 10.1016/S1364-6613(03)00095-0
- 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., Bischof, W. F., & Di Lollo, V. (1999). Attentional switching in spatial and non-spatial domains: Evidence from the attentional blink. *Psychological Bulletin*, *125*, 458–469. doi: 10.1037/0033-2909.125.4.458
- 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
- Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature*, *428*, 748–751. doi: 10.1038/nature02447
- Yeshurun, Y., & Levy, L. (2003). Transient spatial attention degrades temporal resolution. *Psychological Science*, *14*, 225–231. doi: 10.1111/1467-9280.02436
- Zeki, S. M. (1978). Uniformity and diversity of structure and function in rhesus monkey prestriate visual cortex. *Journal of Physiology*, *277*, 273–290.
- Zhang, W., & Luck, S. J. (2009). Feature-based attention modulates feed-forward processing. *Nature Neuroscience*, *12*, 24–25. doi: 10.1038/nn.2223

(RECEIVED January 9, 2012; ACCEPTED March 7, 2012)

Appendix



Appendix figure. Top panel: ERP amplitude in μV elicited on correct trials as a function of time in ms on the Pz electrode in Experiment 1, plotted separately for 40, 70, and 100 ms S1 duration. The left panel represents the integration condition, and the right panel represents the singleton condition. Bottom panel: Overlay of the ERP amplitude in μV at POz as a function of time in ms on (red) singleton correct trials from Experiment 1 and 2. The ERP of Experiment 1 is time-locked to S1 in the left panel, and is locked to S2 in the right panel (i.e., -80 ms).