

Fast temporal event integration in the visual domain demonstrated by event-related potentials

ELKAN G. AKYÜREK,^a ANNA SCHUBÖ,^a AND BERNHARD HOMMEL^b

^aDepartment of Psychology, Ludwig Maximilian University, Munich, Germany

^bPsychological Research & Leiden Institute for Brain and Cognition, Leiden University, Leiden, The Netherlands

Abstract

Four experiments are reported that investigated visual event integration by using a variant of the missing element paradigm. Good performance on this task depends on whether two brief successive stimulus displays are perceived as (or integrated into) one single event. We replicated the classic finding of greater accuracy with shorter duration of the first stimulus and ruled out an attention-related account thereof. In a subsequent electrophysiological experiment we found that successful event integration increased the amplitude of the N1, N2, and late P3 components of the event-related potential and decreased early P3 amplitude. No effect on the P1 was observed. The results provided evidence for an early onset of event integration in time and demonstrated the existence of electrophysiological markers of episodic integration. The implications of these results are related to studies on feature-specific integration and early attentional processes.

Descriptors: Event integration, Visual perception, Event-related potential, N1, N2, P3

Visual perception relies on two kinds of information. The first is featural information about object properties such as location, shape, or color. The second kind is temporal information: a specification of the time course of external events. Put simply, a wholesome visual percept consists of *what* was seen and *when*. To achieve coherent perception, the brain must integrate or bind information that is passed continuously from distributed neuronal populations (even for quite basic visual properties, e.g., Zeki, 1978) while also keeping track of the time course of these sensations. The process by which the brain accomplishes the apparently seamless ongoing integration of distributed representation has been called binding or event coding (Hommel, 2004; Hommel, Müsseler, Aschersleben, & Prinz, 2001; Treisman, 1996). Featural and temporal binding are accomplished by the general principle of proximity. Featural binding, for instance, can use spatial proximity to associate the perception of two features with each other. Thus, the shape and color of an apple come together because they were perceived at the same location. Similarly, events that happen at the same time or quickly after each other are more likely to be perceived as one than events that are more separated in time.

The authors thank Vincent Di Lollo for helpful discussion of the particularities of the experimental paradigm and Asher Cohen and two anonymous reviewers for their helpful comments on an earlier version of this manuscript. A.S. and E.G.A. were supported by the German Research Foundation (DFG) as part of the excellence cluster “Cognition for Technical Systems” (CoTeSys), project #148.

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

An important question with regard to both featural and temporal integration is whether they operate at a relatively early or rather late processing stage. At a later stage, integration could be thought of as an organizational mechanism operating on the contents of working memory. At an earlier stage, integration could give structure to the sensation of individual features. This question has not yet been resolved, although some evidence to date has been collected, mostly pertaining to featural integration.

Featural integration for the case of single defining feature values (e.g., red vs. green dots) has been shown to be extremely rapid, allowing for early attentional selection of whole objects on the basis of featural proximity (Schoenfeld et al., 2003; Valdes-Sosa, Bobes, Rodriguez, & Pinilla, 1998; Zhang & Luck, 2009). Presumably the brain accomplishes rapid feature integration by spreading activation from one neural module that encodes a relevant feature to other modules that encode other features belonging to the same object (with the possible exception of V1; e.g., Duncan, Humphreys, & Ward, 1997). It is not yet clear whether such fast control of integration needs to match the organizational properties of visual cortex to work, but it seems likely. In this case, integration on the basis of color is fast, because color as such is coded very early in the perceptual system. An arbitrary, more complex perceptual property may not yield fast integration because it is not distinctly represented early enough in time.

The case is even less clear for temporal integration. One might be tempted to assume that temporal integration is a hard-wired and perhaps emergent property of the brain, for instance, as a result of periodicity of cortical excitability. In this case, temporal integration could be thought of as the sampling rate of the cognitive system (cf. the perceptual moment hypothesis; Allport,

1968). However, evidence from rapid serial visual presentation (RSVP) studies has shown that the temporal extent of integration (the integration window) can vary as a result of both exogenous and endogenous control, casting doubt on the idea of a hard-wired property.

Exogenous control of temporal integration has been demonstrated to occur when two successive stimuli in an RSVP stream do not match, such as when they belong to different categories (e.g., task-relevant vs. irrelevant). The perception of that conceptual mismatch causes the ongoing integration of one event (episode) to stop and a new one to start (Hommel & Akyürek, 2005; Potter, Staub, & O'Connor, 2002). The primary evidence for the idea that temporal integration is affected comes from the Lag 1 sparing phenomenon (Visser, Bischof, & Di Lollo, 1999). Lag 1 sparing is the escape from the attentional blink, which in turn is the failure to identify the second of two target stimuli when it follows the first within less than about 500 ms (Broadbent & Broadbent, 1987; Raymond, Shapiro, & Arnell, 1992). Lag 1 sparing occurs when the target stimuli are of the same kind (e.g., both a letter) and are presented in direct succession, that is, without an interfering stimulus in between. Lag 1 sparing can be considered a correlate of the temporal integration of both targets into one event representation. When targets do not follow each other directly, the interfering stimuli cause integration to stop after the first target. To perceive the second target, a new event representation has to be created, and the effort associated with this may result in the attentional blink. In support of this view, evidence for the idea that only one event episode is used at Lag 1 and two for blinked (and later) lags has been found in the type of report errors that are made by participants; they are quite different. At Lag 1, although the identities of the targets are preserved, their temporal order is forgotten on a large number of trials. By contrast, identity errors, particularly regarding the second target, are common during blinked lags, whereas order errors are not. Apparently, temporal order information is associated with the "production date" of event episodes, so that stimuli being integrated into the same episode share the same temporal tag and can thus no longer be distinguished with regard to time or order (Akyürek, Toffanin, & Hommel, 2008; Hommel & Akyürek, 2005).

Endogenous control over the temporal parameters of integration has also been demonstrated. Akyürek et al. (2008) showed that implicit expectancies regarding temporal properties of stimuli (i.e., the speed of presentation) tune the integration process. In their study, the expectancy of a slow stimulus presentation rate induced a rather relaxed mode of integration with longer temporal integration windows, whereas shorter windows were induced by a fast presentation rate.

Temporal integration thus seems to be a fairly flexible and powerful cognitive function that is capable of using task meta-knowledge to make minute adjustments to the process of perception rather than being a simple sampling rate function. This might suggest that integration takes place relatively late in the processing chain, for instance, acting to organize memory in a post hoc fashion. Given that the aforementioned studies relied on behavioral report, ample opportunity for such late effects on the eventual response existed indeed. One way to tap into the processing stages related to integration more directly is to make use of the high temporal resolution of electrophysiology. A recent electrophysiological study measured the event-related potential (ERP) of integration in an RSVP paradigm and yielded evidence that integration affected the N2 and P3 components (Akyürek, Riddell, Toffanin, & Hommel, 2007). The P3 is thought to reflect

relatively late processing stages, such as complete identification and consolidation in short-term memory (Donchin & Coles, 1988; Polich, 2007). The role of the N2 in RSVP is not entirely clear, but the N2 component has also been associated with the analysis of task-relevant features in visual search tasks (Barceló, Suwazono, & Knight, 2000), the processing of visual context homogeneity (Schubö, Wykowska, & Müller, 2007), and general cognitive control processes in go/no-go tasks (Nieuwenhuis, Yeung, & Cohen, 2004). These results thus provided a first indication that temporal integration is not exclusively a matter of late, memory-related processing. At the same time, a considerable time gap remains between the N2 component observed in this study of temporal integration and the modulation of P1 and N1 components found in studies of featural integration (e.g., Valdes-Sosa et al., 1998). Unless an earlier correlate of temporal integration can be demonstrated, this gap may be taken to reflect a functional distinction.

In search of earlier ERP correlates of temporal integration, the present study employed a missing element task (MET; described below). This paradigm consists of just two brief stimulus presentations and thus allows the examination of the ERP without the use of difference waves as necessitated by RSVP paradigms. In these paradigms, the ERP elicited by each of the stimuli in the stream distorts the waveforms and obscures early components such as the P1 and N1, which typically have lower amplitude. A further benefit of the MET is that it does not require the processing of alphanumeric stimulus material, so that the possibility that integration is stalled until these stimuli are fully processed can be excluded.

The missing element paradigm used in the present study was inspired by studies on iconic memory that were initially reported over 30 years ago (Hogben & Di Lollo, 1974; Di Lollo, 1977, 1980). In these studies, a square grid or array of regularly spaced dots appeared on a tachistoscope in two successive presentations. The timing of the first display was variable (between 10 and 200 ms), and the second display was fixed at 10 ms, with a 10-ms blank interval in between. The two displays together contained all the dots in the array except for one. One position in the array was not filled in, and participants were asked to indicate the location of the missing element. Doing so successfully in this task is fairly easy if both displays can be integrated into one single event episode, and the results supported this account. Contrary to expectations at the time, increasing the duration of the first display (S1) resulted in a steep decline in performance. According to integration logic this observation makes perfect sense, however: A long duration of the first display leaves enough time for the integration window to be opened and closed again in time, before the next display arrives. When the first display is very brief, there is insufficient time to close the integration window, and the perceptual input from the second display (S2) is merged into the current event episode as well, with beneficial results for the performance on the MET. Thus, this task provides a straightforward test of temporal integration. Before turning to the measurement of the ERP, three behavioral experiments were conducted to control for potential artifacts and to rule out alternative theoretical interpretations.

EXPERIMENT 1

Experiment 1 was designed to replicate and extend the results of missing element integration tasks reported in the literature (Di

Lollo, 1977, 1980; Hogben & Di Lollo, 1974). In the first instance, this experiment served to verify the reported performance on modern computerized hardware, because the original experiments were conducted on tachistoscopes and were, at times, reported without statistical corroboration. Experiment 1 tested the effects of S1 as well as S2 duration.

Method

Participants

Thirteen students (7 female, 6 male) at the Ludwig Maximilian University Munich participated for course credit or monetary compensation. Participants were unaware of the purpose of the experiment and reported normal or corrected-to-normal vision. Mean age was 25.5 years (range 20–31 years).

Apparatus and Stimuli

Participants were individually seated in a comfortable chair in a dimly lit and sound-attenuated testing chamber at a distance of approximately 100 cm from the screen. The 20-in. CRT screen was driven by a Core 2 Duo computer with a discrete graphics board and refreshed at 100 Hz with a resolution of 800×600 pixels in 32-bit color. The experiment was programmed in E-Prime 1.2. Responses were logged on a standard USB mouse polling at 125 Hz. 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. Squares were chosen rather than dots to avoid undue perceptual difficulty. The grid was made up of 25 invisible fields of 20×20 pixels, within which the black squares were centered in turn, each measuring 10×10 pixels.

Procedure and Design

The total number of trials was 600, starting with a practice block of 24 trials that were excluded from analysis. Trials continued without interruption within blocks. There were six experimental blocks of 96 trials each, and after each block participants had the opportunity to take a break. Participants initiated each block of trials by clicking the right mouse button. Each trial started with a blank interval of 600 ms, which was followed by the presentation of the experimental stimuli. The stimuli were presented in two successive display frames, each containing a random selection of 12 out of 25 possible squares (without overlap), so that only one square was not drawn in either display. A blank interval of 10 ms was inserted between these two frames. On half of the trials, the duration of the first display frame varied between 20, 40, 100,

120, 140, and 200 ms, whereas that of the second frame was set at 10 ms. On the other half of the trials, the distribution was mirrored so that the first display frame was held constant while the second varied. All trial types were randomly intermixed and equally distributed.

After the offset of the last stimulus display, another 600-ms blank interval followed before the response screen appeared. The response screen consisted of an array of squares that was similar to the stimulus arrays with the exception 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 5000 ms or until a response was registered. Participants responded by using the left mouse button to click on the outline of the square that had not been filled by either set of squares shown in the two stimulus arrays. Figure 1 shows a schematic representation of the trial structure. The phenomenal impression of the stimulus displays can be captured by trying to derive the location of the missing element from the two displays shown here. This is without doubt a challenging task, somewhat similar to what would happen in the actual trials when the displays are not integrated. Yet, when the two displays shown in Figure 1 could be overlaid (i.e., “integrated”), the missing element would be apparent immediately.

Mean accuracy was analyzed in two separate repeated measures analyses of variance (ANOVAs) with a single variable representing the duration of the variable (S1 or S2, respectively) display. Thus, each analysis considered exactly half of the total number of trials in the experiment. The duration variable had six levels (20, 40, 100, 120, 140, and 200 ms). As noted, the duration of the other display remained constant at 10 ms in the analysis. Trials were counted as correct when the participant had clicked on the square outline that constituted the missing element or within its 20-pixel virtual perimeter. In case of significant tests of sphericity, the degrees of freedom were adjusted using the Greenhouse–Geisser epsilon correction.

Results and Discussion

The ANOVA pertaining to the duration of the first stimulus display (S1) showed a clear effect of duration, $F(5,60) = 37.01$, $MSE = .007$, $p < .001$. Performance peaked at 72.6% at the shortest display duration, dropping down to 58.0% at 40 ms, 42.6% at 80 ms, and 44.2% at 100 ms before stabilizing at 36.2% at 140 and 200 ms. The left panel of Figure 2 shows response accuracy as a function of S1 duration.

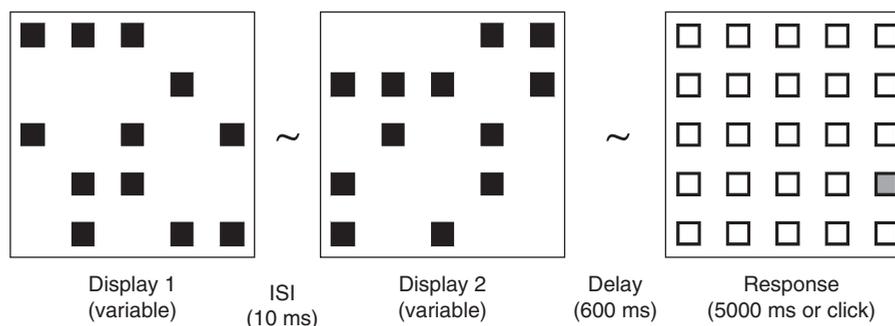


Figure 1. Schematic representation of the experimental design. Two rapid stimulus presentations of variable duration (see main text) each showed 12 out of 25 squares in the grid, with a 10-ms blank interstimulus interval. After another blank delay of 600 ms the response screen appeared. The correct response is highlighted in gray for illustration purposes only.

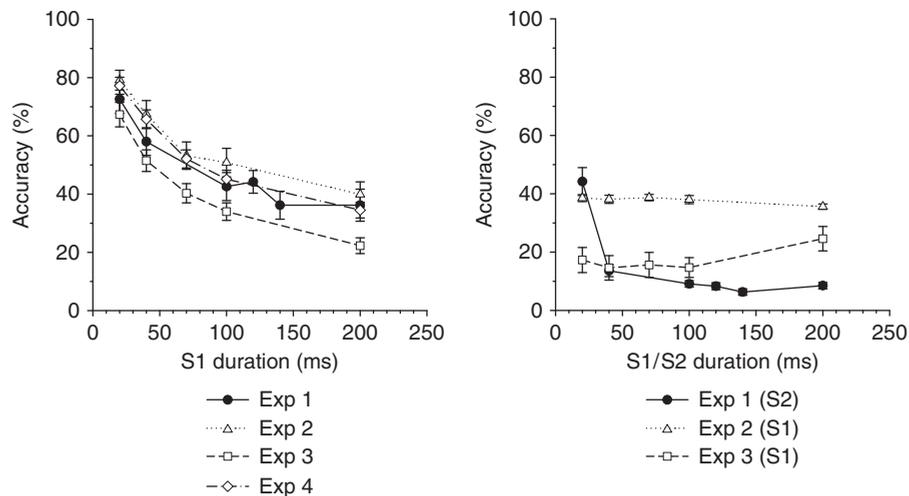


Figure 2. The left panel shows response accuracy for the missing element task in Experiments 1, 2, 3, and 4 in percent correct, plotted as a function of the duration of the first stimulus display. The right panel shows the same as a function of the duration of the second display for Experiment 1. For Experiments 2 and 3, the right panel shows performance on the majority and size judgment tasks, respectively, as a function of the duration of the first display. Error bars represent one standard error of the mean.

The ANOVA on the duration of the second stimulus display (S2) revealed that this variable affected accuracy as well, $F(2,19) = 48.29$, $MSE = .018$, $p < .001$, $\epsilon = .31$. Performance was generally lower on trials in which S2 duration was increased and peaked at 44.2% at 20 ms. Accuracy dropped off steeply to 13.6% at 40 ms and remained below 10% for longer durations (9.1%, 8.3%, 6.3%, and 8.5%, respectively). The right panel of Figure 2 shows response accuracy as a function of S2 duration.

The results confirmed previous work on integration with simple visual stimuli. Shorter S1 durations strongly improved performance, which provides evidence for more successful integration with more rapid presentation. A somewhat similar trend was observed for S2 duration. At the same time, S2 duration seemed to have a stronger effect on overall performance, as only the shortest duration allowed performance to escape from what appeared to be a bottom level. A degree of asymmetry between the effects of S1 and S2 duration might be accounted for in two ways. First, a longer and more clearly distinct S2 may not be so easily added to the event episode that was initiated for S1. The reason for this might be that a longer duration of S2 presumably provided accumulating evidence that it was a new stimulus, which would trigger an episode-closing response. Second, it might be that the short duration of S1 resulted in a relatively weak (sensory) impression, which could then become vulnerable to interference from the longer-lasting S2. In this sense, S2 acted as a strong backward mask (for a review of visual masking, see Enns & Di Lollo, 2000). In any case, however, the overall pattern of results from S1 and S2 duration was qualitatively comparable and in agreement with both previous observations and integration theory.

EXPERIMENT 2

Although the array task is a fairly straightforward test of visual integration and has been successfully tested against other accounts in the past (e.g., Di Lollo & Dixon, 1988; Dixon & Di Lollo, 1994), it might be argued that differences in sustained attention (or alertness) could play a confounding role in the observed performance. In particular, one might suppose that

shorter duration of the stimulus displays might heighten alertness and elicit more elaborate processing on those trials, so that performance improves. Conversely, longer durations may cause the observer to “doze off,” thus degrading performance. The hypothetical differential deployment of sustained attention could, in principle, account for the effect of duration on task accuracy without invoking integration. Thus, Experiment 2 was designed to investigate the feasibility of the differential attention account.

The most critical modification with regard to Experiment 1 was that an additional task was added to the design: Participants were asked to make an additional judgment about the stimulus displays they had been shown. The stimuli from the second display were now colored in blue, and in addition to the classic 12 stimuli per display as before, the number of squares drawn in each display could also consist of 10 or 14 (always adding up to 24). The additional task for the participants was to indicate whether the blue or the black (or neither) set of squares were in the majority. If differential deployment of attention was at least partially responsible for the performance on the MET, then the same effect of stimulus duration should be observed in the majority judgment task.

Method

Participants

Nineteen new students (14 female, 5 male) participated for course credit or monetary compensation. The recruitment procedures and requirements were identical to those used in Experiment 1. Mean age was 23.5 years (range 19–31 years).

Apparatus and Procedure

Experiment 2 was identical to Experiment 1 with the following exceptions: S2 duration held constant at 10 ms, and the middle S1 duration was modified slightly to approach the 50% performance point (to improve the power of the later ERP comparisons between error and correct trials in Experiment 4). The new duration was 70 ms. As Experiment 1 furthermore showed that the durations of 120 and 140 ms were somewhat uninformative, these were omitted to simplify the design, leaving 20, 40, 70, 100,

and 200 ms. As mentioned, the stimuli of the second display were now always blue. The number of stimuli in each display was varied between three alternative configurations: 12 stimuli each, 10 (S1) and 14 (S2), or 14 (S1) and 10 (S2). All trials were randomly intermixed and equally distributed between the experimental conditions. Finally, an additional response screen was added to the end of the trial, lasting for 5000 ms or until a response was given. The screen showed three double-size squares aligned on the horizontal axis. The first square was an outline, the second was solid black, and the third one was solid blue.

Participants used the left mouse button to click on the outline square if they thought that neither black nor blue squares were in the majority and on one of the other ones if they thought its corresponding color had been in the majority. As before, a click within the perimeter (double sized, at 40 pixels) of the correct alternative was acknowledged as such. The total number of trials in this experiment was 510, the first 30 of which were practice.

The results were analyzed for both tasks in separate ANOVAs (i.e., for the MET and for the majority judgment task), with the variable duration as before. The variable now had five levels (20, 40, 70, 100, and 200 ms).

Results and Discussion

Performance on the MET was similarly affected by duration of S1 as it was in Experiment 1, $F(3,45) = 92.01$, $MSE = .008$, $p < .001$, $\epsilon = .63$. The shortest duration resulted in 79.1% correct responses, dropping to 67.4% at 40 ms, 53.2% at 70 ms, 50.1% at 100 ms, and finally 39.9% at 200 ms. The left panel of Figure 2 shows response accuracy on the MET as a function of S1 duration.

Performance on the majority judgment task was not affected by S1 duration at all, $F < 1.3$, and hovered around 37.8% on average. The right panel of Figure 2 shows performance on this task as a function of S1 duration.

As expected, the results replicated those from Experiment 1 by showing a strong effect of S1 duration, whereas no such effect was observed on the majority judgments. If S1 duration had caused a differential deployment of attention in the MET, a comparable effect should have been obtained in the majority judgment task. Because this was not the case, our findings suggested that performance on the MET reflects integration processes rather than differential attentional allocation.

EXPERIMENT 3

Experiment 2 reinforced the idea that the MET is an appropriate measure of integration. However, a couple of objections need to be considered. First, it is possible that the addition of the majority task in Experiment 2 has led participants to adopt a different, “dual task” mode of processing the stimulus displays, even though the performance on the MET did not really indicate that this might have happened. Second, one might argue that differential deployment of attention does not affect performance during the whole trial but only the processing of S2. Thus, one might argue that although performance on the majority judgment task in Experiment 2 was not affected by duration, this could be so because possible difficulties with perceiving S2 were compensated for by improved perception of S1. Experiment 2 offered no way to distinguish between sustained performance on a trial level and specific S2-related performance, because the majority judgment

task could (theoretically) be performed by attending to only one stimulus display and to infer the number of squares in the other.

Experiment 3 was designed to check the possibility that attentional allocation specific to S2 might have played a role. It was similar to Experiment 2, but the stimulus displays were as in Experiment 1 with 12 black stimuli each. On 25% of trials, the stimuli displayed in the second array were enlarged. Participants were asked to detect the location of the missing element unless the second set of stimuli was enlarged. In the latter case, the MET should not be performed; instead an alternative response field had to be clicked to indicate that the size change had been detected. As the size of the second set of stimuli was increased on only 25% of the trials, participants were likely to be prepared for just the MET. Performance on the size judgment task was dependent on the perception of the second display only and could not be inferred from the perception of the first.

Method

Participants

Twenty new students (17 female, 3 male) participated. Recruitment and selection procedures were as in Experiment 1. Mean age was 22.3 years (range 19–26 years).

Apparatus and Procedure

The experiment was identical to Experiment 2 with the following exceptions. On 25% of trials, the squares in the second display were enlarged by 1 pixel in each direction. The spacing of the stimuli in the grid remained unchanged, so that they were not displaced. The response screen was furthermore changed to accommodate the new response that the size of the stimuli had increased. On all trials, a new response field was added below the grid array of 30×30 pixels (depicting a cascaded set of squares). The total number of trials was 660, including 20 practice trials at the start of the experiment.

Results and Discussion

The analysis of the MET showed a significant effect of S1 duration, $F(2,36) = 82.37$, $MSE = .015$, $p < .001$, $\epsilon = .47$. Performance replicated the previous results, peaking at 20 ms (67.3%) and dropping thereafter (51.5% at 40 ms, 40.3% at 70 ms, 34.0% at 100 ms, and 22.3% at 200 ms). The left panel of Figure 2 shows performance on the MET as a function of S1 duration.

The analysis of the size judgment task failed to show a reliable effect of S1 duration, $F(1,27) = 2.69$, $MSE = .036$, $p < .1$; if anything, there was a slight trend toward better performance at 200 ms duration. Performance was generally quite low, indicating that this task was difficult: 17.3% at 20 ms, 14.6% at 40 ms, 15.6% at 70 ms, 14.7% at 100 ms, and 24.6% at 200 ms. Note that because of the combined nature of the MET and size judgment task, chance level for the second task is actually dependent on the response mode of the observers: Performing just the size judgment task would yield 25%, but doing just the MET would come to 0%. Given that performance was clearly above the 0 point (and above the combined chance level of 12.5%), it can be assumed that observers did mind the size judgment task. The right panel of Figure 2 shows performance on the size judgment task as a function of S1 duration.

These findings again showed that the MET was sensitive to S1 duration, whereas the size judgment task was not. Taken to-

gether, the evidence suggested that performance on the MET reflects visual integration over time and cannot be accounted for by (differential deployment of) attentional resources.

EXPERIMENT 4

Having verified that performance on the MET is indeed diagnostic of visual integration, the purpose of Experiment 4 was to examine the time course of visual event integration. The principal issue of interest was the onset of visual event integration. Three potential moments were considered. The earliest of these is reflected in the P1 and N1. The onset of temporal integration in the time range of these components would indicate that temporal integration acts on the very first phases of visual (attentional) processing, involved in basic feature detection and discrimination (e.g., Heinze, Luck, Mangun, & Hillyard, 1990). The middle ground was covered by the N2 component, an attentional component that reflects processing beyond pop-out stimulus detection (Luck & Hillyard, 1994). If temporal integration started here, it could be considered a process that acts on partially coherent visual percepts. It is assumed that some critical links between basic visual properties are available at this stage (e.g., a color associated with a particular location), but full identification has not yet been completed. Finally, the latest moment under consideration was the time range of the P3, a component typically associated with memory updating (e.g., Polich, 2007). If temporal integration were to be reflected in this but not earlier components, this would support the idea that temporal integration is a late process that organizes memory and acts on virtually complete percepts.

To establish the onset of visual event integration, the approach taken in this experiment was to compare the ERP to the stimuli on trials on which integration failed to trials on which it succeeded. It should be noted that a fair comparison of this kind requires (1) considering only trials that were physically identical and (2) using a roughly equal number of trials in each condition. These criteria were met by using the trials of the 70-ms S1 duration condition, which ensured that the stimuli were physically identical, and that error and correct trials were of an approximately equal distribution. The earliest difference between the ERP in these two conditions can thus be taken to reflect the start of temporal integration.

Method

Participants

Twenty-one new students (18 female, 3 male) participated. Recruitment and selection procedures were as in Experiment 1. Mean age was 23.0 years (range 19–30 years).

Apparatus and Procedure

For Experiment 4, the size judgment task from Experiment 3 was omitted, and the distribution (but not the number) of trials was modified. Of all trials, 8 out of 20 were of 70 ms duration to maximize statistical power in this crucial condition where about 50% of errors were expected. The remaining four durations were shown on 3 trials out of 20. The delay at the start of each trial was increased by a random jitter to reduce temporal predictability and now varied randomly between 600 and 800 ms. Finally, an additional blank delay of 200 ms was added after the response screen at the end of each trial, during which the participant's

response was coded and sent to the electroencephalogram (EEG) acquisition computer.

Electrophysiological Recording and Data Analysis

EEG was recorded with Ag-AgCl electrodes from 64 electrodes (laid out according to the extended international 10–20 system). The electrodes were referenced to Cz and re-referenced off-line to the average of both mastoids. 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 amplifier used a 125 Hz cutoff and a 0.1-Hz highpass filter. EEG was recorded at a frequency of 500 Hz.

EEG was averaged off-line into 1000-ms segments, starting 200 ms prior to the onset of S1 and ending 800 ms afterward. Trials with amplitudes exceeding $\pm 80 \mu\text{V}$, voltage steps exceeding $\pm 50 \mu\text{V}$ between two sampling points, and trials with voltages lower than $0.10 \mu\text{V}$ for 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). Visual inspection of the data did not indicate any notable qualitative change in the ERP as a result of this procedure. The data were filtered off-line with a 40-Hz lowpass filter at -12 dB (48 dB/oct roll-off), and a 0.1-Hz highpass at -6 dB (24 dB/oct roll-off). 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 all analyses.

ANOVAs were performed for mean amplitude values obtained in four time windows corresponding to the occipital P1 (90–130 ms after the onset of the first stimulus) and occipital N1 (160–190 ms), the parietal-occipital N2 (220–260 ms), and finally the parietal P3 in both an early (260–390 ms) and a late (450–600 ms) time window. Three sets of single electrodes were chosen for analysis: Oz, O1, and O2 for the P1 and N1; POz, PO3, and PO4 for the N2; and finally Pz, POz, P3, and P4 for the P3. The analyses were designed to compare successful and unsuccessful integration at 70-ms S1 duration, contrasting error trials with correct ones while keeping physical stimulation constant. Recall that the 70-ms condition was purposefully chosen because it averaged close to 50% correct/error trials and was therefore also shown with higher frequency than the other durations. Thus, the analyses were aimed at integration itself, rather than at exploring differences due to S1 duration, which would involve not just stimulus duration but also potentially confounding contributions from trial frequency and error frequency. In all of the ERP analyses, a second independent variable was added to the design for individual electrode locations to explore the spatial distribution of the ERP at the scalp.

Results and Discussion

Behavioral Results

The analysis showed a significant effect of S1 duration, $F(2,49) = 134.95$, $MSE = .007$, $p < .001$, $\epsilon = .62$. Performance again replicated the familiar pattern, with peak performance at 20 ms (77.2%) and a clear dropoff thereafter (65.7% at 40 ms, 52.1% at 70 ms, 45.1% at 100 ms, and 34.5% at 200 ms). The left panel of Figure 2 shows performance as a function of S1 duration.

Electrophysiological Results

The integration analysis of the P1 did not show a reliable main effect of the success of integration nor an interaction of that variable with electrode position, $F_s < 1.4$. Electrode position did have a main effect of its own, indicating that ERP amplitude was more positive on the O1 (2.87 μV) and O2 (2.14 μV) electrodes than on Oz (1.67 μV), $F(2,31) = 8.15$, $\text{MSE} = 2.42$, $p < .005$, $\epsilon = .79$.

For the N1, the picture was quite different; integration had a clear effect, $F(1,20) = 6.11$, $\text{MSE} = .447$, $p < .05$, whereas electrode position did not, $F < 1.01$. The interaction term was not reliable either, $F < 1$. Average amplitude across the three electrodes was $-1.67 \mu\text{V}$ for successful integration and $-1.37 \mu\text{V}$ for unsuccessful integration. The top panel of Figure 3 shows ERP amplitude as a function of time for the Oz, O1, and O2 electrodes.

The integration analysis of the N2 showed an effect similar to the one observed for the N1. Integration had a main effect, $F(1,20) = 7.02$, $\text{MSE} = 1.57$, $p < .05$, which seemed to be uniform across the electrode positions; the interaction was not significant, $F < 1$. As can be seen from the middle panel of Figure 3, successful integration across the POz, PO3, and PO4 electrodes averaged 0.75 μV , whereas its counterpart reached 1.34 μV . Electrode position was not significant, $F(2,40) = 2.34$, $\text{MSE} = 7.31$, $p < .11$.

Integration also affected the P3 in the early time window, $F(1,20) = 5.85$, $\text{MSE} = 1.90$, $p < .05$, as decreased amplitude was associated with successful integration (2.12 μV compared to 2.64 μV). Electrode position did not have a main effect, $F < 1$, but it did interact with integration, $F(2,43) = 2.93$, $\text{MSE} = .317$, $p < .05$, $\epsilon = .71$. The difference elicited by integration seemed slightly smaller at the Pz electrode (0.31 μV delta), compared to

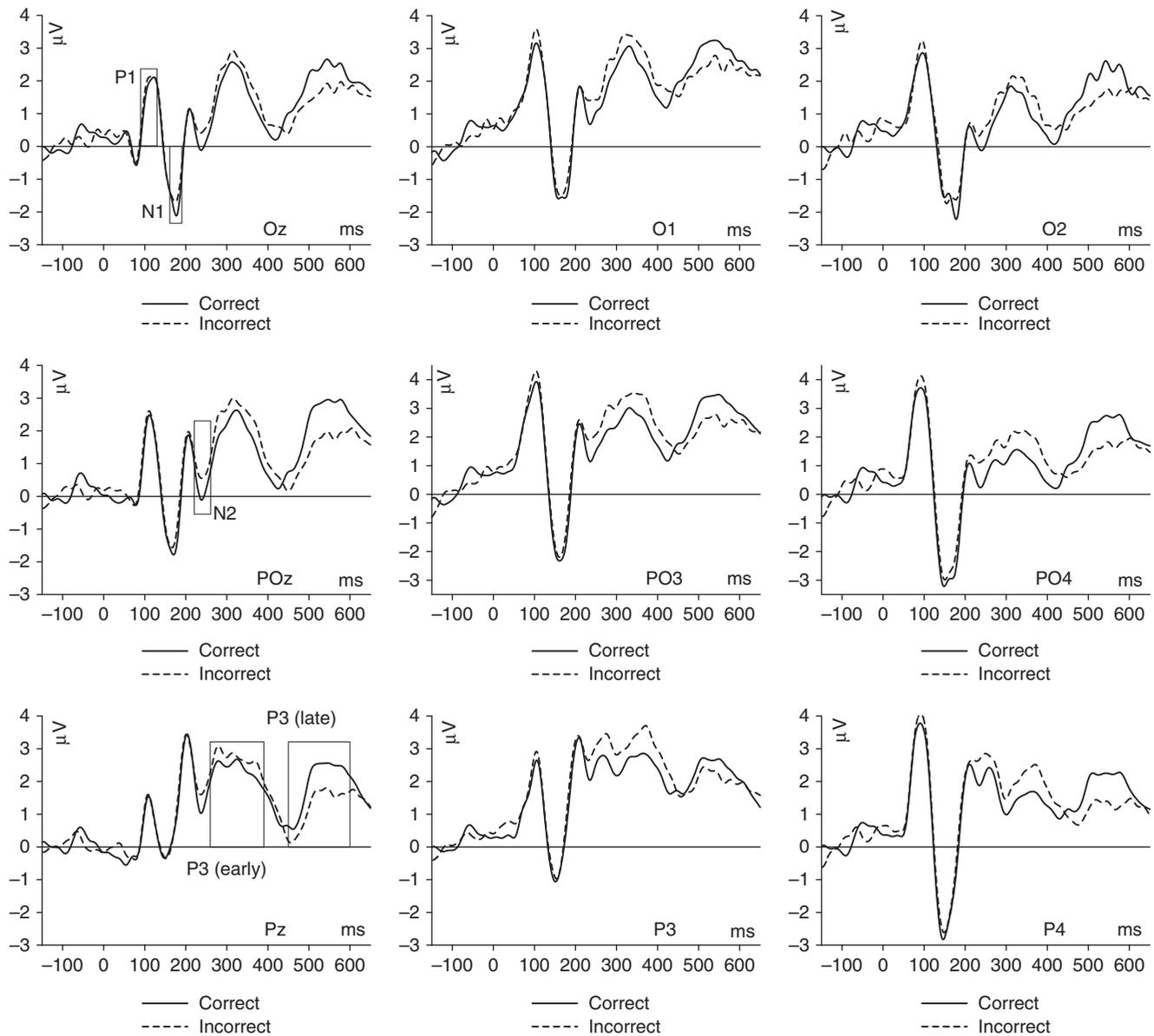


Figure 3. ERP amplitude in microvolts as a function of time in milliseconds. Shown are the Oz (top left panel), O1 (top center), O2 (top right), POz (middle left), PO3 (middle center), PO4 (middle right), Pz (bottom left), P3 (bottom center), and P4 (bottom right) electrodes. The zero time point represents the onset of the first stimulus array, and box outlines delineate analysis windows.

the others (0.50 μV delta at POz, 0.65 μV delta at P3, and 0.59 μV delta at P4). The P3 in the late time window also showed effects of integration, although the main effect was just short of significance, $F(1,20) = 4.17$, $MSE = 4.393$, $p > .06$. In this case, however, mean amplitude in correct trials was higher than that in incorrect trials (2.19 μV and 1.53 μV , respectively). Integration did interact reliably with electrode position, $F(2,42) = 6.27$, $MSE = .146$, $p < .005$, $\epsilon = .70$, even though the latter variable did not affect the ERP overall ($F < 1$). The interaction was caused by a decrease in amplitude during successful integration on the P3 electrode ($-0.30 \mu\text{V}$), whereas amplitude increased for the other electrodes (0.72 μV at Pz, 0.86 μV at POz, and 0.76 μV at P4). ERP amplitude over Pz, P3, and P4 as a function of time is shown in the bottom panel of Figure 3.

An additional analysis of the error trials was furthermore conducted. Error trials were categorized into two categories (nearby and far), which reflected the average spatial discrepancy between the location of the missing element and the response. No effects of this spatial factor were apparent in the P1 range ($F < 1.2$). The N1 elicited by these error trials was also not affected by integration ($F < 1$), but there was a trend toward an interaction with electrode position, $F(1,25) = 3.48$, $MSE = .178$, $p > .07$, $\epsilon = .63$. Errors falling into the nearby category elicited a weaker N1 on the Oz electrode ($-1.48 \mu\text{V}$) than those in the far category ($-1.60 \mu\text{V}$), a pattern not seen on the O1 and O2 electrodes. The N2 and P3 analyses did not reveal any reliable effects ($F < 1.4$). Thus, it can be concluded that the average spatial correspondence between errors and the location of the missing element barely affected the integration process.

Finally, an analysis was conducted to investigate possible effects on lateralized components. To this end, we examined the PO7/PO8 electrode pair and computed the ERP elicited by the missing element when it appeared ipsilateral to the electrode site (i.e., left hemisphere electrode site with the missing element appearing in the left visual field and the same for right hemisphere site and right visual field) and subtracted these from the corresponding contralateral waveforms (i.e., left hemisphere electrode site and right visual field and the same for right hemisphere site and left visual field). The resulting difference waveform reflects lateralized brain activity. Such difference waves were computed for both correct and incorrect trials. Both an early and a late window were examined; the first was a typical N2pc range window between 180 and 260 ms, and the second window corresponded to the observed lateralization in the present study, from 300 to 480 ms. No effect was observable in the early window, $F < 1$, suggesting that lateralized attentional components, as associated with the N2pc (e.g., Luck & Hillyard, 1994) were not involved in the present task. In the late window, an increased negativity of a rather sustained nature was observed contralateral to the location of the missing element for correct trials only ($-0.95 \mu\text{V}$ compared to $-0.23 \mu\text{V}$ for incorrect trials). The difference between correct and incorrect trials was reliable, $F(1,20) = 11.15$, $MSE = .476$, $p < .005$. Given the relatively late occurrence of this effect, an interaction with the earlier effects associated with the integration process can be ruled out.

Current source density and ERP maps of the difference between successful and unsuccessful integration are shown in Figure 4, as well as these maps for both categories separately. There was no evidence for a change due to integration success in the topographical properties of any of the observed components, suggesting that they had identical neural generators. The P1, N1, and N2 all showed strong signal in posterior regions. Notably

missing was any evidence for an anterior N1. The (early) P3 showed a modest central distribution, whereas posterior regions also showed increased (and slightly lateralized) positivity. The differences observed in the early P3 window were similar to those in the N2 range, suggesting a qualitative change compared to the differences seen in the late P3 window.

In summary, the physiological results demonstrated that visual event integration is, in fact, a very fast process, as evidenced by the modulation of the N1. Thus, it can be concluded that temporal integration already acts on basic perceptual processes. Further modulations in the time ranges of the N2 and P3 components were also observed, confirming that temporal integration continues to affect visual perception up to the phase of working memory consolidation.

General Discussion

The present results provide new insights into the temporal properties of event integration over time. It was established that temporal event integration in the MET is independent of potential differences in the deployment of sustained attention on the trial level and independent of the deployment of attention to S2 in particular. As we were able to show, S1 duration strongly affects performance in the integration-dependent MET but not in other, nonintegrative perceptual tasks, such as the majority and size judgment tasks. This is not to say that attention is completely irrelevant for the MET, but rather that the process of integration has a unique, observable effect of its own.

The ERP results demonstrated that visual event integration is able to act on early visual processing, as evidenced by the modulation of the N1. The effects of integration persisted across later components; it increased N2 amplitude, decreased early P3 amplitude, and increased late P3 amplitude. Temporal integration has been shown to be responsive to endogenous control (Akyürek et al., 2007, 2008), and the early locus of temporal integration that was presently observed thus suggests that such endogenous control can exert effects on some of the most basic phases of visual processing.

Whereas N1 amplitude was enhanced during successful integration, P1 amplitude was not affected. Although P1 and N1 amplitude are often modulated concurrently as a function of spatial attention in experimental tasks, they have also been dissociated (see Mangun, 1995). In the present study, the finding that P1 amplitude was unaffected by the success of integration supported the idea that the very first phase of attentional deployment was constant.

Modulation of the N1 in the auditory domain has previously been attributed to temporal integration of successive tones (Loveless, Levänen, Jousmaki, Sams, & Hari, 1996). Indeed, Müller, Widmann, and Schröger (2005) have shown an increased N1 in response to successive tones originating from the same auditory stream as compared to tones from different streams. If the N1 can be taken to underlie temporal integration, then these results can be interpreted as an increase in the temporal integration of successive tones, which in turn supports the idea that the N1 is sensitive to event-based modulation.

N1-related activity in the visual domain has been attributed to the reorienting of attention but also to a discriminative process that is not directly related to attention (Heinze et al., 1990; Luck, Heinze, Mangun, & Hillyard, 1990; Vogel & Luck, 2000). The present N1 modulation did not seem to fit either category very

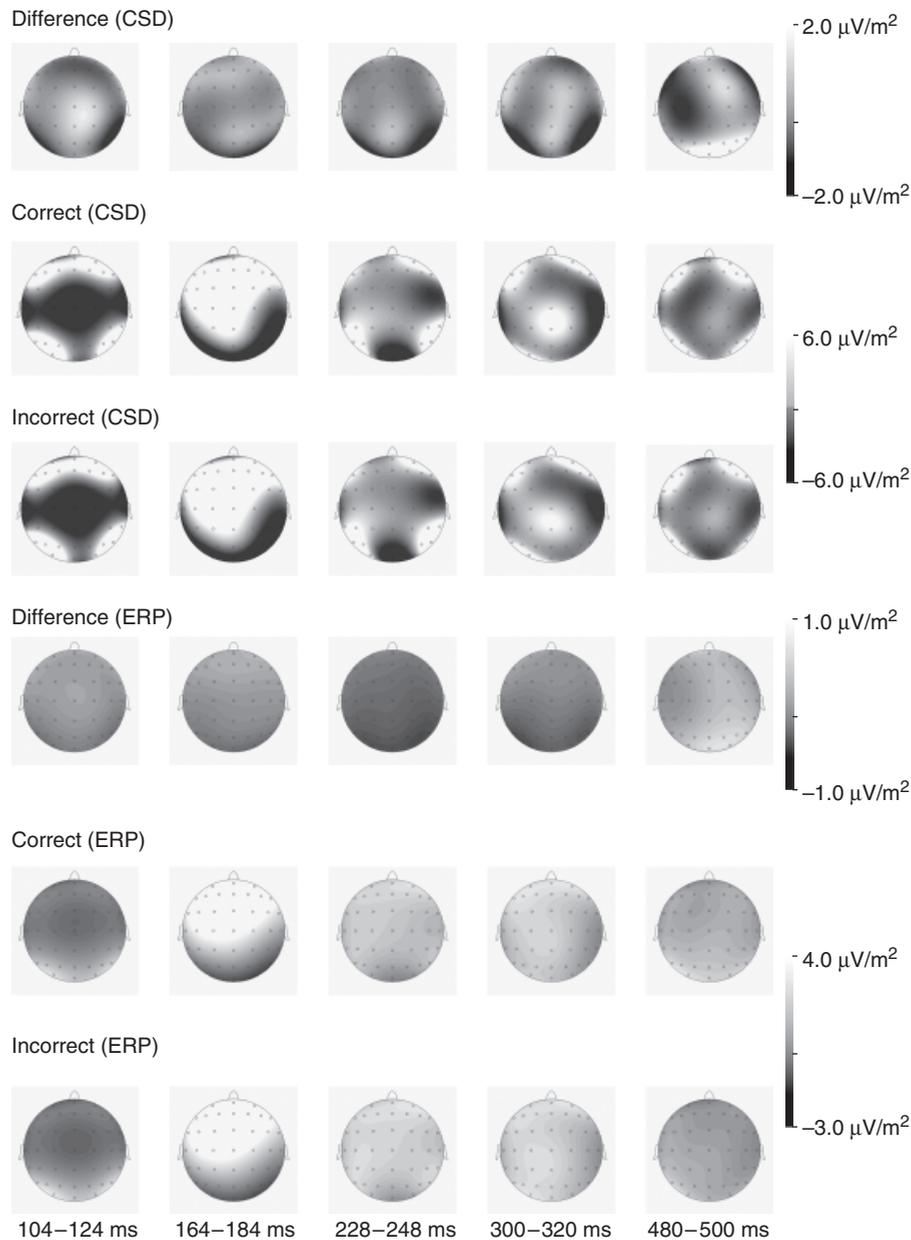


Figure 4. Topographical maps of the brain activity at the P1, N1, N2, and early and late P3 waveform peaks. The top panel shows CSD maps for the difference between successful and unsuccessful integration (top row) as well as for each of these separately (middle and bottom rows). The bottom panel shows the same, but visualized as ERP maps. Maps use spherical spline interpolation and represent a 20-ms average centered on the observed waveform peaks.

well, as neither attentional reorienting nor increased discrimination is immediately evident when integration succeeds. When S1 and S2 are processed as two separate events (a failure to integrate), then an attentional reorienting response to S2 might have been expected; instead, N1 amplitude was decreased. An increased discriminative response could be associated with successful integration in two ways. One possibility is that integration in the present paradigm serves a function that is in some way similar to discrimination in choice-RT tasks (Vogel & Luck, 2000). It could be argued, therefore, that what has been described as the N1 discriminative process can also be interpreted as a particular instance of (featural) integration. A second possibility is that the modulation of the N1 is a correlate of the *consequence* of successful integration rather than a correlate of integration

itself. In this view, integration might be taking place even before the N1, and the modulation of this component observed in the present paradigm could be attributed to successful perception of the location of the missing element.

Attention to nonspatial features has been associated with relatively broad selection negativity (SN; Hillyard & Münte, 1984), an early component that is nonetheless distinct from the N1 and seems to occur in the range of the N2 (e.g., Anllo-Vento & Hillyard, 1996). The SN has been associated with feature-specific selection and has been linked to a potential generator source in intermediate extrastriate cortex (Hopf, Boelmans, Schoenfeld, Luck, & Heinze, 2004). The enhancement of the N2 and the attenuation of the early P3 observed in the present study may bear some semblance to the SN, both with regard to time range as

well as to its topographical scalp distribution over occipital regions. If the presently observed modulations across the N2 and P3 can indeed be taken to reflect a form of SN, then this is necessarily a feature-agnostic variant of it: The stimulus arrays in the present study did not allow for selection on the basis of feature values. Further study is required to determine the relationship between the negativity observed presently and the SN before conclusive claims can be made. An alternative explanation of the current modulation of the N2 is that it reflected the grouping of the stimuli by similarity or homogeneity coding (Duncan & Humphreys, 1989). It has been shown that the posterior N2 is modulated by factors affecting texture segmentation without depending on featural properties (Schubö, Schröger, & Meinecke, 2004; Schubö et al., 2007). This account fits well with the current paradigm. Once temporal integration has succeeded, it enabled the grouping of all stimuli in the array. Indeed, the N2 modulation might be thought of as a correlate of spatial integration, performed in the present paradigm as a second step, after the two displays were temporally integrated.

The increased amplitude of the late P3 component could be attributed to an increase in efficiency with regard to consolidating the stimuli in memory. When integration was successful, one event representation was sufficient for full representation. In case of a failure to integrate the stimuli into one event episode, an inefficient set of two separate episodes had to be established, and the increased effort associated with this process was presumably reflected by lower P3 amplitude. A response-related account of the P3 modulation can be discounted. In the experimental paradigm the response was deferred, which minimizes if not eliminates any influence of motor- and response-related factors on the ERP.

Previous studies on featural integration have shown even earlier effects than those reported here for temporal integration,

tracing back to the P1. Feature integration in these studies was accomplished by grouping according to a single basic feature value, such as the color of a swarm of dots (Schoenfeld et al., 2003; Valdes-Sosa et al., 1998; Zhang & Luck, 2009), or even by grouping input within distinct sensory modalities (Giard & Peronnet, 1999). In terms of “integrated competition” as proposed by Duncan and colleagues (Desimone & Duncan, 1995; Duncan et al., 1997), this may reflect the speed at which a neural module that encodes a particular feature (e.g., color) early in the visual processing stream can spread its activity to other modules (e.g., location), thereby binding features together at an early stage. In any case, a slightly earlier locus of featural integration, as compared to temporal integration, might be expected for logical reasons: Feature integration can rely on information that is available from one glance of the visual scene, whereas temporal integration requires the passage of some time by definition.

The present study provides the first demonstration of very fast temporal event integration and, as such, bears some relevance for the study of attention to temporal stimulus properties. Indeed, the present task in some sense required a kind of implicit temporal judgment of the visual input, that is, a “choice” to perceive the two displays as one extended event or as two separate successive ones. One study on attention to temporal stimulus properties was reported by Griffin, Miniussi, and Nobre (2002). It revealed that a temporal cue modulates the ERP to a probe stimulus, starting at 250 ms at the earliest (in unilateral displays). These findings led the authors to conclude that temporal attention had a later effect than its spatial counterpart. The present results are not necessarily in disagreement with this conclusion, yet they do show how visual information processing can be influenced by temporal integration almost as fast as it is by spatial attention, divided by a temporal gap only as wide as the lag between P1 and N1.

REFERENCES

- 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.
- Akyürek, E. G., Toffanin, P., & Hommel, B. (2008). Adaptive control of event integration. *Journal of Experimental Psychology: Human Perception and Performance*, *34*, 569–577.
- Allport, D. A. (1968). Phenomenal simultaneity and the perceptual moment hypothesis. *British Journal of Psychology*, *59*, 395–406.
- Anllo-Vento, L., & Hillyard, S. A. (1996). Selective attention to the color and direction of moving stimuli: Electrophysiological correlates of hierarchical feature selection. *Perception & Psychophysics*, *58*, 191–206.
- Barceló, F., Suwazono, S., & Knight, R. T. (2000). Prefrontal modulation of visual processing in humans. *Nature Neuroscience*, *3*, 399–403.
- 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.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, *18*, 193–222.
- Di Lollo, V. (1977). Temporal characteristics of iconic memory. *Nature*, *267*, 241–243.
- Di Lollo, V. (1980). Temporal integration in visual memory. *Journal of Experimental Psychology: General*, *109*, 75–97.
- Di Lollo, V., & Dixon, P. (1988). Two forms of persistence in visual information processing. *Journal of Experimental Psychology: Human Perception and Performance*, *14*, 671–681.
- 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.
- Donchin, E., & Coles, M. G. (1988). Is the P300 component a manifestation of context updating? *Behavioral & Brain Sciences*, *11*, 357–374.
- Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychological Review*, *96*, 433–458.
- Duncan, J., Humphreys, G., & Ward, R. (1997). Competitive brain activity in visual attention. *Current Opinion in Neurobiology*, *7*, 255–261.
- Enns, J. T., & Di Lollo, V. (2000). What’s new in visual masking? *Trends in Cognitive Sciences*, *4*, 345–352.
- Giard, M. H., & Peronnet, F. (1999). Auditory-visual integration during multimodal object recognition in humans: A behavioral and electrophysiological study. *Journal of Cognitive Neuroscience*, *11*, 473–490.
- 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.
- Griffin, I. C., Miniussi, C., & Nobre, A. C. (2002). Multiple mechanisms of selective attention: Differential modulation of stimulus processing by attention to space or time. *Neuropsychologia*, *40*, 2325–2340.
- 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.
- 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.
- Hogben, J. H., & Di Lollo, V. (1974). Perceptual integration and perceptual segregation of brief visual stimuli. *Vision Research*, *14*, 1059–1069.
- Hommel, B. (2004). Event files: Feature binding in and across perception and action. *Trends in Cognitive Sciences*, *8*, 494–500.

- 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.
- Hommel, B., Müsseler, 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.
- Hopf, J.-M., Boelmans, K., Schoenfeld, M. A., Luck, S. J., & Heinze, H.-J. (2004). Attention to features precedes attention to locations in visual search: Evidence from electromagnetic brain responses in humans. *Journal of Neuroscience*, *24*, 1822–1832.
- 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.
- 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.
- Luck, S. J., & Hillyard, S. A. (1994). Electrophysiological correlates of feature analysis during visual search. *Psychophysiology*, *31*, 291–308.
- Mangun, G. R. (1995). Neural mechanisms of visual selective attention. *Psychophysiology*, *32*, 4–18.
- Müller, D., Widmann, A., & Schröger, E. (2005). Auditory streaming affects the processing of successive deviant and standard sounds. *Psychophysiology*, *42*, 668–676.
- Nieuwenhuis, S., Yeung, N., & Cohen, J. D. (2004). Stimulus modality, perceptual overlap, and the go/no-go N2. *Psychophysiology*, *41*, 157–160.
- Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology*, *118*, 2128–2148.
- 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.
- 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.
- Schoenfeld, M. A., Tempelmann, C., Martinez, A., Hopf, J. M., Sattler, C., Heinze, H. J., et al. (2003). Dynamics of feature binding during object-selective attention. *Proceedings of the National Academy of Sciences, USA*, *100*, 11806–11811.
- 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.
- 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.
- Treisman, A. (1996). The binding problem. *Current Opinion in Neurobiology*, *6*, 171–178.
- 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.
- 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.
- Vogel, E. K., & Luck, S. J. (2000). The visual N1 component as an index of a discrimination process. *Psychophysiology*, *37*, 190–203.
- 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 feedforward processing. *Nature Neuroscience*, *12*, 24–25.

(RECEIVED March 5, 2009; ACCEPTED July 9, 2009)