



What processes are disrupted during the attentional blink? An integrative review of event-related potential research

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Abstract

Reporting the second of two targets is impaired when these appear in close succession, a phenomenon known as the attentional blink (AB). Despite decades of research, what factors limit our ability to process multiple sequentially presented events remains unclear. Specifically, two central issues remain open: does failure to report the second target (T2) reflect a structural limitation in working memory (WM) encoding or a disruption to attentional processes? And is perceptual processing of the stimulus that we fail to report impaired, or only processes that occur after this stimulus is identified? We address these questions by reviewing event-related potential (ERP) studies of the AB, after providing a brief overview of the theoretical landscape relevant to these debates and clarifying key concepts essential for interpreting ERP studies. We show that failure to report the second target is most often associated with disrupted attentional engagement (associated with a smaller and delayed N2pc component). This disruption occurs after early processing of T2 (associated with an intact P1 component), weakens its semantic processing (typically associated with a smaller N400 component), and prevents its encoding into WM (associated with absent P3b). However, failure to encode T2 in WM can occur despite intact attentional engagement and semantic processing. We conclude that the AB phenomenon, which reflects our limited ability to process sequential events, emerges from the disruption of both attentional engagement and WM encoding.

Keywords Attentional blink · Attentional engagement · Working memory · Semantic processing · P1 · N2pc · P3 · N400

Introduction

How fast we process successive events in a highly dynamic environment plays a crucial role in guiding our actions and determining their outcomes. For example, as any driver knows, a tiny delay in detecting a sudden change on the road can mean the difference between safely stopping the car and a fatal accident. It is therefore unsurprising that one of the main endeavors of psychological research is to understand what factors affect the timing of information processing. Such research has uncovered that we are severely limited in our

ability to process sequential events (e.g., a ringing cellphone and a pedestrian running across the road). In particular, when two events occur in close temporal succession, our performance at reporting the second event is poor, a phenomenon known as the “attentional blink” (AB, Raymond et al., 1992). To create the AB effect in the lab, participants are usually required to search for two targets (T1 and T2) embedded among distractors presented in a rapid serial visual presentation (RSVP) stream. The typical pattern of results is that T2 identification is impaired when this target appears within half a second from T1 (the blink period), and gradually returns to baseline. When T2 immediately follows T1 and appears at the same location, performance is spared (Lag-1 sparing; Potter et al., 1998).

The discovery of the AB spurred one of the most comprehensive research efforts in cognitive psychology (for reviews, see Dux & Marois, 2009; Martens & Wyble, 2010). Yet, the key limitations underlying the low performance observed during the blink remain elusive. In particular, two central questions are still unanswered: (i) Does failure to report the second target reflect a disruption to attentional processes or a

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structural limitation in encoding information into working memory (WM)? And (ii) is perceptual processing of the stimulus that we fail to report impaired, or only processes that occur after this stimulus is identified? The answers to these fundamental questions have far-reaching implications because the AB is extensively used as a diagnostic tool both in basic research (in order to explore the mechanisms underlying processes such as emotion perception (Anderson & Phelps, 2001; McHugo et al., 2013) or conscious perception (e.g., Sergent et al., 2005)), and in applicative and clinical research (as a tool to study individual differences (e.g., Beech et al., 2008; Lahar et al., 2001; Mason et al., 2005; Wynn et al., 2006)).

In the present review, we survey the AB studies that relied on the event-related potential (ERP) methodology to explore the factors limiting our ability to process successive events. ERP research relies on the assumption that different cognitive processes are associated with unique and predictable neural fingerprints. Under certain conditions (Luck, 2012), the neural activity related to a given event manifests as transient changes in voltage that can be recorded from the surface of the scalp, using electroencephalogram (EEG) electrodes. ERPs are calculated by averaging segments of the ongoing EEG waveform that are time-locked to this event, a procedure that allows one to isolate the event-related brain activity from unrelated noise. Unlike behavioral studies, in which only the end outcomes of the identification process (i.e., the response) can be directly measured, ERP studies allow one to track how the processes that lead to target reports unfold in time, with high temporal precision. Thus, ERPs are particularly well suited to pinpoint what stages of processing are disrupted during the blink period (Luck & Vogel, 2001).¹ However, ERP studies that relied on the AB paradigm have yielded conflicting results, and, so far, there has been no attempt to integrate their findings. Previous reviews of the AB were broad in scope, both in terms of the methodologies they surveyed (behavioral, ERPs and fMRI) and of the issues they covered (Dux & Marois, 2009; Martens & Wyble, 2010). Here, we present a thorough but narrowly focused review of the studies that capitalized on the unique advantages of the ERP methodology to elucidate the factors that limit our ability to process successive events, as manifested in the AB effect.

We first provide a brief overview of the theoretical landscape relevant to these questions. Next, after a general description of the ERP method and relevant ERP components, we propose a classification of the extant ERP literature relying on the AB paradigm, according to the comparisons used to measure the AB: *lag effects*, *T2-identification effects* and *T1-task*

effects. We then use this classification to review the findings in two separate sections: (i) *Attention and working memory encoding during the AB* and (ii) *Perceptual processing during the AB*. Finally, we summarize the conclusions of our review and spell out their theoretical implications.

Selective theoretical overview

The two questions at the heart of this review can be traced back to disagreements between the first two major theories of the AB, Raymond et al.'s (1992) *Attentional Gating Theory* and Chun and Potter's (1995) *Two-Stage Model*. According to Raymond et al. (1992), attentional processes that are necessary for high-level perceptual processing are disrupted during the blink, whereas according to Chun and Potter (1995), the AB reflects a structural limitation in WM encoding that takes its toll after T2 is attended and identified (see also Jolicoeur & Dell'Acqua, 1998). While the distinctions between attentional selection and WM encoding on the one hand and between perceptual and post-perceptual processes on the other hand cleanly map onto the Attentional Gating Theory and Two-Stage Model, making sense of the differences between later theories requires a finer-grained categorization. For this purpose, we rely on a framework inspired by Eimer's (2014) four-stage model of selective attention in visual search.

According to our variant of Eimer's (2014) model, when participants search for a target, they go through four functionally dissociable stages. During the *preparation* stage (stage 1), observers prepare for the upcoming task by representing the search goals in WM (i.e., they generate an attentional template). During the *guidance* stage (stage 2), template-matching inputs are enhanced, which allows detecting a candidate target. Then, during the *attentional engagement* stage (stage 3), observers selectively allocate visual processing resources to the candidate target. Finally, during the *WM encoding* stage (stage 4), the target is encoded in WM, and the resulting representation is maintained there until it is no longer needed.

Two theories (Di Lollo et al., 2005; Taatgen et al., 2009) propose that the early stages that lead to target detection (stages 1 and 2) are disrupted during the blink period. We refer to these theories as the *disrupted-control* account (see also Zivony & Lamy, 2016, for a more detailed discussion). Di Lollo et al. (2005) suggested that control over the attentional filter is lost during the AB, such that target-monitoring processes are exogenously reconfigured by incoming irrelevant information. Taatgen et al. (2009) suggested that after the first target is detected, any mismatch between new information and the attentional template results in the suspension of target detection processes. Although important differences exist between the two accounts, they both assume that T2 is not

¹ Another sub-field of electrophysiology is the study of steady and synchronized brain states, such as activity in the alpha frequencies. The relationship between synchronized brain activity and the AB is outside the scope of this review and is not covered here (but see Janson & Kranczioch, 2011, for a review; see also Glennon et al., 2016; Petro & Keil, 2015; Pincham & Szűcs, 2012; Shapiro et al., 2017; for recent studies).

recognized as a target during the blink, and is therefore not selected for further processing.

Several theories propose that the AB effect emerges as a result of suppressed (e.g., Raffone et al., 2014; Raymond et al., 1992) or slowed (e.g., Nieuwenstein et al., 2005; Olivers & Meeter, 2008; Wyble et al., 2009) attentional engagement (stage 3). We refer to these theories as the *disrupted-engagement account*. Raymond et al. (1992) suggested that during the blink period, the operation of an attentional gate that grants perceptual information access to higher-level cognitive processes is temporarily disrupted. The attentional gate rapidly opens following a target's detection, but because it does not immediately close, irrelevant and conflicting information may be allowed through. When that happens, the gate shuts down for a short period, denying all incoming inputs access to further processing, until the information that passed through the gate is sorted and encoded (see Raffone et al., 2014, for a similar account). According to the more recent account suggested by Nieuwenstein et al. (Nieuwenstein et al., 2005; see also Bowman & Wyble, 2007; Olivers & Meeter, 2008), attentional engagement is not entirely suppressed during the blink. Instead, they suggest that the transient attentional enhancement that normally occurs rapidly following target detection, becomes sluggish during the blink. As a result, attention is engaged in the distractor that follows T2 rather than in T2 itself.

Finally, two theories referred to as the *bottleneck account* suggest that during the AB, access to WM (stage 4) becomes temporarily blocked (Chun & Potter, 1995; Jolicoeur & Dell'Acqua, 1998). According to this account, WM encoding is a serial process that can take several hundred milliseconds and is limited to one item (or one chunk of items) at a time. This structural capacity limitation creates a “bottleneck” through which additional targets cannot pass. Thus, even though during the blink T2 is correctly detected and selected (i.e., stages 1–3 are completed without disruption), its representation remains in an unstable state before it is encoded in WM, and can therefore be overridden by trailing masking stimuli.

According to the foregoing classification, the dividing line between theories that focus on attentional processing and theories that focus on WM encoding is crisp: the former postulate that one of several stages prior to encoding in WM (stages 1–3) is disrupted during the blink, whereas the latter posit that only encoding in WM (stage 4) is impaired. Notably, these theories all assume that a single mechanism is compromised during the attentional blink, and the possibility that a less parsimonious model may better explain the plurality of AB findings has typically been overlooked (but see, e.g., Kranczioch et al., 2007; Wong, 2002).

What stance do these theories adopt on the second question addressed in this review: is perceptual processing of a blinked target impaired? Perceptual processing refers to any

operations involved in forming sensory representations (e.g., Vogel et al., 2005; Zivony, Shanny, & Lamy, 2018b). Low-level perceptual processes, such as registration of basic features (e.g., color and orientation), are widely assumed to occur early, automatically, and in parallel across the visual field (Itti & Koch, 2000; Treisman, 2014; Wolfe, 2014). While AB theories generally agree that these processes remain unaffected during the blink, whether later, higher-level perceptual processes, and in particular semantic processing, are disrupted, is more controversial. The term “semantic processing” may refer to a variety of cognitive processes. For example, semantic processing of the word “doctor” may refer to its lexical identification, to its semantic categorization (e.g., doctor is a profession), or to the activation of related representations (e.g., nurse, syringe). For the present purposes, semantic processing refers to the perceptual processes required for lexical identification.

According to bottleneck theories (Chun & Potter, 1995; Jolicoeur & Dell'Acqua, 1998), semantic processing is intact during the blink period, since these theories posit that only WM encoding, which is thought to occur after semantic processing is complete, is disrupted during the blink. For attention-based theories of the AB, however, whether or not semantic processing suffers from the blink depends on whether attentional selection is thought to occur early or late, that is, before or after semantic processing – an issue that has a long and complex history (see Lachter et al., 2004, for a review of the “early vs. late selection” debate).

Raymond et al. (1992) initially adopted an early-selection view and suggested that the AB deficit results from attentional factors that occur at a relatively early stage prior to identification. Thus, according to their model, semantic processing is impaired during the blink. However, newer findings soon overturned this conclusion by demonstrating that a stimulus appearing during the blink primed a subsequent semantically related target (Maki et al., 1997; Shapiro et al., 1997). In light of these findings, virtually all later models of the AB embraced a post-perceptual account of the AB (see Dux & Marois, 2009). Specifically, attention-based theories adopted a late-selection view (Di Lollo et al., 2005; Raffone et al., 2014; Taatgen et al., 2009), according to which semantic analysis occurs independently of attentional enhancement and can affect response selection, even if semantic information is not available for conscious report. However, this theoretical consensus may be unwarranted. In contradiction with the post-perceptual account, several behavioral studies showed that semantic priming from blinked items is either severely reduced or entirely eliminated (e.g., Martens et al., 2002; Murphy & Bloom, 2015; Zivony & Lamy, 2016). These findings raise the possibility that although semantic processing may occur during the blink, it is weakened to the extent that it may have little effect on downstream processes. Closer scrutiny of the extant ERP studies may help resolve this issue.

Studying the attentional blink (AB) with event-related potentials (ERPs)

ERP components

Event-related potentials (ERPs) refer to waveforms resulting from the averaging of EEG activity time-locked to a specific event (for reviews, see Luck, 2014; Woodman, 2010). These waveforms consist of successive positive and negative deflections often called “components,” that are typically named according to their polarity (positive or negative) and the order of their appearance (e.g., P1 and N1 followed by P2 and N2). A prominent advantage of ERPs is that they provide a continuous measure of the neural activity that occurs between the onset of the critical event and the response – unlike behavioral measures, such as response times or accuracy, which reflect the final outcome of the many intervening processes.

One challenge encountered by ERP researchers is that recorded neural activity often reflects the combined outcome of multiple co-occurring processes. This is especially true in RSVP experiments, as activity related to target processing typically overlaps with activity related to the processing of temporally adjacent distractors. In order to address this problem, many ERP researchers use what is called the *subtraction method*. This method relies on the rationale that by subtracting one EEG waveform from another, the resulting difference wave reflects only the neural activity that is not shared between the two original waveforms. In other words, if only one waveform contains activity related to the process of interest and the two waveforms are identical in all other respects, unrelated activity should be cancelled out in the subtraction. How this method can be used to isolate the EEG activity related to the target in an RSVP paradigm is illustrated in Fig. 1.

In order to study psychological processes using ERPs, a connection must first be established between a process and its electrophysiological signature. This association is recognized when considerable similarity is found in the component activity (e.g., in timing and scalp distribution) from different experiments thought to tap the same process. It is important to note that a component merely reflects neural activity that is consistently associated with a given process (and not the process itself). Nevertheless, experimental manipulations that modulate the activity of a component can shed light on the factors that affect the time course of the associated cognitive process.

As ERP research has accumulated since the 1960s, many reliable associations have been established between specific cognitive processes and ERP components. Here, we focus on the components that have been most extensively investigated

in the context of the AB: P1, N2pc, P3, and N400.² As we explain in more detail below, the P1 component is typically associated with early perceptual processing, the N2pc with attentional selection, the P3 with a variety of processes including updating in WM, and the N400 with detection of semantic anomalies. We thus examine the extent to which these components are modulated during the blink in order to answer the questions that are the focus of the present review (the findings from ERP studies of the AB are summarized in Table 1). Note, however, that despite the relative consensus regarding the mechanisms indexed by these components, their characterization is an ongoing endeavor. Therefore, any conclusions drawn from the present review may need revising if new findings modify the current interpretation of these components.

The P1 component P1 is the first positive deflection in the ERP waveform. It is widely distributed across the scalp, emerges within 60–100 ms of stimulus onset, and is thought to reflect registration of the eliciting stimulus’ physical attributes in the extrastriate cortex (Hillyard & Picton, 1987; see Pratt, 2012, for a review). In line with this interpretation, P1 was found to be sensitive to the luminance of unattended objects (Johannes et al., 1995). Therefore, for the purposes of the present review, we consider P1 as an index of early perceptual processing.

The N2pc component The N2-posterior-contralateral (N2pc) component typically emerges within a 180- to 300-ms window from stimulus onset over posterior sites. The N2pc manifests as a larger amplitude at electrodes contralateral to the target’s visual field relative to ipsilateral electrodes and is calculated as the difference wave between these (see Fig. 1). Therefore, the N2pc can be recorded only in response targets that appear laterally. While it is generally agreed that the N2pc indexes spatially specific attentional processes (Eimer, 1996; Woodman & Luck, 1999) that occurs downstream from attentional shifting (e.g., Hoffman et al., 2020; Kiss et al., 2008; Luck, 2012; Theeuwes, 2010; Zivony, Allon, et al., 2018a), a more precise characterization of these processes remains a matter of debate, with the most prominent candidates being: individuation of a potential target from surrounding objects (Mazza & Caramazza, 2011), precise localization of the target’s spatial coordinates (Tan & Wyble, 2015), the onset of transient attentional enhancement (Zivony, Allon, et al., 2018a), a combination of target enhancement and distractor suppression that relies on correct feature binding (Luck, 2012), and the process that grants objects access to conscious recognition (Berggren & Eimer, 2020). Note, however, that a common denominator of these accounts is that the N2pc is tightly linked to either the attentional engagement stage itself or to its immediate precursors (individuation, localization) or consequences (feature binding, conscious access). Therefore, for the purposes of the present review, we consider the N2pc as an index of attentional engagement.

² For completeness, we refer to AB studies that reported additional ERP components (N1, P2, N2, and P3a) in Table 1.

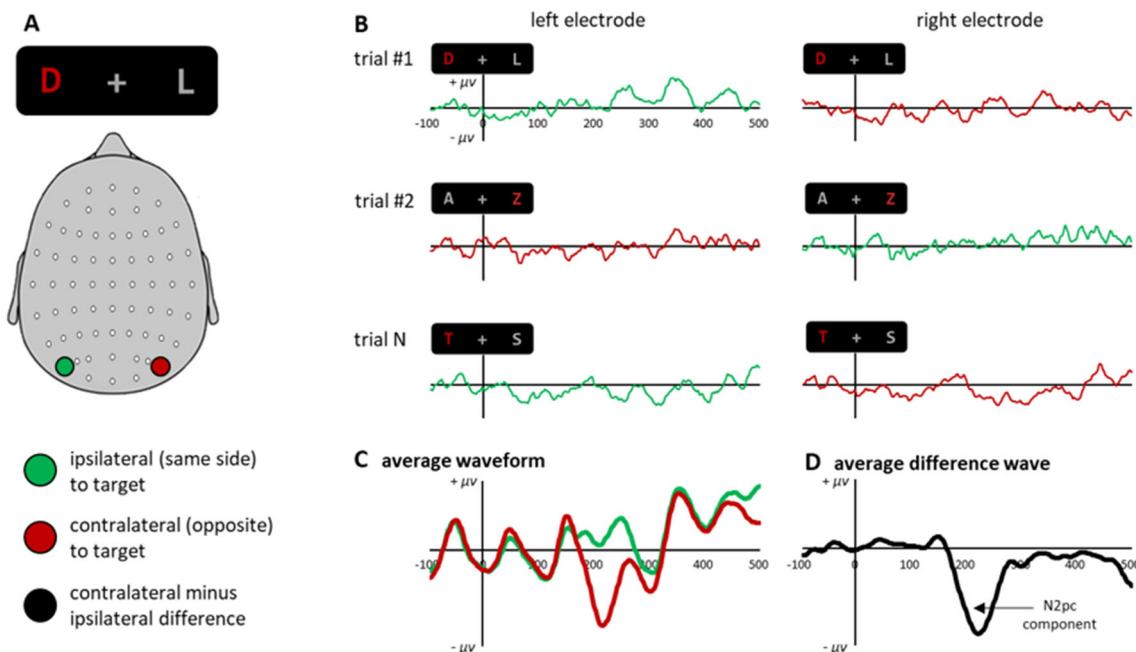


Fig. 1 Illustration of event-related potential (ERP) averaging and subtraction used to isolate the target-related N2pc component. A target is presented left or right from screen center. (A) The target is the red letter. Electrodes (represented as dots) record neural activity from the scalp. The N2pc is calculated based on activity recorded in two occipital electrodes, one ipsilateral and the other contralateral to the target's side (marked green and red, respectively). (B) Neural activity is recorded and segmented offline, relative to the time of target onset. Because neural activity from unrelated events is also recorded in the two electrodes, clear target-related

activity is difficult to detect on a trial-by-trial basis. Averaging the activity from each electrode reduces noise and enhances the target-related neural signal (C). In rapid serial visual presentation (RSVP) experiments, the rapidly onset and offset stimuli result in neural activity that overlaps with the ERP component. However, this activity is similar on both ipsilateral and contralateral electrodes. Therefore, subtracting the average ipsilateral waveform from the average contralateral waveform (D), retains only lateralized neural activity, and allows one to isolate the target-related N2pc

The P3 component The P3 (also called P3b) is a positive deflection with a typical peak latency between 300 and 500 ms from stimulus onset over midline sites. The P3 is widely thought to reflect processes related to WM updating, downstream from attentional enhancement (see Polich, 2007, for a review). A central finding supporting this account is that P3 is larger for infrequent than for frequent targets, regardless of their physical saliency. Given the robustness of this finding, many researchers opt to isolate the P3 by computing a frequency-related difference wave, which results from the subtraction of the waveform associated with a frequent target from the waveform associated with an infrequent target. Other accounts include potentiation of responses to motivationally significant events (e.g., Nieuwenhuis et al., 2005), conscious perception (e.g., Rutiku et al., 2015; Salti et al., 2012; Sergent et al., 2005), and post-perceptual processing related to report (e.g., Pitts et al., 2014). A common denominator of these interpretations is that the P3 occurs after the target is encoded in WM but prior to response selection. Therefore, for the purposes of the present review, we consider the P3 as an index of WM encoding.

The N400 component The N400 is a negative deflection that emerges approximately 400 ms after stimulus onset over centroparietal sites. The N400 is particularly sensitive to

semantic anomalies: after a specific semantic context is established, the N400 is larger for semantically incongruent stimuli (e.g., “medicine-banana”) than for semantically congruent stimuli (e.g., “medicine-doctor”). Accordingly, the N400 is often thought to index the detection of semantic relationships (see Kutas & Federmeier, 2011, for a review). It is usually isolated by subtracting the congruent- from the incongruent-condition waveforms, resulting in a congruency-related difference waveform. Note, however, that three processes are logically necessary for a reliable congruency-related N400: participants must retain the semantic context established by the experimental procedure, extract semantic information from the target, and compare the two. On the one hand, for the purposes of the present review, the presence of the N400 component can be taken to indicate that semantic information was extracted. On the other hand, however, finding that this component is reduced or eliminated is more difficult to interpret, because it may indicate that processes other than semantic identification were impaired.

ERP measures of the AB

The studies reviewed here investigate which cognitive processes are disrupted during the blink period by measuring changes in the ERP component activity associated with T2.

Table 1 Event-related potential (ERP) studies of the attentional blink (AB)

Component	Article	Condition /experiment	Isolation method	Comparison	Finding
P1/N1	Batterink et al., 2012	Experiment 1	Raw waveform	T2-identification	Ø
	Koivisto & Revonsuo, 2008	Raw waveform	Raw waveform	T1-task	Ø
	Kranzioch et al., 2007	T2 waveform	T2 present minus T2 absent	T2-identification	Ø
	Lasaponara et al., 2015	T2 present minus T2 absent	T2 present minus T2 absent	T2-identification	Ø
	Sergent et al., 2005	T2 present minus T2 absent	T2 present minus T2 absent	T2-identification	Ø
	Vogel et al., 1998	Probe present minus probe absent	Probe present minus probe absent	Lag effect × T1-task	Ø
	Weller et al., 2019	Raw waveform	Raw waveform	Lag effect	Ø
	Akyurek et al., 2010	T2 present minus T2 absent	T2 present minus T2 absent	Lag effect	S
	Batterink et al., 2012	Raw waveform	Raw waveform	T2-identification	Ø
	Koivisto & Revonsuo, 2008	Experiment 1	T1-task	T2-identification	Ø
P2	Kranzioch et al., 2003	Experiment 1	T2-identification	T2-identification	Ø
	López et al., 2008	Raw waveform	Raw waveform	Lag effect	Ø
	Berti, 2011	Probe present minus probe absent	Probe present minus probe absent	Lag effect × T1-task	Ø
	Vogel et al., 1998	Inrequent minus frequent T2	Inrequent minus frequent T2	Lag effect	S
	Vogel & Luck, 2002	Infrequent minus frequent T2	Infrequent minus frequent T2	Lag effect	S
	Unmasked T2	Infrequent minus frequent T2	Infrequent minus frequent T2	Lag effect	S
	Dell'Acqua et al., 2006	T2 present minus T2 absent	T2 present minus T2 absent	T2-identification	R
	Experiment 1	T2 present minus T2 absent	T2 present minus T2 absent	T2-identification	R
	Experiment 2	T2 present minus T2 absent	T2 present minus T2 absent	T2-identification	S*
	Kranzioch et al., 2003	Raw waveform	Raw waveform	T2-identification	R
N2pc	Nakatani et al., 2012	T2 present minus T2 absent	Contralateral minus ipsilateral	Lag effect × T1-task	R
	Sergent et al., 2005	Contralateral minus ipsilateral	Contralateral minus ipsilateral	T2-identification	R
	Akyurek et al., 2010	Contralateral minus ipsilateral	Contralateral minus ipsilateral	T1-task, T2-identification	Ø
	Chennu et al., 2008	Contralateral minus ipsilateral	Contralateral minus ipsilateral	Contralateral minus ipsilateral	S
	Dell'Acqua et al., 2006	Contralateral minus ipsilateral	Contralateral minus ipsilateral	Contralateral minus ipsilateral	R
	Easy T1	Difficult T1	Difficult T1	Contralateral, T2-identification	R
	Jolicœur, Sessa, Dell'Acqua, & Robitaille, 2006a	Contralateral minus ipsilateral	Contralateral minus ipsilateral	Lag effect	R
	Jolicœur, Sessa, Dell'Acqua, & Robitaille, 2006b	Contralateral minus ipsilateral	Contralateral minus ipsilateral	Lag effect × T1-task	S
	Lagoix et al., 2015	Contralateral minus ipsilateral	Contralateral minus ipsilateral	Lag effect	D
	Losier et al., 2017	Contralateral minus ipsilateral	Contralateral minus ipsilateral	Lag effect	Ø
Z1/Z2	Pomerleau et al., 2014	Contralateral minus ipsilateral	Contralateral minus ipsilateral	Lag effect	R
	Robitaille et al., 2007	Contralateral minus ipsilateral	Contralateral minus ipsilateral	T1-task	R
	Verleger et al., 2009	Contralateral minus ipsilateral	Contralateral minus ipsilateral	Lag effect	R
	Zivony, Allou, et al., 2018a	Contralateral minus ipsilateral	Contralateral minus ipsilateral	Lag effect	R,D

Table 1 (continued)

Component	Article	Condition /experiment	Isolation method	Comparison	Finding
P3a	Batterink et al. 2012 Dell'Acqua et al., 2015 Lasaponara et al., 2015	Raw waveform T2 present minus T2 absent	T2-identification Lag effect	Ø R	
	Experiment 1 Experiment 2	T2 present minus T2 absent	T2-identification	R	
	Masked T3	T2 present minus T2 absent	T2-identification	R	
	Losier et al., 2017	T3 present minus T3 absent	Lag effect	R	
	Unmasked T3	T3 present minus T3 absent	Lag effect	R	
	Sergent et al., 2005	T2 present minus T2 absent	T2-identification	S	
	Akyurek et al. 2010	T2 present minus T2 absent	Lag effect	R	
	Batterink et al. 2012	T2 present minus T2 absent	T2-identification	Ø	
	Arnell, 2006	Raw waveform	T2-identification	R, D	
	Bourassa et al., 2015	Inrequent minus frequent T2	Lag effect		
	Crastan et al. 2009	Inrequent minus frequent T2	Lag effect × T2-identification	S	
	Damsma et al., 2018	Raw waveform	Lag effect × T2-identification	S*	
	Dell'Acqua et al., 2003	Inrequent minus frequent target	Lag effect × T2-identification	S*	
	Dell'Acqua et al., 2015	T2 present minus T2 absent	Lag effect × T1-task	R, D	
	Kranzioch et al. (2003)	T2 present minus T2 absent	Lag effect		
	Kranzioch et al., 2007	Raw waveform	Lag effect × T2-identification	S*	
	Lasaponara et al., 2015	T2 present minus T2 absent	T2-identification	R	
	Experiment 1	T2 present minus T2 absent	T2-identification	R	
	Experiment 2	Raw waveform	Lag effect	S*	
	Control group	T3 present minus T3 absent	Lag effect	R, D	
	Masked T3	T3 present minus T3 absent	Lag effect	R, D	
	Unmasked T3	Raw waveform	T1-task, T2-identification	R	
	Lopez et al. 2008	Raw waveform	Lag effect	D	
	Losier et al., 2017	Raw waveform	Lag effect	S*	
	Martens et al., 2006	Raw waveform	T2-identification	S	
	Morimoto & Yagi 2013	Raw waveform	T2-identification	S*	
	Nakatani et al., 2012	Raw waveform	Lag effect × T2-identification	S*	
	Pesciarellia et al. 2007	Raw waveform	Lag effect	R	
	Pincham & Szűcs 2012	Raw waveform	T2-identification	S	
	Pincham & Szűcs, 2014	Raw waveform	Lag effect × T2-identification	R	
	Ptitó et al., 2008	Inrequent minus frequent T2	Lag effect	S	
	Robitaille et al., 2007	Inrequent minus frequent T2	T1-task	S	
	Rölke et al., 2001	T2 present minus frequent T2	T2-identification	R	
	Sergent et al., 2005	Inrequent minus frequent T2	T2-identification	S	
	Sessa et al. 2009	Inrequent minus frequent T2	Lag effect × T1-task	R	
	Vogel et al. 1998	Inrequent minus frequent T2	Lag effect × T1-task	R, D	
	Experiment 4		Lag effect × T1-task	S	

Table 1 (continued)

Component	Article	Condition /experiment	Isolation method	Comparison	Finding
N400	Vogel & Luck, 2002	Masked T2 Unmasked T2	Inrequent minus frequent T2 Inrequent minus frequent T2	Lag effect Lag effect	S D
	Batterink et al., 2010	Easy T1 Difficult T1	Congruent minus incongruent T2 Congruent minus incongruent T2 Congruent minus incongruent T2 Congruent minus incongruent T2	Lag effect × T2-identification Lag effect Lag effect Lag effect	S Ø S
	Giesbrecht et al., 2007		Congruent minus incongruent T2 Congruent minus incongruent T2 Congruent minus incongruent T2 Congruent minus incongruent T2	Lag effect T2-identification T2-identification T2-identification	Ø S
	Loonis, 2006		Congruent minus incongruent T2 Congruent minus incongruent T2 Congruent minus incongruent T2 Congruent minus incongruent T2	T2-identification T2-identification T2-identification T2-identification	S S S R
	Peressotti et al., 2012		Congruent minus incongruent T2 Congruent minus incongruent T2 Congruent minus incongruent T2	T1-task Lag effect Lag effect	Ø Ø Ø
	Pesciarellia et al. 2007		Congruent minus incongruent T2	Lag effect	Ø
	Rolke et al., 2001		Congruent minus incongruent T2	Lag effect	Ø
	Sy et al. 2012	Unmasked T2 Experiment 2	Congruent minus incongruent T2 Congruent minus incongruent T2	Lag effect Lag effect	Ø Ø
	Vachon & Jolicœur, 2011		Congruent minus incongruent T2	Lag effect	Ø
	Vogel et al., 1998		Congruent minus incongruent T2	Lag effect	Ø
	Weller et al., 2019		Congruent minus incongruent T2	R	

Notes. Ø no effect on either amplitude or latency, R reduced amplitude, D latency is delayed, S amplitude is entirely suppressed, S* amplitude seems to be entirely suppressed based on visual inspection, but the relevant statistical analysis was not reported

However, they differ in the comparisons on which they rely in order to measure this disruption. These can be divided into three types.

One comparison relies on the temporal signature of the AB effect and contrasts T2-locked activity when T2 appears within the blink relative to when it appears outside the blink (i.e., at short vs. long T1–T2 lags). As the averaging of ERP waveforms requires many repetitions, most studies use two lags, with only a few using more lags (e.g., López et al., 2008; Morimoto & Yagi, 2013). We refer to this comparison as the “*lag effect*.” A second comparison builds on the notion that ongoing processing of T1 determines the depth of the AB (e.g., Chun & Potter, 1995; Ouimet & Jolicoeur, 2007; Seiffert & Di Lollo, 1997). It relies on one of two manipulations of the task associated with T1: T2-locked activity is contrasted either (i) between a single-task condition, where participants have to report only T2, and a dual-task condition, where they are required to respond to both T1 and T2, or (ii) between an easy and a difficult T1 task. We jointly refer to these comparisons as the “*T1-task effect*.” Finally, a third comparison focuses on the neural fate of blinked targets, by contrasting T2-locked activity for incorrectly identified versus correctly identified T2s, inside the blink. We refer to this comparison as the “*T2-identification effect*.”

An important advantage of the T2-identification effects over the two other comparisons is that it can shed light on the extent to which a process that is disrupted during the AB nevertheless survives. Given that the AB is not an all-or-none phenomenon, residual activity at short T1–T2 lags, or when the T1 task is difficult, might stem only from trials where T2 simply escaped the blink. By contrast, finding residual activity when T2 is incorrectly identified, provides convincing evidence that the process under study remains operational during the AB.

With all three comparisons, finding that a component’s activity remains intact during the blink indicates that the limitation underlying the difficulty to report the second of two targets is unrelated to the process indexed by this component—barring spurious null effects. By contrast, interpretation issues may arise with regard to positive effects, and these issues differ across the three comparisons.

With the *lag effect*, processing of T2 does not differ between the two lags only in the fact that T2 occurs during versus outside the blink, but also in the temporal attention that T2 receives: because T2 occurs on every trial, the expectation that it will soon appear is higher at the long than at the short lag (Kranjcioch & Bryant, 2011; Nobre et al., 2007). With the *T1-task effect*, manipulating the amount of processing resources devoted to T1 not only affects the depth of the blink, but also overall cognitive load—which is higher for dual than for single T1 tasks and for difficult than for easy T1 tasks. Finally, with the *T2-identification effect*, incorrectly identified T2s may represent a mixture of blinked targets and targets that

participants failed to report accurately for other reasons. This problem arises only when T2 is below ceiling outside the blink, which entails that many T2 errors at the short lag are likely to be unrelated to the AB effect.

Accordingly, any component modulation found using the lag, T1-task, or T2-identification comparisons may reflect effects of temporal expectations, cognitive load or any factor impairing T2 processing, respectively, and may therefore be unrelated to the blink. Several studies used more than one comparison to measure the AB effect within the same experiment,³ thereby circumventing this problem. For instance, overall cognitive load stemming from the T1 task should affect T2 processing regardless of lag; conversely, temporal expectations should affect T2 processing regardless of T1-task difficulty. Therefore, when the lag effect and T1-task effect are concomitantly measured, finding a larger T1-task effect at the short lag than at the long lag invalidates overall cognitive load as an alternative account; conversely, finding a lag effect only in the dual-task condition but not in a single-task condition, invalidates temporal expectations as an alternative account. Likewise, when the T2-identification effect is measured together with either the lag effect or the T1-task effect,⁴ finding that the T2-identification effect emerges only at the short lag but not at the long lag, or in the dual-task but not in the single-task condition, invalidates the alternative account according to which this effect might be attributed to errors unrelated to the blink.⁵

Attention and working memory encoding during the AB

In this section, we review the ERP studies investigating the roles of attentional engagement and WM memory encoding in the AB effect. Based on the ERP literature briefly referred to in the foregoing *ERP components* section, we therefore focus on modulations of the N2pc and P3 components during the blink.

³ Using a manipulation to isolate the component of interest (e.g., a frequency manipulation for the P3 component) may also allow one to reject alternative accounts, while relying on only one comparison.

⁴ Note that this solution can pose a methodological challenge, because there may be too few incorrect responses outside the blink to allow a reliable ERP analysis.

⁵ It is noteworthy that unlike in behavioral analyses, ERP analyses often did not exclude trials on which T1 was incorrectly reported (e.g., Akyürek et al., 2010; Giesbrecht et al., 2007; Jolicoeur et al., 2006; López et al., 2008; Robitaille et al., 2007; Sessa et al., 2007; Sy et al., 2013; Verleger et al., 2008). This procedure should have no consequential incidence on the interpretation of the ERP results when T1 error rates are low. However, when T1 error rates are high, interpretation problems may arise. For instance, the lag effect (e.g., López et al., 2008) and T1 effects (Robitaille et al., 2007) might be underestimated, because failing to process T1 should increase the probability to successfully process T2 during the blink (but not outside the blink).

Effects of the AB on the N2pc component

Lag effect Most studies that examined lag effects on the T2-locked N2pc found that at short lags (inside the blink) relative to longer lags (outside the blink), the amplitude of the T2-locked N2pc was reduced (Jolicoeur, Sessa, Dell'Acqua, & Robitaille, 2006a; Jolicoeur, Sessa, Dell'Acqua, & Robitaille, 2006b; Pomerleau et al., 2014; Verleger et al., 2009; Zivony, Allon, et al., 2018a; but see Losier et al., 2017) and its latency delayed by approximately 20 ms (Lagroix et al., 2015; Zivony, Allon, et al., 2018a; see Fig. 2). Jolicoeur, Sessa, Dell'Acqua, and Robitaille (2006b) reported additional results that tie these effects to the AB. In their study, T1 was a gray digit embedded in a central RSVP stream of gray letters, whereas T2 was a digit drawn in a pre-specified color that randomly appeared in one of two lateral streams. A lag effect on both T2 accuracy and the N2pc was found when participants had to report T1, but not when they had to ignore T1.

A more confusing picture emerges from studies in which the effects of the blink were examined for a distractor instead of a target. In Zivony, Allon, et al. (2018a), one of two RSVP streams sometimes included a square outline that shared the target's defining feature (i.e., its color) and appeared prior to T2 (see Fig. 2A). The N2pc amplitude associated with this distractor was clearly smaller at the short relative to the long lag. In Pomerleau et al. (2014), T2 was a circle in a prespecified color (e.g., red), embedded among gray distractors presented in multiple RSVP streams. A salient distractor in a non-target color (e.g., green) appeared simultaneously with T2. When this distractor was lateral (and the target appeared on the midline), it produced an N2pc of equal magnitude irrespective of whether the T2 appeared at the short or long lag. However, Pomerleau et al.'s (2014) finding may be due to floor effects: unlike in Zivony et al.'s study, the distractor competed with T2 and produced a considerably

smaller N2pc than T2, outside the blink. Thus, there is no strong evidence for the notion that the AB affects the N2pc associated with a distractor versus a target in qualitatively different ways.

T1-task effect Three studies reported effects of the T1-task on the N2pc's amplitude (single vs. dual task: Dell'Acqua et al., 2006; easy vs. difficult task: Akyürek et al., 2010; Robitaille et al., 2007). In two of these (Dell'Acqua et al., 2006; Robitaille et al., 2007), the N2pc was measured only at short lags. Thus, the lower N2pc amplitude observed for the more demanding task could be driven by overall cognitive load. However, Akyurek et al. (Akyürek et al., 2010) reported findings that do not lend themselves to this alternative interpretation. In their study, two identical colored letters (T1) appeared, one in each of two streams of black letters. The T1 task was to match T1 either to a single letter (easy condition) or to one of four possible letters (difficult condition). The T2 task was to identify the colored digit (T2) in one of the streams. The amplitude of the N2pc was smaller when the T1 task was difficult than when it was easy, at both the short and the long lags. However, this effect could not be entirely attributed to differences in overall cognitive load, because it was more pronounced at the short lag, that is, inside the blink.

T2-identification effect Only two studies examined T2-identification effects on the N2pc (Chennu et al., 2008; Dell'Acqua et al., 2006), and both reported that its amplitude was reduced for blinked relative to correctly identified targets. Notably, T2 accuracy outside the blink was below ceiling in these studies, which indicates that many T2-identification errors were unrelated to the blink. However, additional findings reinforce the conclusion that the reported T2-identification effects can be attributed to the AB effect. Chennu et al. (2008) found that T1, which was physically identical to T2,

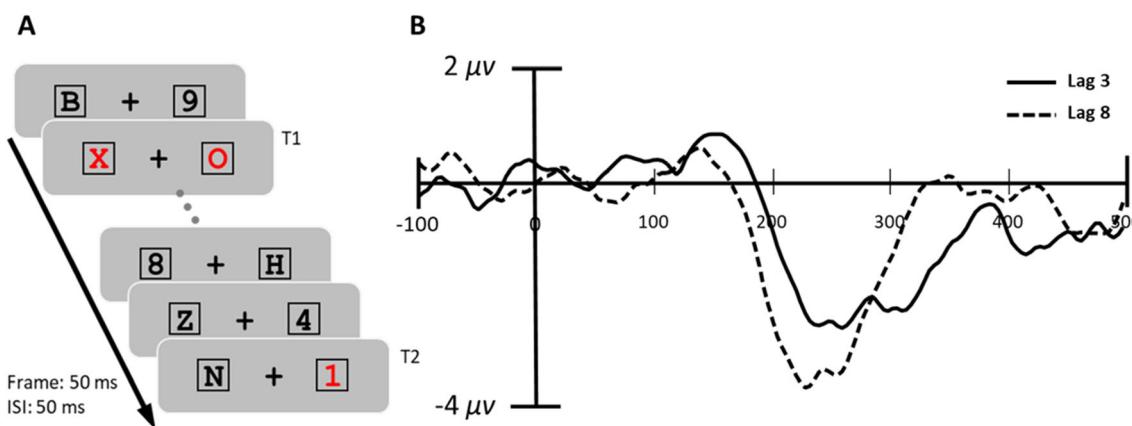


Fig. 2 Paradigm and results from Zivony, Allon, et al. (2018a). (A) Illustration of the stimulus sequence. The T1 task was to indicate whether the two red letters were identical or different. The T2 task was to report whether the red digit was smaller or larger than 5. T1–T2 lag was either 3

or 8. (B) N2pc difference waveforms (contralateral minus ipsilateral at electrodes PO7/PO8). The N2pc inside the AB (lag 3) was delayed and attenuated relative to the N2pc outside the AB (lag 8). Redrawn with permission from Elsevier

produced an N2pc of equal magnitude whether it was correctly or incorrectly identified. In Dell'Acqua et al. (2006), the T2 task was to detect a gap in a colored square outline embedded among gray letters presented in two streams. The T1 task was either to detect two identical gray “=” symbols (easy condition) or to indicate whether two gray digits were the same or different (difficult condition). The authors found the T2-identification effect on the N2pc to be larger when the T1 task was difficult than when it was easy.

Finally, whether the N2pc survives during the blink period appears to depend on task difficulty. For incorrectly identified T2s, Dell'Acqua et al. (2006) found an intact N2pc when the T1 task was easy and no residual N2pc when it was difficult, while Chennu et al. (2008) reported a residual N2pc with a letter-identification T1 task that may be considered to be of intermediate difficulty.

Effects of the AB on the P3 component

Lag effect Many studies showed a clear lag effect on the P3 amplitude (Bourassa et al., 2015; Damsma et al., 2018;

Dell'Acqua et al., 2003; Sessa et al., 2007; Vogel et al., 1998). Two of these (Sessa et al., 2007; Vogel et al., 1998) examined the lag effect in combination with a T1-task manipulation (single vs. dual task), and found the P3 amplitude to be reduced at short relative to long lags only in the dual-task condition. Notably, some studies manipulated T2 masking and yielded findings that set important constraints on the interpretation of these lag effects. For example, in Vogel and Luck (2002; see Fig. 3A) the T2 task was to identify a white letter (E on 25% of the trials, and another randomly selected letter on 75% of the trials). The authors examined lag effects on the T2-locked frequency-related P3 (resulting from the subtraction of the frequent “non-E” waveform from the infrequent “E” waveform). T2 was either the last item in the RSVP (i.e., it was unmasked) or the item before last (i.e., it was masked). The P3 amplitude was entirely suppressed at short lags when T2 was masked. When T2 was unmasked, the P3 amplitude was intact at the short relative to the long lag, but its onset latency was delayed (see Fig. 3B). This pattern of results was replicated in several studies (Arnell, 2006; Brisson, 2015; Brisson & Bourassa, 2014; Dell'Acqua et al., 2015; Morimoto

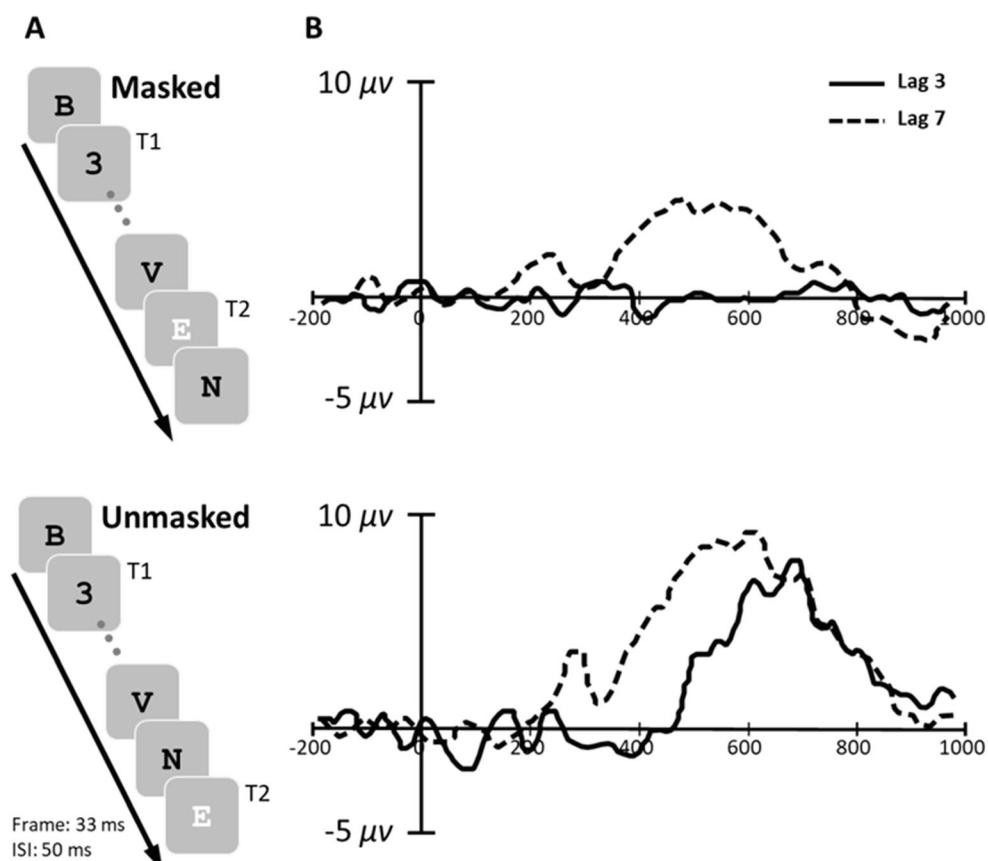


Fig. 3 Paradigm and results from Vogel and Luck (2002). (A) Illustration of the stimulus sequence. The T1 task was to identify the digit and the T2 task was to identify the white letter. T2 was either the item before last (masked condition, upper row) or the last item in the stream (unmasked condition, bottom row). (B) Frequency-related P3 difference waveforms

(infrequent minus frequent at electrode Pz). When T2 was masked (upper row), P3 inside the AB (lag 3) was suppressed relative to P3 outside the AB (lag 8). When T2 was unmasked (lower row), P3 inside the AB (lag 3) was delayed relative to P3 outside the AB (lag 8). Redrawn with permission

& Yagi, 2013; Ptito et al., 2008; Sessa et al., 2007), with P3 delayed by an average of 70 ms at the short relative to the long lag (but this latency difference varied considerably across studies). Among these, however, four studies (Arnell, 2006; Dell'Acqua et al., 2015; Losier et al., 2017; Ptito et al., 2008) reported that the P3 amplitude for an unmasked T2 was still slightly but significantly reduced at the short lag relative to the long lag.

T1-task effect Two studies reported T1-task effects on the P3 amplitude at short lags (Akyürek et al., 2010; Robitaille et al., 2007), but did not report whether the T1 effects were modulated by lag. Since the P3 amplitude is known to be smaller for dual tasks than for single tasks across T1–T2 lags (Dell'Acqua et al., 2015; Sessa et al., 2007; Vogel et al., 1998; Vogel & Luck, 2002), these findings might simply reflect an effect of cognitive load.

T2-identification effect Most studies found reduced P3 amplitude for blinked relative to correctly identified target at the short lag (Bourassa et al., 2015; Craston et al., 2009; Damsma et al., 2018; Kranczioch et al., 2003; Kranczioch et al., 2007; López et al., 2008; Martens et al., 2006; Pesciarelli et al., 2007; Rolke et al., 2001; Sergent et al., 2005). The only exception is Batterink et al. (2012), but their failure to observe this effect is likely to result from a floor effect: in that study, no P3 activity was observed at the short lag when T2 was correctly identified.

While most of the studies found that P3 does not survive during the AB (Bourassa et al., 2015; Craston et al. 2009; Damsma et al., 2018; Dell'Acqua et al., 2003; Kranczioch et al., 2003; López et al., 2008; Pesciarelli et al., 2007; Pincham & Szűcs 2012, Pincham & Szűcs, 2014; Nakatani et al., 2012; Robitaille et al., 2007; Sergent et al., 2005; Vogel et al., 1998; Vogel & Luck, 2002), three studies reported residual P3 activity when T2 was incorrectly identified (Kranczioch et al., 2007; Lasaponara et al., 2015; Rolke et al., 2001). Note, however, that these studies did not use the subtraction method and instead measured the P3 from the raw waveform. The residual P3 in these studies may therefore reflect overlapping processes unrelated to T2 processing.

Summary of N2pc and P3 studies

As is clear from the foregoing sections, both the N2pc and the P3 components are disrupted during the blink period. The results show that the N2pc amplitude is reduced and its latency delayed during the AB, and that the N2pc survives to a variable extent during the AB, depending on how difficult the T1 task is. These findings suggest that attentional engagement is disrupted, but not necessarily prevented,⁶ during the blink period. Because N2pc studies rely on tasks involving lateralized displays, one may claim (i) that this conclusion

cannot be generalized to instances where the target appears at fixation (e.g., with single-stream displays) and (ii) that not attentional engagement per se, but the shift of spatial attention to the target's location that precedes it (Dell'Acqua et al., 2006a) may be compromised during the blink. However, several findings invalidate these potential criticisms. First, single-stream behavioral studies (Nieuwenstein, 2006; Nieuwenstein et al., 2005; Zivony & Lamy, 2016, Experiment 1) and N2pc studies where the target appeared only 1° from fixation (Akyürek et al., 2010; Verleger et al., 2009) also reported findings supporting the disrupted-engagement account. Furthermore, many behavioral studies reported that attentional shifting is intact during the blink period (Bae et al., 2018; Ghorashi et al., 2010; Ghorashi, Enns, et al., 2009a; Ghorashi, Spalek, et al., 2009b; Zivony, Allon, et al., 2018a; Zivony & Lamy, 2014, 2016), while ERP studies reported modulations of the N2pc during the blink when no attentional shift time-locked to T2 was required, namely, when T1 and T2 were on the same side (Verleger et al., 2009), as well as when their locations were known in advance (Chennu et al., 2008).

The foregoing review also shows that in most studies, the P3 component is entirely suppressed during the blink when T2 is masked, but is only delayed when T2 is unmasked – in line with behavioral studies showing that when T2 is unmasked, the AB effect manifests in longer reaction times rather than in reduced T2 accuracy (Giesbrecht & Di Lollo, 1998; Zuvic et al., 2000). These findings suggest that consolidation of information in WM is delayed rather than altogether prevented, and the finding that P3 is entirely suppressed when T2 is masked merely indicates that T2 is not encoded on these trials (and therefore does not produce a P3).

Perceptual processing during the AB

In this section, we review the ERP studies investigating whether perceptual processing is impaired during the blink. We therefore focus on the P1 component, which is associated with low-level perceptual processing, and on the N400, which is taken as evidence that semantic processing occurred.

Effects of the AB on the P1 component

Relatively few AB studies examined the P1 component. These studies showed no lag effect (Vogel et al., 1998; Weller et al., 2019), no T1-task effect from contrasting a single versus a

⁶ This conclusion relies on the relatively few studies that examined T2-identification on the N2pc. However, additional findings from the posterior N2 and P3a components also support this conclusion. Similar to the N2pc, the P3a and posterior N2 are associated with attentional enhancement (Suwazono et al., 2000; Polich, 2007). Studies that examined T2-identification effects on these components consistently found reduced posterior N2 activity and P3a activity for blinked targets that was not entirely suppressed (see Table 1).

dual task (Vogel et al., 1998), and no T2-identification effect (Koivisto & Revonsuo, 2008; Kranczioch et al., 2007; Lasaponara et al., 2015; Sergent et al., 2005).

Effects of the AB on the N400 component

Lag effect The hallmark paradigm used to examine the effect of T1 processing on the N400 was developed by Vogel et al. (Vogel et al., 1998, Fig. 4A). In that study, a prime word that established an explicit semantic context was presented prior to the RSVP stream, and the T2 task was to indicate whether or not T2 was semantically related to this prime. The results showed a clear congruency-related N400 (resulting from the subtraction of the congruent waveform from the incongruent waveform) that was not modulated by lag (see Fig. 3B). This null effect of lag was replicated using unmasked T2s (Vachon & Jolicœur, 2011; lag 2 vs. lag 7). However, later studies that used Vogel et al.'s task with minor (Loomis, 2006) or more notable changes (Batterink et al., 2010, see Fig. 4C; Giesbrecht et al., 2007; see also: Sy et al., 2013, Weller et al., 2019) reported large lag effects on the N400.

T1-task effect Two studies also relied on a variant of Vogel et al.'s (1998) paradigm to examine T1-task effects on the N400 (Giesbrecht et al., 2007; Sy et al., 2013). They used the same stimuli but yielded conflicting findings. Giesbrecht et al. (2007) reported a significant N400 when the T1-task was easy, but not when it was difficult, and this T1-task effect was

modulated by T1-T2 lag. By contrast, Sy et al. (2013) found no effect of T1-task difficulty on the N400 during the blink. However, because these authors also failed to show the expected T1-task effect on T2 accuracy, it is difficult to draw strong conclusions from their findings about the relationship between T1-task difficulty and the N400.

T2-identification effect All the studies that examined T2-identification effects on the N400 reported a modulation of this component's amplitude. Batterink et al. (2010) used a paradigm similar to Vogel et al.'s (1998) and reported that the N400 emerged when T2 was correctly reported but was entirely suppressed when T2 was missed. Other studies (Peressotti et al., 2012; Pesciarelli et al., 2007; Rolke et al., 2001) used a different, three-target paradigm developed by Shapiro et al. (1997). In this paradigm, the targets are white words embedded within a stream of black distractor words. The lags between these targets are fixed, such that T2 always appears at a short lag from T1, and the third target (T3) is presented at a long lag after T2. Importantly, T2 is either semantically related or unrelated to T3. Unlike in Vogel et al.'s (1998) paradigm, participants are simply asked to identify the target, and are therefore not required to explicitly notice the semantic relationship between the targets. Instead, semantic processing of T2 is expected to establish a semantic context and to benefit T3 processing when T3 is semantically congruent with T2. These studies all showed T2-identification effects on the T3-locked N400 (though the effect was only

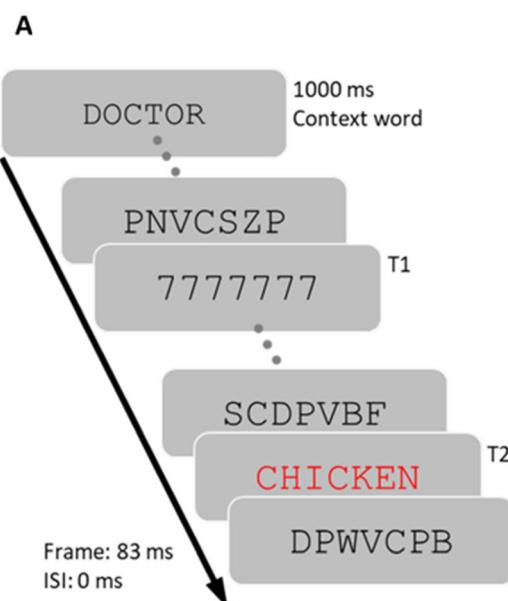
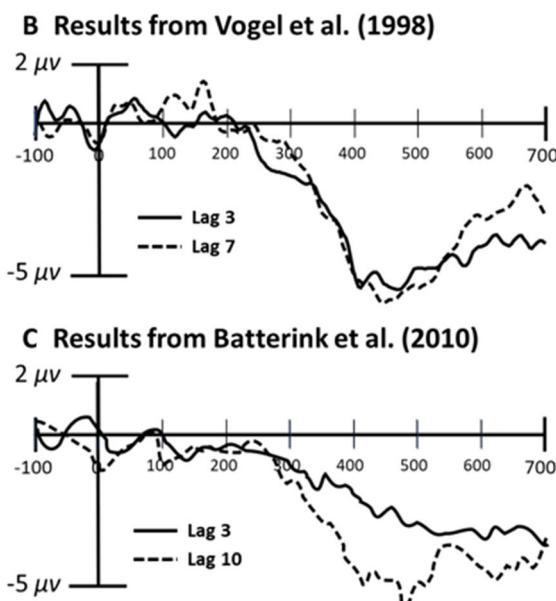


Fig. 4 Paradigm and results from Vogel et al. (1998, Experiment 2) and results from Batterink et al. (2010). (A) Illustration of the stimulus sequence. The T1 task was to indicate whether the digit was odd or even. The T2 task was to indicate whether the red word was related or unrelated to the context word. (B and C) Congruency-related N400 difference waveforms (incongruent minus congruent at electrode Cz). In Vogel



et al. (1998), N400 amplitude was similar inside (lag 3) and outside (lag 7) the AB. In Batterink et al. (2010), using a similar paradigm, N400 amplitude was smaller inside (lag 3) than outside (lag 10) the AB. Redrawn with permission from American Psychological Association and MIT press

marginally significant in Rolke et al., 2001). Moreover, following an incorrectly identified T2, the T3-locked N400 was either entirely suppressed (Peressotti et al., 2012; Pesciarelli et al., 2007) or present but nevertheless smaller relative to trials where T2 was correctly identified (Rolke et al., 2001).

Summary of P1/N1 and P400 studies

The reviewed studies clearly show that the blink does not modulate the P1 component and is therefore unlikely to affect low-level perceptual processes (see also Berti, 2011, for converging evidence showing no lag effect on the visual mismatch negativity component, thought to reflect automatic change detection at the sensory level). By contrast, most studies show that the N400 amplitude is reduced during the AB, suggesting that semantic processing is often disrupted during the AB.

Before this conclusion can be fully embraced, however, three remarks are in order. First, interpreting the finding that the T2-related N400 component is weaker during the blink is not straightforward. Since the N400 emerges from the comparison between the semantic input and an established semantic context, this finding may indicate that the comparison process, rather than semantic processing of T2, is disrupted. This possibility arises for studies that used a paradigm similar to Vogel et al.'s (1998) and found a lag effect on the T2-locked N400 (Batterink et al., 2010; Giesbrecht et al., 2007; Loomis, 2006). In this task, the semantic context is provided outside the blink and the T2 task requires both extracting semantic information from T2 and comparing it to the context. However, this alternative account does not apply to the three-target paradigm (Peressotti et al., 2012; Pesciarelli et al., 2007; Rolke et al., 2001; Shapiro et al., 1997). In this paradigm, T2 establishes the semantic context, and the N400 emerges from the comparison between T2 and T3. As T3 always appears outside the blink period, any AB-induced reduction of the N400 cannot be attributed to disruption of the post-perceptual processes involved in semantic comparison. Instead, such a reduction can be directly attributed to impaired semantic processing of T2.

Second, one may also argue that T2 initially undergoes full semantic analysis, but its representation rapidly decays unless it is attended and subsequently encoded in WM. While this account is possible, it entails that the post-perceptual account cannot be falsified by measuring the consequences of semantic processing (e.g., by measuring the N400 or semantic priming). Moreover, it substantially departs from the notion that T2's semantic representation can feed downstream processes irrespective of whether or not it is encoded in WM (Chun & Potter, 1995; Shapiro et al., 1997; Vogel et al., 1998).

Finally, three studies (Vachon & Jolicoeur, 2011; Vogel et al., 1998; and the easy T1 task condition in Giesbrecht et al., 2007) reported an intact N400 during the blink. These

exceptions raise the possibility that semantic processing may be impaired during the blink only in certain conditions. In particular, semantic processing may remain unaffected during the blink when the task is easy enough. The findings of Giesbrecht et al. (2007) provide direct evidence supporting this hypothesis, and a comparison between Vogel et al.'s (1998) and Batterink et al.'s (2010) studies is also consistent with this conjecture: in the former, participants reported the identity of a digit presented as a string (e.g., "7777777") and the N400 was intact, whereas in the latter, participants performed the more difficult task of naming a word flanked by # signs (e.g., "#SEVEN#") and the N400 was reduced. However, Loomis (2006) used the same (easy) task as Vogel et al. (1998) and, yet, found an AB effect on the N400. Further research is therefore needed to establish the role of T1-task difficulty on semantic processing of T2 during the blink.

General discussion

A fairly clear and consistent picture emerges from the foregoing review. The findings converge to show that early perceptual processing (indexed by P1) is unaffected during the blink period, whereas attentional engagement (indexed by N2pc), WM encoding (indexed by P3), and semantic processing (indexed by N400) are disrupted to various degrees. Next, we evaluate how different theories of the AB can accommodate these findings.

Re-evaluation of current attentional blink models

Disrupted-control theories While disrupted-control theories (Di Lollo et al., 2005; Taatgen et al., 2009) can account for the findings that the N2pc, P3, and N400 are disrupted during the blink, they do not explain why the N2pc can survive to varying degrees. According to these theories, attentional control is lost during the blink and, therefore, T2 cannot be categorized as a target and attentional engagement should be entirely prevented (see Nieuwenstein, 2006; Zivony & Lamy, 2016; Zivony, Allon, et al., 2018a, for additional evidence against the disrupted-control account).

Bottleneck theories Bottleneck models (Chun & Potter, 1995; Jolicoeur & Dell'Acqua, 1998) posit that WM encoding is disrupted during the blink and therefore naturally account for the finding that the P3 component is compromised. However, these theories also predict that attentional engagement and semantic processing should be spared by the blink. Therefore, they do not explain findings showing that both the N2pc and N400 are often disrupted. In addition, ERP studies that examined distractor intrusions argue against the idea that encoding into WM is prevented during the blink. Distractor intrusions refer to the finding that when a target is embedded

among distractors that share the target's response dimension (e.g., a target letter embedded among letter distractors; see Fig. 5A), participants often erroneously report a distractor instead of the target (e.g., Botella et al., 2001; Zivony & Eimer, 2021). Bourassa et al. (2015) reported that the distractor immediately following T2 produced a P3 on trials where T2 was blinked and that this distractor-locked P3 was equal in size to the T2-locked P3 when T2 was correctly reported (see Fig. 5B). These results are therefore incompatible with the idea that WM-encoding mechanisms are unavailable during the blink.

Disrupted-engagement theories Disrupted-engagement theories (Bowman & Wyble, 2007; Nieuwenstein et al., 2005; Olivers & Meeter, 2008; see also Nieuwenstein, 2006; Zivony & Lamy, 2016) predict that, as attentional engagement merely becomes sluggish during the blink period, the T2-locked N2pc should be reduced and delayed. Moreover, they predict that downstream processes that depend on attentional amplification should also be impaired, and in particular, WM encoding, as indexed by the P3 component.

Thus, the reviewed findings provide more support for disrupted-engagement theories than for competing accounts. However, in their present form, these theories do not provide an adequate explanation for three findings. First, they cannot explain the findings from studies showing intact N2pc during the blink (Dell'Acqua et al., 2006; Losier et al., 2017). Second, the reviewed findings suggest that WM encoding is substantially more impaired during the blink period than attentional engagement: while the AB delays the N2pc by approximately 20 ms (Lagroix et al., 2015; Zivony, Allon, et al., 2018a), it delays the P3 (e.g., Sessa et al., 2007; Vogel & Luck, 2002) as well as reaction times (Zivony et al., 2018; Zivic et al., 2000)

by much longer durations. Finally, these models have generally embraced the late-selection view, according to which semantic processing is independent of attention. Therefore, they predict that semantic processing should be intact during the blink, a conclusion that is invalidated by many of the N400 studies reviewed here.

To summarize, none of the current models of the attentional blink can fully accommodate the findings that emerged from the present review. In the next section, we first explain what core tenets of disrupted-engagement theories must be modified to account for the finding that semantic processing is impaired during the blink. We then suggest that a dual-disruption account of the AB may best account for the extant data.

Disrupted engagement and semantic processing during the blink

The findings from N400 studies reviewed here show that semantic processing is most often disrupted during the blink period (Batterink et al., 2010; Giesbrecht et al., 2007; Peressotti et al., 2012; Pesciarelli et al., 2007; Rolke et al., 2001; Weller et al., 2019). Considering that many behavioral studies demonstrated that semantic priming is also reduced (e.g., Martens et al., 2002; Murphy & Bloom, 2015; Zivony & Lamy, 2016), it is surprising that the post-perceptual account of the AB was so widely embraced. This state of affairs is likely to result from the implicit assumption that at any given moment, semantic information is either fully represented or not at all, and, accordingly, that it should be either unaffected or entirely suppressed by the blink. The intermediate possibility – that semantic processing may be weakened during the blink – was typically not considered (but see Zivony,

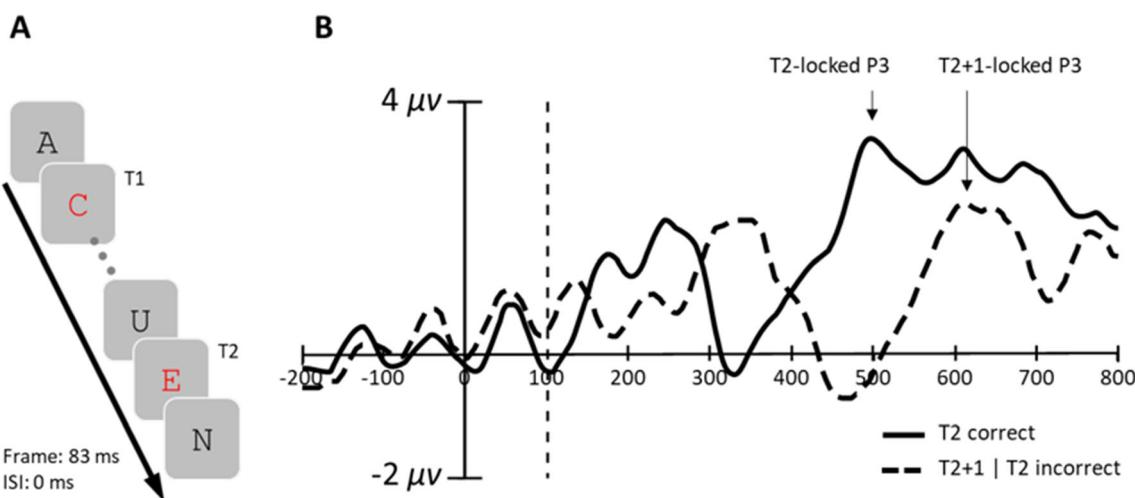


Fig. 5 Paradigm and results from Bourassa et al. (2015). (A) Illustration of the stimulus sequence. The T1 and T2 tasks were to identify the red digits. (B) T2-locked frequency-related P3 difference waveforms (infrequent minus frequent at electrode Pz) on correct T2 trials and T2+1-

locked frequency-related P3 on incorrect T2 trials. The broken vertical line represents the onset of T2+1. Redrawn with permission from John Wiley and Sons

Shanny, & Lamy, 2018b). Indeed, the first studies that supported the post-perceptual account (Maki et al., 1997; Shapiro et al., 1997) focused on whether semantic processing is at all possible during the blink. Consequently, they overlooked evidence showing that relative to unblinking targets, semantic priming from blinked targets was substantially reduced (e.g., Shapiro et al., 1997, Fig. 3) – a result that nicely dovetails the N400 findings of the present review.

The idea that semantic processing does not require attention is not a core tenet of disrupted-engagement theories (Bowman & Wyble, 2007; Nieuwenstein et al., 2005; Olivers & Meeter, 2008). We therefore suggest that these can be modified to accommodate the finding that semantic processing is impaired during the blink. To do that, we mainly rely on the computational episodic simultaneous type serial token (eSTST) model (Bowman & Wyble, 2007; Wyble et al., 2009, 2011), on Reeves and Sperling's (1986) attentional gating model, as well as on models that emphasize the distinction between feedforward and recurrent brain processing (e.g., Lamme & Roelfsema, 2000; Sligte et al., 2008; Zivony & Eimer, 2021; Zylberberg et al., 2009).

Accordingly, we consider perceptual processing as a process of evidence accumulation, during which activation of sensory representations is continuously strengthened (Reeves & Sperling, 1986). Activation strength determines how durable and sensitive to masking a perceptual representation is, and how likely it is to affect downstream processes. Perceptual processing of each stimulus in the RSVP stream starts when information reaches the visual cortex, approximately 50–70 ms after stimulus onset (as reflected by P1). Low-level features (e.g., color) are activated faster than high-level features (e.g., semantic identity; see Zivony, Shanny, & Lamy, 2018b). Nevertheless, feedforward processing may result in the extraction of semantic information but, as such information is fragile and vulnerable to perceptual competition, it may not be sufficiently activated to be encoded in WM (Sligte et al., 2008).

Target processing benefits from attention in two ways. First, a top-down set for specific target features selectively enhances perceptual processing at an early stage (e.g., Schoenfeld et al., 2007; Zhang & Luck, 2008). Second, approximately 150 ms after target onset, attentional engagement is deployed (as reflected by the N2pc) when the evidence for the target's defining feature presence reaches a certain threshold (Zivony & Eimer, 2021). Attentional engagement recruits recurrent processing (Lamme & Roelfsema, 2000; Zylberberg et al., 2009) and exponentially strengthens the representations at the attended location. Finally, the most highly activated item or items are encoded in WM, and consolidation of these items into WM takes several hundred milliseconds (as indicated by P3).

This modification of the disrupted engagement account provides a straightforward explanation for many of the reviewed findings. At a presentation rate of approximately

100 ms per item, recurrent processing in the visual cortex following T2's detection coincides with the feedforward processing of the post-T2 item. The processing of two signals in the same brain areas results in an intense competition for perceptual representation between the two items, the result of which determines which item will gain access to WM. Therefore, as shown in previous studies (Zivony & Eimer, 2020, 2021), even a 20-ms delay in attentional engagement can upset the balance between the two items and enhance the post-T2 item more than T2. As a consequence of such delays, the target is not sufficiently activated to be encoded in WM (see Fig. 6). This explains why when T2 is missed during the blink, some N2pc activity survives (Chennu et al., 2008; see also footnote 5), whereas P3 activity is entirely suppressed (Bourassa et al., 2015; Kranczioch et al., 2003; Vogel et al., 1998; Vogel & Luck, 2002; but see Lasaponara et al., 2015; see also Sergent et al., 2005, for a similar difference between the N2 and P3 components), and the trailing distractor is encoded instead (Bourassa et al., 2015). Finally, although the semantic representation of the target can be extracted even if it does not benefit from attentional engagement, this representation is weaker, which explains why the N400 is attenuated but not eliminated during the blink.

A dual-disruption account of the AB

The modified disrupted engagement account we just described illustrates how disruption to a single process can parsimoniously account for many of the AB findings reviewed above, including impaired semantic processing and increased distractor intrusions during the blink period. However, even though impaired attentional engagement explains much of the AB effect (Nieuwenstein, 2006; Zivony & Lamy, 2016), it does not tell the whole story. Specifically, it does not explain why the time-locked performance impairment that characterizes the blink is sometimes observed together with intact N2pc (Dell'Acqua et al., 2006; Losier et al., 2017), intact N400 (Giesbrecht et al., 2007; Vachon & Jolicoeur, 2011; Vogel et al., 1998), and intact semantic priming (Harris et al., 2010; Harris & Little, 2010): as these effects are sensitive to attentional engagement, they should at least be reduced during the blink.

These findings suggest that the AB might reflect the disruption of two processes – a possibility that was raised by several authors (e.g., Kranczioch et al., 2007; Wong, 2002), but never took hold among the major theories of the AB. The observation that arises from the present review and is most consistent with this idea is that the experiments that generated the aforementioned null effects on the N2pc, N400 and semantic priming, all used a relatively easy T1 task and reported a modest AB effect on performance accuracy. These findings suggest that the AB may reflect (i) an early disruption to attentional engagement (with impaired encoding into WM

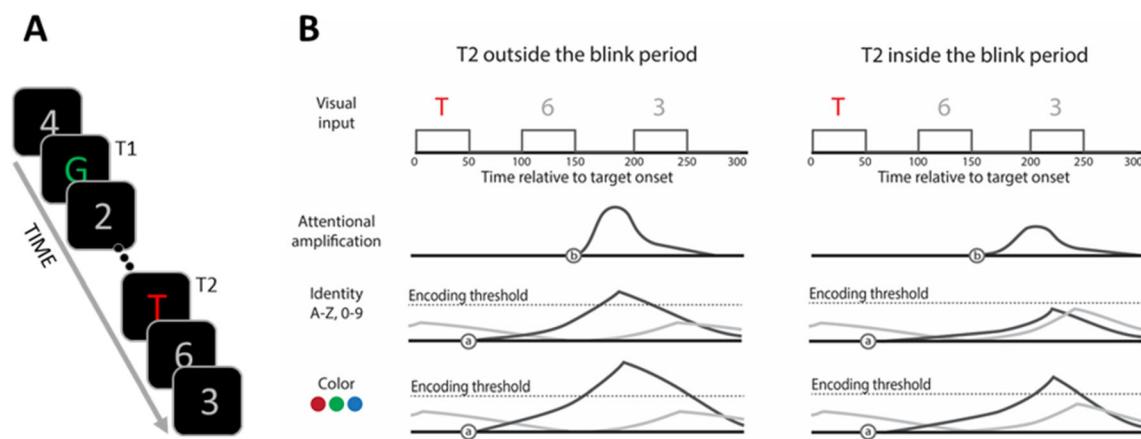


Fig. 6 Schematic outline of how disrupted engagement affects perceptual processing. (A) An example of a rapid serial visual presentation (RSVP) task where the targets are colored letters embedded among gray digits. (B) The two panels follow the time course of attentional amplification and sensory representations after T2 onset, on trials where T2 is outside the blink period (left) and inside the blink period (right). Sensory representations of the different feature dimensions, alphanumeric identity and color, are represented separately. Feedforward visual processing of the target starts shortly after the target's onset (a). Activation levels initially increase

and then decrease due to backward masking. At a specific time point (b) attentional engagement is triggered, but its build up is either fast (left panel) or attenuated and delayed (right panel). Stimuli are encoded if they cross an encoding threshold. Task-relevant colors are more strongly activated than task-relevant identities in the absence of attentional engagement. Therefore, delayed engagement is more likely to result in incorrectly reporting T2's identity than in incorrectly reporting its color (Zivony, Shanny, & Lamy, 2018b)

occurring downstream), as suggested by disrupted engagement theories, that occurs only when the T1 task is difficult enough, and (ii) a later disruption that emerges even with easy T1 tasks and delays WM encoding. This “dual-disruption” account predicts that with easy T1 tasks, the AB should affect only processes related to WM encoding, and should thus leave semantic priming, the N2pc, and N400 intact.⁷ Under such conditions, T2’s representation is initially strongly activated, but degrades over time. Therefore, even when engagement is intact, delays to WM encoding can result in reduced T2 accuracy and substantially slower reaction times.

Indirect evidence in favor of this dual-task account comes from studies of the psychological refractory period (PRP). The PRP refers to the finding that, when people respond to two successive simple tasks, reaction times for the second task linearly decrease with the temporal lag between the two targets. Importantly for our purposes, Lien et al. (2011) examined the effect of task difficulty of the first task on the PRP and on the N2pc. While PRP emerged in both the easy and the difficult tasks, the N2pc was intact when the task was easy, but was reduced when the task was difficult. Since the

mechanisms underlying the PRP and AB overlap at least partly (Marti et al., 2012), this finding is consistent with the possibility that a small reduction in T2 accuracy may emerge even when attentional engagement is intact.

Conclusion

By making sense of apparent inconsistencies in the ERP literature on the AB over the last two decades, the present review paints a clear picture of the processes that are impaired during the blink, and thereby takes a step towards resolving some of the oldest theoretical questions about this phenomenon. It shows that processing a target impairs the deployment of attentional engagement that follows the detection of a subsequent target during the blink period, which in turn affects perceptual (semantic) processing of T2 as well as the probability that it is encoded in WM. However, impaired attentional engagement alone cannot adequately explain the finding that perceptual processing is intact when the T1 task is easy (e.g., Dell’Acqua et al., 2006; Giesbrecht et al., 2007) nor why attentional engagement is delayed to a much lesser extent than WM encoding (e.g., Zivony, Allon, et al., 2018a vs. Vogel & Luck, 2002, respectively). Our review suggests that delays to WM encoding also contribute to the performance cost incurred when we process multiple sequentially presented events – independently of attentional engagement. If confirmed by future research, this conclusion should encourage the field to let go of the entrenched assumption that our ability to process multiple sequentially presented events is constrained by a single mechanism and pave the way for

⁷ Note, however, that disrupted N2pc, semantic priming, and N400 were sometimes reported with relatively easy tasks (e.g., Loomis, 2006). One may speculate that individual differences account for these findings. The argument goes as follows: because no given task is equally demanding for all participants, a small subset of participants may find so-called “easy” T1 tasks to be difficult. As a consequence, whether or not AB effects on processes that depend on attentional engagement emerge in a given study, depends on whether the sample includes such participants. This should always be the case with large enough samples, but the samples used in ERP studies of the AB were typically small, which explains why null effects were sometimes reported (e.g., Vogel et al., 1998).

more complete accounts of this fundamental limitation of our cognitive system.

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