Psychonomic Bulletin & Review
2009, 16 (6), 1106-1111
doi:10.3758/PBR.16.6.1106

Target–distractor interference in the attentional blink implicates the locus coeruleus–norepinephrine system

Christopher M. Warren, Andreas T. Breuer, and Justin Kantner
University of Victoria, Victoria, British Columbia, Canada

Daniel Fiset and Caroline Blais
University of Montreal, Montreal, Quebec, Canada

and

Michael E. J. Masson
University of Victoria, Victoria, British Columbia, Canada

We provide evidence that the locus coeruleus–norephinephrine (LC–NE) system is the neurophysiological basis of the attentional blink. The attentional blink refers to decreased accuracy for reporting the second of two targets in a rapid serial visual presentation of distractors. The LC–NE account of the attentional blink posits that targets elicit a facilitative LC–NE system response that is available for the first target but subsequently unavailable to the second, due to the autoinhibitory nature of the LC–NE system. We propose a modification of the LC–NE account, suggesting that the LC–NE system response is elicited by interference between mutually exclusive responses demanded by temporally proximal targets and distractors. We increased the interference between the first target and the following distractor by reducing the time between them. For identifying the second target this high-interference condition yielded a benefit up to 200 msec after onset of the first, followed by a decrease in accuracy. Consistent with our modification of the LC–NE account, this result suggests a temporarily enhanced LC–NE system response to increased target–distractor interference.

When two targets are inserted into a rapid serial visual presentation (RSVP) of distractors, there is decreased accuracy for identification of the second target (T2) if it occurs approximately 100–600 msec after the first target (T1). This phenomenon is referred to as the *attentional blink* (AB; Raymond, Shapiro, & Arnell, 1992). The AB is considered an important phenomenon because of its relation to the process of consolidating an iconic memory into working memory, inferred from evidence that perceptual and semantic information is extracted from T2 during the AB even when T2 cannot be identified (e.g., Vogel, Luck, & Shapiro, 1998). This finding suggests that the AB deficit is particular to an attentional process that facilitates successful encoding of a stimulus into working memory for later report.

Figure 1 illustrates our variation of the AB task. The temporal profile of the AB is described using accuracy scores for the identification of T2 at varying *lags*. When T2 follows T1 consecutively, it is said to follow at lag 1. If a single distractor occurs between T1 and T2, T2 follows at lag 2, and so on. Identification of T2 is typically preserved at lag 1 and then most impaired at lags 2 and 3, with performance gradually recovering from lags 4–6, when the deficit typically ends. The unimpaired accuracy at lag 1 is termed *lag 1 sparing*. Most AB research uses a presentation rate of about 10 items/sec, so lag 1 typically corresponds to a stimulus onset asynchrony (SOA) of 100 msec after the onset of T1, and successive lags occur at 100-msec intervals.

Nieuwenhuis, Gilzenrat, Holmes, and Cohen (2005) described how the AB phenomenon maps onto the behavior of a neuromodulatory system theorized to play a role in attention. The locus coeruleus–norepinephrine (LC–NE) account of the AB is based on evidence that the LC responds to the occurrence of a motivationally salient event by releasing NE into the forebrain. Computational analyses of the effects of NE in the forebrain suggest that the presence of NE will increase the responsivity of target neurons, enhancing signal detection and stabilizing a neural representation in the face of noise or interference (Cohen, Aston-Jones, & Gilzenrat, 2004). Critical to accounts of the AB, the LC is autoinhibitory, so that a large release of NE will be followed by a short period of reduced NE release. This event sequence means that a short period of benefit will be followed by a period of deficit. Under the LC–NE account of the AB, NE is released by

C. M. Warren, cwarren@uvic.ca

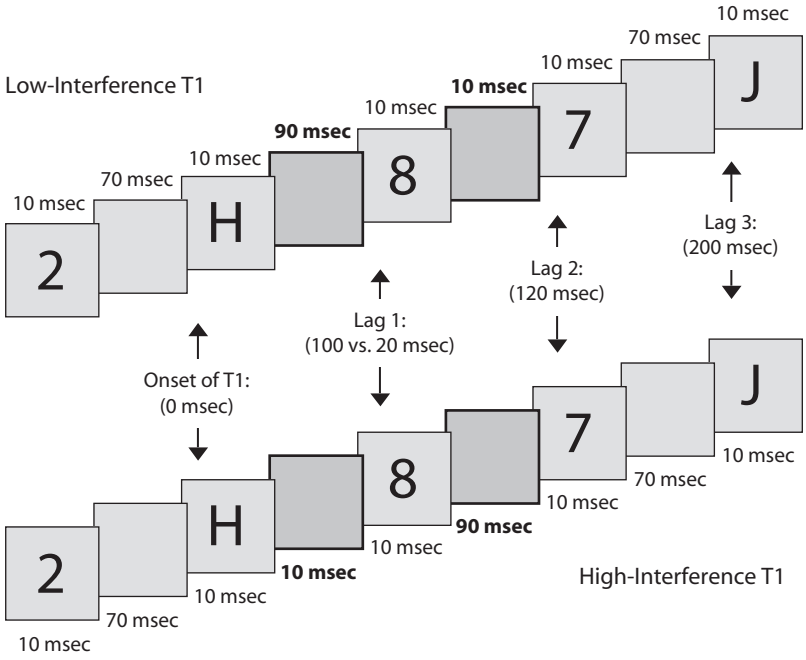

Figure 1. Graphic representation of the critical portion of one trial from each of the two conditions in the attentional blink task. Actual events involved 20 stimuli, 20 interstimulus intervals (ISIs), and a beginning fixation cross. The stimuli were displayed for 10 msec each. Blank ISI screens were displayed for 70 msec each, except for the two highlighted ISI screens, which were displayed for either 10 or 90 msec. Each condition was also complemented by a control condition in which the timing of distractors was the same but the first target (T1) was replaced with a distractor.

the LC upon target detection, facilitating target processing. Sparing observed at short SOAs following T1 (typically represented by lag 1 sparing at 100 msec) represents the continuing presence of NE before it dissipates, and the AB deficit corresponds to the period after T1 when the initial recruitment of NE has dissipated and further release is inhibited. The LC–NE theory of the AB makes physically explicit the idea of an attentional resource that is available for T1, but less so for T2. Most theories of the AB prior to and since the LC–NE theory posit some sort of limited capacity resource, and most are loosely compatible with the idea that NE might be the physical manifestation of that resource (e.g., Nieuwenstein, 2006; Raymond et al., 1992).

A more recent computational model of the AB argues against the idea of a limited capacity resource and, instead, emphasizes the critical role of the distractor following T1 in producing an AB. The boost and bounce theory (Olivers & Meeter, 2008) posits bottom-up excitatory and inhibitory feedback mappings that develop according to task parameters, so that targets activate excitatory feedback and distractors activate inhibitory feedback. In addition, the theory includes a top-down, transient attentional enhancement that is triggered when a target is detected, enhancing whatever recurrent feedback mapping is active. Olivers and Meeter noted that the attentional enhancement that they described could potentially be the manifestation of LC–NE system activity. However, rather than the AB being caused by the temporary unavailability of this enhancement, it is caused by the *enhancement's being applied to the inhibitory feedback activated by the distractor following T1*. The theory holds that the enhancement recruited in response to T1 is (inappropriately) maximal during exposure to the item following T1. When that item is a distractor, it enhances the inhibitory feedback to sensory processing, reducing the chance that subsequent targets will be detected for a short time.

Support for the boost and bounce theory has come from experiments in which the distractor following T1 has been replaced with another target. When three targets (T1, T2, and T3) are inserted consecutively into an RSVP, the third target demonstrates significantly greater accuracy, as compared with a condition in which T2 is replaced by a distractor (e.g., Kawahara, Kumada, & Di Lollo, 2006). The boost and bounce theory accounts for these results parsimoniously: There is no AB for T3 because there is no intervening distractor between T1 and T3 to elicit the inhibitory response. The boost and bounce theory is further supported with evidence that the salience of the distractor following T1 impacts the AB. Olivers and Meeter (2008) conducted an AB experiment with red letters as targets amid black numbers. The critical manipulation was the color of the distractors following T1: The two distractors following T1 could be either red or black. When the distractors were red, they were less salient (following red targets) and were predicted to produce less inhibition, reducing or delaying the AB. As was predicted, when both the lag 1 and lag 2 distractors were red, the lag 3 target

exhibited sparing. Furthermore, this late sparing was followed by a longer-lasting AB deficit, so that although T2 accuracy recovered by about 552 msec in the standard AB condition, accuracy for T2 was still comparatively low up to 1,154 msec after onset of T1 in the two-red-distractor condition. This finding represents a crossover interaction of distractor salience and time on T2 accuracy: T2 accuracy was improved at early lags but worsened at later lags. Olivers and Meeter claimed that this result indicated a delayed AB, so that reducing the salience of the distractors immediately following T1 displaced both sparing and deficit onward in time, to the first salient distractor following T1.

However, very similar work has been explained within the framework of the LC–NE account. Nieuwenstein (2006) reported that when T2 is preceded by a distractor that shares a feature with T2 (e.g., the color red), the distractor works as a cue, facilitating detection and subsequent report of T2 even though it is presented during the period of the AB. Against the claims of the boost and bounce theory, this result held even when a distractor that did not share a feature with the targets intervened; only the distractor preceding and sharing a feature with T2 was necessary to produce the benefit. Nieuwenstein cited the LC–NE system in interpreting his results. He suggested that "cuing T2 mitigates the effect of the AB because a cue will trigger the disinhibition of mechanisms mediating resource allocation in advance of the target, with the result that the following target can be responded to rapidly" (pp. 983–984).

Just as Nieuwenstein's (2006) cuing explanation can account for the sparing results observed in Olivers and Meeter (2008), we submit that it can also account for the observations suggestive of a delayed recovery period. We suggest that sustained cuing of the LC response by the colored distractors would extend the subsequent refractory-like period of the LC–NE system when T2 was not presented immediately following the cues. In support of this, we point out that the supposed delay of the AB recovery period in Olivers and Meeter was not displaced as precisely as the period of sparing. In the two-red-distractor condition, the AB should be delayed by only 180 msec, but the T2 deficit is still apparent 552 msec after the AB deficit appears to have completely recovered in the standard AB condition. This timing is more suggestive of a prolonged than a delayed AB. Thus, the same observations that are interpreted as a delayed AB in support of the boost and bounce theory could be interpreted under the LC–NE account as a prolonged AB due to sustained (greater) LC activity following T1 and, subsequently, a greater period of LC inhibition. The question we examine here is whether this pattern of results can be demonstrated in additional circumstances consistent with only one of these accounts. Although they were not discussed in this context, the data from the Nieuwenhuis et al. (2005) experiments speak to this issue.

In two AB experiments, Nieuwenhuis et al. (2005; see also Martin & Shapiro, 2008) inserted an additional distractor into the RSVP. In Experiment 1, the additional distractor was placed 50 msec after onset of T1, and in Experiment 2, it was superimposed on T1. In both experiments, the ability to report T2 at 200 msec in the condition with the additional distractor was facilitated relative to a control condition, whereas accuracy was decreased at 700 msec. This difference was not discussed in the original article, but Nieuwenhuis (personal communication, June 26, 2009) has confirmed that the lag 2 differences were significant in both experiments, whereas the lag 7 differences were significant only in Experiment 1. These experiments were not designed to address the issue we are raising. Should the effect we highlight persist under more controlled and sensitive circumstances, it cannot be explained by the boost and bounce theory: There is no reason why the insertion of the distractor should delay the AB. However, this effect can be accommodated by the LC–NE account with a simple and reasonable modification: by assuming that the addition of another distractor so close to T1 increased the size of the LC response.

There is neurophysiological support for this modification. The LC receives prominent innervation from the anterior cingulate cortex (ACC), an area of the brain associated with the detection and resolution of response conflict (e.g., Aston-Jones & Cohen, 2005). Increased activation in the ACC has been observed during the AB when targets were followed by distractors, as compared with a no-distractor condition and other conditions under which target–distractor interference was increased (Marois, Chun, & Gore, 2000). We posit that the ACC detects conflict within the AB paradigm, due to temporal overlap between *remember* and *ignore* responses to targets and distractors, and recruits the LC–NE system accordingly.

Our modification of the LC–NE account is consistent with the appearance of a larger LC–NE system response when T1 and the following distractor were moved closer in time. We replicated the effect seen in Nieuwenhuis et al. (2005) within the context of this reasoning, with additional controls to eliminate possible confounds (see the Method and Discussion sections). We created two conditions of the typical AB task, a low-interference condition and a high-interference condition. The conditions were distinguished by the amount of time available to process T1 before the subsequent distractor appeared. The LC–NE account predicts that the high-interference condition will exhibit greater T2 accuracy at early lags (up to an SOA of 200 msec, represented by lag 3 in our task), followed by worse accuracy at later lags, relative to the low-interference condition.

METHOD

Subjects

Sixteen undergraduate students at the University of Victoria took part in the experiment for extra credit.

Apparatus and Stimuli

The stimuli consisted of black digits and uppercase letters presented in rapid succession on a light gray background (25.0 cd/m^2). The stimuli subtended, on average, 1º of visual angle horizontally. They were presented on a monitor refreshed at 100 Hz. The subjects were stabilized with a chinrest and viewed the stimuli from a distance of 55 cm.

Procedure

The experiment consisted of two sessions, approximately 45 min each, separated by 1–7 days. The first session began with a 24-trial practice block, followed by three 96-trial experimental blocks. The second session consisted of three 96-trial experimental blocks. The experimental manipulation was implemented randomly within blocks, with the constraint that each block contained an equal number of trials from each condition.

The critical events in a single trial are illustrated in Figure 1. The subjects triggered the beginning of each trial by pressing the space bar. A fixation cross was displayed at the center of the screen for 1 sec and was immediately replaced by an RSVP sequence. The sequence consisted of 20 characters (18 digits as distractors and 2 letters as targets). The 18 digits in the sequence were chosen randomly, with replacement, from the numbers 2–9, with the constraint that a number could not be repeated consecutively. The targets consisted of 2 letters drawn randomly, with replacement, from 21 of the 26 letters of the alphabet. We excluded the letters B, I, O, Q, and S because of their visual similarity to digits. T1 was randomly presented at any location between the 6th and 10th frames inclusively. T2 could appear at any of four lags defined by temporal position following T1: lag 2, lag 3, lag 5, or lag 8. There were always at least two distractors following the second target. After the RSVP finished, two response screens sequentially appeared requesting the identity of T1 and T2. The subjects responded using the keyboard.

Each stimulus in the RSVP sequence was presented for 10 msec, followed by a blank screen displayed for an additional 70 msec. With this interstimulus interval (ISI), the majority of the stimuli were associated with 80 msec of processing time before onset of the next stimulus. However, the timing of two critical ISIs was manipulated to produce differences in T1-distractor interference. In the low-interference condition, the ISI following T1 (ISI-1) was increased from 70 to 90 msec, allowing T1 to be processed for a total of 100 msec before onset of the following distractor. In the high-interference condition, ISI-1 was decreased to 10 msec, allowing only 20 msec for T1 to be processed before the next distractor. This lengthening and shortening of ISI-1 was balanced by a complementary lengthening and shortening of the ISI following the next distractor (ISI-2), so that when the critical ISI-1 was 90 msec, the critical ISI-2 was 10 msec, and vice versa. This manipulation resulted in lag 1's falling either 20 or 100 msec after onset of T1. However, T2 was never presented at lag 1 in this experiment, so that the difference is inconsequential. In both conditions, lag 2 fell at an SOA of 120 msec after T1, lag 3 occurred at 200 msec, lag 5 at 360 msec, and lag 8 at 600 msec. In addition, there were two control conditions, in which the critical ISIs were manipulated exactly as in the experimental conditions but a distractor was presented in place of T1. This condition was included to assess whether T2 accuracy would be impacted by the variation in ISIs in the absence of T1.

RESULTS

Target accuracies for T1 and T2 are plotted separately as a function of lag and interference level in Figure 2. Analysis of T2 accuracy was conditional on accurate reporting of T1, and accuracy was defined as reporting the correct target irrespective of order. We note that the following results held when accurate responding was defined as reporting the targets in the correct order and also held when T2 accuracy was scored independently of T1 accuracy. Our interference manipulation impacted T1 accuracy such that T1 accuracy was significantly lower in the high-interference condition than in the low-interference condition, as indicated by a two-factor ANOVA of T1 accuracy, with lag and interference level as repeated measures factors [$F(1,15) = 147.99$, $p < .001$]. There was also a main effect of lag [$F(3,45) = 16.17$, $p < .001$] and a lag × interference level interaction [$F(3,45) = 12.37$, $p < .001$].

T2 accuracy followed our prediction that in the high-interference condition, a relative benefit would be observed at both lag 2 and lag 3. A two-factor ANOVA was performed with lag and interference level as repeated measures factors. This analysis yielded a significant main effect of interference level [$F(1,15) = 9.76$, $p = .007$], a significant effect of lag [$F(3,45) = 4.63$, $p = .007$], and a significant lag × interference level interaction [$F(3,45) = 24.09$, $p < .001$]. A separate ANOVA at each lag, with interference level as the repeated measures factor, demonstrated that, as was predicted, accuracy for T2 was sig-

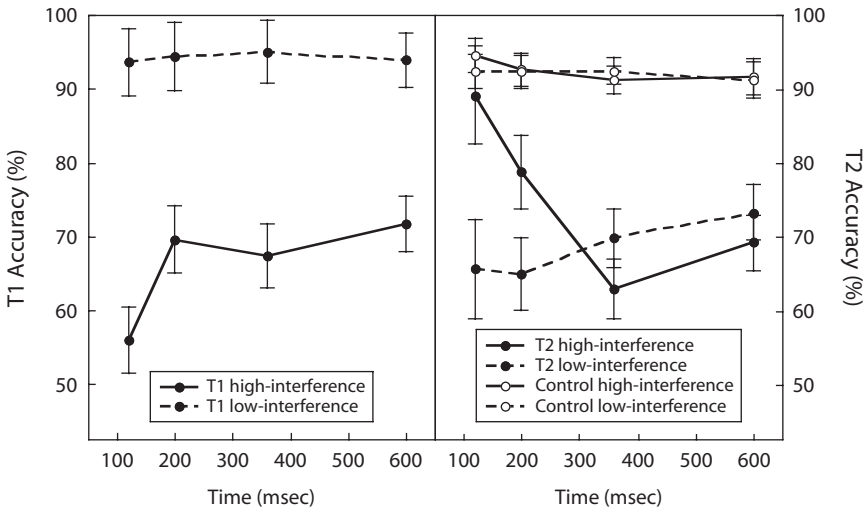

Figure 2. Mean percentages of correct responses for the first target (T1) and the second target (T2) as a function of the lag at which T2 occurred. Analysis of T2 accuracy was conditional on accurate reporting of T1. Error bars represent 95% within-subjects confidence intervals.

nificantly greater in the high-interference condition than in the low-interference condition at both lag 2 [$F(1,15) = 27.65$, $p < .001$] and lag 3 [$F(1,15) = 17.97$, $p = .001$], but accuracy at lag 5 was significantly worse in the high-interference condition [$F(1,15) = 6.35$, $p = .024$] and was still lower at lag 8, but the difference had fallen below significance [$F(1,15) = 2.56$, $p = .130$]. No significant difference appeared in the control condition at any lag [lag 2, $F(1,15) = 2.18$, $p = .160$; lag 3, $F(1,15) = 0.05$, $p = .817$; lag 5, $F(1,15) = 1.00$, $p = .333$; lag 8, $F(1,15) = 0.05$, $p = .826$].

DISCUSSION

We theorized that a larger LC–NE response to the interference between T1 and the following distractor would lead to improved T2 accuracy at early lags, followed by reduced accuracy at later lags. When we moved T1 and the following distractor closer together in time, we found that accuracy for identifying T2 was significantly better at lags 2 and 3. This was followed by lower accuracy at lag 5.

Our experimental results highlight an inverse relationship between T2 accuracy at early lags (the period of sparing) and T2 accuracy at later lags (the period of deficit). The LC–NE theory holds that accurate reporting of T2 is directly related to the availability of NE in relevant processing areas at any given time following T1. As such, the more NE released at T1, the greater the sparing that should be observed and, subsequently, the greater the deficit due to inhibition of the LC by the initial NE release. Especially large NE releases can produce evidence of sparing as late as 200 msec after onset of T1. We should note here that when we discuss the LC–NE account, we refer only to the general idea that the LC–NE system underlies the AB; we are making inferences here that were not put forth in the original theory.

In contrast to the LC–NE account, the boost and bounce theory does not predict the observed relationship between the period of sparing and the period of deficit. Under the boost and bounce theory, a condition will yield only the *appearance* of greater sparing, followed by a greater deficit when the AB has been delayed: There is no mechanism for impacting sparing except by delaying or eliminating the inhibition-eliciting distractor. If a manipulation impacted either the attentional enhancement or the inhibitory feedback postulated in the boost and bounce theory, the theory still would not predict the results that we report. Manipulating the strength of the posited attentional enhancement or distractor-elicited sensory inhibition would impact only the period of deficit. Sparing would be unchanged, confined to targets that were not preceded by a salient distractor. One might point out that our manipulation may have reduced the salience of the distractor in our high-interference condition, but the observation that T2 accuracy was improved at lag 3 (200 msec) in the high-interference condition, despite a distractor's intervening at 120 msec in both conditions, works against this interpretation.

We included the control condition in this study to rule out two additional alternative explanations of our results. It is possible that the disruption of the timing of the RSVP may have drawn attention to T2 to varying degrees according to the differences in the disruption across conditions. However, if this were the case, we should have seen effects in our control condition. Furthermore, because T2 at lag 2 was preceded by a blank ISI of either 10 or 90 msec across conditions, it is possible that differences in forward masking from the distractor preceding T2 may have driven the lag 2 results. Again, our control condition did not show any differences in accuracy for targets preceded by a distractor by 10 versus 90 msec. Moreover, the benefit we predicted extended past lag 2 to lag 3 and then crossed over to become a deficit by lag 5, despite there being no differences in masking at these later lags.

It is interesting to note that T1 accuracy was worst when T2 occurred at lag 2 in the high-interference condition. Potter, Staub, and O'Connor (2002) highlighted the phenomenon that at SOAs of approximately 120 msec or less, sparing of T2 is accompanied by a deficit in reporting T1. They suggest that when T1 and T2 appear in close temporal proximity, they compete for a limited pool of resources, such that if T2 appears before T1 has been processed to the point of identification, the resources recruited for T1 will benefit T2 over T1. This interpretation is consistent with the LC–NE account. NE is theorized to facilitate signal processing by enhancing the difference between stronger and weaker signals, reducing interference from background noise or less relevant signals. This means that when NE arrives in the forebrain, the strongest representations will receive the greatest benefit. We assume that targets will always represent the strongest signals by virtue of their motivational salience, so that NE will always benefit targets over distractors. However, in the case in which processing of two targets overlaps, T2 may represent the strongest signal by virtue of being the target currently presented on the screen, and it will thus be facilitated more than, and at the expense of, T1.

The primary goal of this study was to test whether target–distractor interference impacts the AB in a manner consistent with a modified version of the LC–NE account of the AB and inconsistent with the recently proposed boost and bounce theory (Olivers & Meeter, 2008). Although our experimental evidence is only preliminary support for our proposed modification of the LC–NE theory, we have presented reliable evidence that cannot be accommodated by the boost and bounce theory. In addition, we highlight the effect of the ISI between T1 and the following distractor on T2 accuracy as an important characteristic of the AB.

AUTHOR NOTE

This research was supported by a discovery grant from the Natural Sciences and Engineering Research Council (NSERC) of Canada to M.E.J.M. C.M.W. was supported by a doctoral NSERC Canadian Graduate Scholarship and a Michael Smith Foundation for Health Research Junior Trainee Award. A.T.B. was supported by a doctoral NSERC postgraduate scholarship. J.K. was supported by an Erich and Shelley Mohr Fellowship. D.F. was supported by a postdoctoral scholarship from Le Fond Québécois de Recherche en Nature et Technologies (FQRNT). C.B. was supported by a Ph.D. scholarship from FQRNT. Correspondence should be sent to C. M. Warren, Department of Psychology, Uni-

versity of Victoria, P.O. Box 3050 STN CSC, Victoria, BC, V8W 3P5 Canada (e-mail: cwarren@uvic.ca).

REFERENCES

ASTON-JONES, G., & COHEN, J. D. (2005). An integrative theory of locus coeruleus–norepinephrine function: Adaptive gain and optimal performance. *Annual Review of Neuroscience*, **28**, 403-450. doi:10.1146/annurev.neuro.28.061604.135709

COHEN, J. D., ASTON-JONES, G., & GILZENRAT, M. S. (2004). A systems level theory of attention and cognitive control. In M. I. Posner (Ed.), *Cognitive neuroscience of attention* (pp. 71-90). New York: Guilford.

KAWAHARA, J.-I., KUMADA, T., & DI LOLLO, V. (2006). The attentional blink is governed by a temporary loss of control. *Psychonomic Bulletin & Review*, **13**, 886-890.

MAROIS, R., CHUN, M. M., & GORE, J. C. (2000). Neural correlates of the attentional blink. *Neuron*, **28**, 299-308.

MARTIN, E. W., & SHAPIRO, K. L. (2008). Does failure to mask T1 cause lag-1 sparing in the attentional blink? *Perception & Psychophysics*, **70**, 562-570. doi:10.3758/PP.70.3.562

NIEUWENHUIS, S., GILZENRAT, M. S., HOLMES, B. D., & COHEN, J. D. (2005). The role of the locus coeruleus in mediating the attentional blink: A neurocomputational theory. *Journal of Experimental Psychology: General*, **134**, 291-307. doi:10.1037/0096-3445.134.3.291

NIEUWENSTEIN, M. R. (2006). Top-down controlled, delayed selection in the attentional blink. *Journal of Experimental Psychology: Human Perception & Performance*, **32**, 973-985. doi:10.1037/0096-1523.32.4.973

OLIVERS, N. L., & MEETER, M. (2008). A boost and bounce theory of temporal attention. *Psychological Review*, **115**, 836-863.

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 & Performance*, **28**, 1149-1162. doi:10.1037//0096-1523.28.5.1149

RAYMOND, J. E., SHAPIRO, K. L., & ARNELL, K. M. (1992). Temporary suppression of visual processing in an RSVP task: An attentional blink? *Journal of Experimental Psychology: Human Perception & Performance*, **18**, 849-860.

VOGEL, E. K., LUCK, S. J., & SHAPIRO, K. L. (1998). Electrophysiological evidence for a postperceptual locus of suppression during the attentional blink. *Journal of Experimental Psychology: Human Perception & Performance*, **24**, 1656-1674.

(Manuscript received October 2, 2007;
revision accepted for publication June 25, 2009.)