CORTEX 71 (2015) 15–33

Available online at www.sciencedirect.com

ScienceDirect

Journal homepage: www.elsevier.com/locate/cortex

Research report

The "serendipitous brain": Low expectancy and timing uncertainty of conscious events improve awareness of unconscious ones (evidence from the Attentional Blink)

Stefano Lasaponara [a,b], *Alessio Dragone* [a,b], *Francesca Lecce* [b,d], *Francesco Di Russo* [b,c] *and Fabrizio Doricchi* [a,b,*]

[a] *Dipartimento di Psicologia, Università "La Sapienza", Roma, Italy*
[b] *Fondazione Santa Lucia IRCCS, Roma, Italy*
[c] *Dipartimento di Scienze Motorie, Umane e della Salute, Università "Foro Italico", Roma, Italy*
[d] *Institute of Cognitive Neuroscience, University College London, UK*

ARTICLE INFO

Article history:
Received 30 September 2014
Reviewed 21 November 2014
Revised 16 January 2015
Accepted 11 May 2015
Action editor Jason Mattingley
Published online 11 June 2015

Keywords:
N2
P300
Visual awareness
Attentional Blink
ERPs

ABSTRACT

To anticipate upcoming sensory events, the brain picks-up and exploits statistical regularities in the sensory environment. However, it is untested whether cumulated predictive knowledge about consciously seen stimuli improves the access to awareness of stimuli that usually go unseen. To explore this issue, we exploited the Attentional Blink (AB) effect, where conscious processing of a first visual target (T1) hinders detection of early following targets (T2). We report that timing uncertainty and low expectancy about the occurrence of consciously seen T2s presented outside the AB period, improve detection of early and otherwise often unseen T2s presented inside the AB. Recording of high-resolution Event Related Potentials (ERPs) and the study of their intracranial sources showed that the brain achieves this improvement by initially amplifying and extending the pre-conscious storage of T2s' traces signalled by the N2 wave originating in the extra-striate cortex. This enhancement in the N2 wave is followed by specific changes in the latency and amplitude of later components in the P3 wave (P3a and P3b), signalling access of the sensory trace to the network of parietal and frontal areas modulating conscious processing. These findings show that the interaction between conscious and unconscious processing changes adaptively as a function of the probabilistic properties of the sensory environment and that the combination of an active attentional state with loose probabilistic and temporal expectancies on forthcoming conscious events favors the emergence to awareness of otherwise unnoticed visual events. This likely provides an insight on the attentional conditions that predispose an active observer to unexpected "serendipitous" findings.

* *Corresponding author*. Dipartimento di Psicologia, Università "La Sapienza", Via dei Marsi 78, 00185 Roma, Italy.
E-mail address: fabrizio.doricchi@uniroma1.it (F. Doricchi).

http://dx.doi.org/10.1016/j.cortex.2015.05.029
0010-9452/

1. Introduction

One of the salient properties of the brain is the ability to pick up statistical regularities in the environment. These regularities can be exploited to generate predictions about upcoming sensory events and minimize the discrepancy between predicted and observed events (Friston, 2010). Stimuli that are not consciously perceived can prime temporally adjacent visual, semantic and motor choices (Dehaene et al., 2001; van Gaal, Ridderinkhof, Fahrenfort, Scholte, & Lamme, 2008; Van den Bussche, Notebaert, & Reynvoet, 2009; van Gaal, Ridderinkhof, Scholte, & Lamme, 2010; Kouider, Eger, Dolan, & Henson, 2009; De Lange, Van Gaal, Lamme, & Dehaene, 2011; Melloni, Schwiedrzik, Müller, Rodriguez, & Singer, 2011; Naccache & Dehaene, 2001; Naccache, Blandin, & Dehaene, 2002; Pessiglione et al., 2007). Unconscious stimuli can also affect more complex activities like deciding to perform one out of two competing cognitive tasks (Capa, Bouquet, Dreher, & Dufour, 2013; Lau & Passingham, 2007; Weibel, Giersch, Dehaene, & Huron, 2013) or estimating the likelihood of having made a response error (Charles, Van Opstal, Marti, & Dehaene, 2013). Nonetheless, the predictive influence of unconscious prime-stimuli is typically short lasting and limited to events presented within the same trial in which the unconscious prime occurs. In contrast to this, available investigations show that higher order predictions that are driven by the exploitation of statistical regularities in the task set and that yield long lasting changes on strategies of cognitive control over different trials, are mainly, if not exclusively, gathered from consciously perceived stimuli (De Lange et al., 2011; Wacongne et al., 2011).

A task that is frequently used to investigate the functional and neural correlates of conscious visual processing is the Attentional Blink (AB) (Broadbent & Broadbent, 1987; Raymond, Shapiro, & Arnell, 1992; Shapiro, Raymond, & Arnell, 1994; for review see Dux & Marois, 2009; Martens & Wyble, 2010). In this task, participants are asked to report two visual targets, T1 and T2, that are successively presented embedded in a rapid stream of visual items [i.e., rapid serial visual presentation (RSVP); Fig. 1]. T2s that are presented within 200–400 msec from T1 are typically missed, i.e., blinked. Initially, the predominant interpretation of the AB was that it arises because serial and capacity-limited operations engaged by the conscious processing of T1 cannot be oriented to parallel conscious processing of T2 (for review see Craston, Wyble, Chennu, & Bowman, 2009; Dux & Marois, 2009; Martens & Wyble, 2010). T2s that are presented early after T1 go undetected because their pre-conscious sensory trace decays during conscious processing of T1. In contrast, T2s that are presented at longer time intervals after T1 are consciously detected because at the end of T1 processing their pre-conscious trace is not decayed and can access conscious processing (Chun & Potter, 1995; Raymond et al., 1992; Sergent, Baillet, & Dehaene, 2005; Shapiro et al., 1994).

More recently, several pieces of evidence have challenged the idea that the AB is due to inherent central capacity limitations in conscious processing (Martens & Wyble, 2010). These studies emphasised the role played by attentional control in managing the competition between targets and distractors in the RSVP and in allowing the emergence to conscious perception of targets. As an example, boosting the salience of T2s through attentional cuing (Nieuwenstein, Chun, van der Lubbe, & Hooge, 2005), reducing the number of distractors within the RSVP (Di Lollo, Kawahara, Ghorashi, & Enns, 2005; Nieuwenstein & Potter, 2006; Olivers, Van Der Stigchel, & Hulleman, 2007; Potter, Nieuwenstein, & Strohminger, 2008) or including the report of T1 and T2 in a single goal, i.e., reporting a combination of T1 and T2 (Ferlazzo, Lucido, Di Nocera, Fagioli, & Sdoia, 2007; Ferlazzo, Fagioli, Sdoia, & Di Nocera, 2008; Sdoia & Ferlazzo, 2012) can induce a recovery of attentional resources and reduce the AB.

In line with this new set of evidences, a number of investigations have pointed out that both indirect and direct cuing of the time point to be attended in the RSVP improves the conscious detection of T2s presented at that time point. Choi, Chang, Shibata, Sasaki, and Watanabe (2012) showed that when participants undergo a training session in which salient-coloured T2s are always presented at one specific lag within the AB (Choi et al., 2012), detection of non-coloured/non-salient T2 presented at the same time lag is improved in a subsequent session of assessment. Tang, Badcock, and Visser (2014), pointed out that this improvement largely depends on temporal expectancies set by salient-coloured T2s during training, as at assessment the AB is no more reduced when more distractors are presented ahead of T1 so that, being equal the time lag between T1 and T2, the absolute temporal position of T2 in the RSVP is different with respect to training. Another series of studies showed that the AB is significantly reduced when the timing of T2 is explicitly cued on a trial-by-trial or block of trials-by-block of trials basis. Martens and Johnson (2005) first showed that cuing the length of the time lag separating T1 from T2 at the beginning of each trial consistently reduces the AB. This was observed both with symbolic cuing, i.e., in the form of short or long line segments (Exp 2), and when direct cuing of the time lag was provided in the form of a time interval interposed between two visual events (Exp 3). Hilkenmeier & Scharlau (2010) reported a similar reduction when in each trial the digit-number defining T1 also indicated the ensuing lag-position of T2. More recently, Shen and Alain (2011) showed that instructing participants to attend, during an entire block of trials, a specific short, middle or long temporal position after T1 consistently reduces the AB for T2 presented at that position.

At variance with these homogenous sets of findings, contrasting results are reported by investigation that have assessed whether blocking the presentation of uncued T2 at a specific time point leads to a reduction of the AB. Martens & Johnson (2005; Experiment 1) found no difference in the magnitude of the AB depending on whether T2s were all presented inside the AB, i.e., 270 msec after T1, or whether they were presented inside the AB in half of the trials and outside the AB, i.e., 720 msec after T1, in the other half of the trials. This finding first suggested that the repeated presentation of T2s at a specific time lag is not automatically detected and exploited by observers and does not produce a drop in the AB. Nonetheless, using the same experimental paradigm, in a recent study Visser, Tang, Badcock, and Enns (2014) showed that a significant reduction of the AB is observed when the voluntary exploration and exploitation of timing

regularity in the occurrence of T2s is induced by informing participants that T2s will predominantly appear at a specific time lag. This set of findings is made even more complex by the results of an investigation into auditory AB by Shen and Alain (2012) in which T2s were presented inside the AB (lag 2) on 80% of trials and outside the AB (lag 8) on 20% of trials or viceversa. As in Martens and Johnson (2005), participants were not informed on the probability distribution of T2s. Shen and Alain (2012) found an improvement of the AB when T2s appeared inside the AB on 80% of trials: nonetheless this improvement was marginal and did not raise T2 detection above chance level, i.e., did not suppress the AB. Though differing from previous findings by Martens and Johnson (2005), this result still does not provide clear-cut support for the influence on the AB of uncued timing regularities in the occurrence of T2s. In addition, in the same study the probability of T2 occurrence inside the AB was inversely related to that of T2 occurrence outside the AB. As a consequence, the non-independent manipulation of T2 occurrence inside and outside the AB does not allow clarifying whether the slight improvement of T2 detection inside the AB was due to the implicit perception of the frequent occurrence of T2s inside the AB or, in contrast, to the perception of the infrequent occurrence of T2s outside the AB. In summary, the set of findings reported in these studies leaves open a number of relevant questions and does not allow concluding whether uncued statistical and timing regularities in the occurrence of consciously and non-consciously perceived target events modify the strength of the AB or not.

Based on evidence suggesting that strategies of cognitive control are mainly driven by consciously perceived stimuli (De Lange et al., 2011; Wacongne et al., 2011), in the present study we were specifically interested in assessing whether the frequency of occurrence and the timing of conscious T2s that are presented outside the AB modulate the access to awareness of unconscious T2s inside the AB. The findings reported by Martens and Johnson (2005; Exp 1) might already suggest that when observers are not explicitly informed on the preferential occurrence of T2s at a specific time lag, a simple change in the frequency of T2s presented outside the AB, i.e., 0% *vs* 50%, does not modify the conscious processing of T2s presented inside the AB. However, one should consider the possibility that these negative findings were reported because: a) when T2s were all presented inside the AB they remained, on average, unconscious and failed to produce a strategic orienting of attention toward the AB period; b) when the probability of occurrence of conscious T2s outside the AB was at chance, i.e., 50% of trials, no strategic change in the reallocation of attentional resources toward shorter lags inside the AB was triggered, because no probabilistic information was offered by T2s occurring outside the AB. On these grounds, we argued that a more suitable way of testing whether changes in the probability of occurrence of conscious T2s outside the AB modify the AB would be to keep constant the number of trials in which T2s are presented inside the AB and make informative the occurrence of T2s outside the AB by presenting these T2s in a clear minority or majority of the remaining trials. This experimental design should allow verifying whether the detection and exploitation of statistical regularities in the occurrence of conscious stimuli modify the access to awareness of stimuli that would otherwise remain non-conscious. We hypothesized that poor predictability of conscious T2 outside the AB would have induced a widening of the focus of attention over larger time sectors of the rapid visual stream of stimuli presented in the task and a reduction of the AB. It is worth noting that the idea that conscious processing is improved when the attention of an active observer is not tied up to precisely defined expectations of incoming sensory inputs, can be originally traced back to the, often misused, concept of "serendipity" (Merton & Barber, 2006). "Serendipity" generally refers to the ability of picking up and appreciating the relevance of involuntary and incidental observations. Its role in scientific discovery has been emphasised, among others, by scientist like the biologist Louis Pasteur (1854) and the physiologist Walter Bradford Cannon (1945). Thus, by exploring the role of expectancy in the conscious processing of incoming visual stimuli, in the present study we also wished to acquire insights on the attentional conditions that predispose an active observer to unexpected "serendipitous" findings.

To pursue the aims of our study, we ran two AB experiments. The main experimental manipulation was to make more or less predictable the occurrence of conscious T2s outside the AB. To get this, we manipulated the two main sources of stimulus predictability that can be considered in a conventional AB task where targets always appear at the same spatial position and no spatial uncertainty is present: a) the probability of occurrence of T2s outside the AB; b) the regular versus irregular timing of occurrence of T2s outside the AB. Therefore, while in both experiments of our study we maintained constant the probability of occurrence and the timing of early non-conscious T2s inside the AB, we varied, the probability of occurrence and the timing of late conscious T2s outside the AB. In Experiment 1 (Fig. 1A), in half of the trials T2s were presented inside the AB at three different time lags from T1. Crucially, in the remaining half of the trials late T2s were presented outside the AB at a fixed time lag from T1 in two different experimental conditions. In a Frequent condition (Fr) T2s were presented on 80% of trials, whereas in a second Infrequent condition (InFr) they were presented only on 20% of trials. In Experiment 2 (Fig. 1B), we additionally introduced uncertainty in the timing of late T2s presented outside the AB so that, both in the Fr and InFr condition, late T2s appeared with equal probability at three different lags from T1. In both experiments participants received no information about the frequency of occurrence and the timing of T2s.

Previous investigations with Event-Related Potentials (ERPs) have well characterized the timing of neural events that are correlated to the competing processing of T1 and T2 and to the conscious detection of T2s (see for example Sergent et al., 2005; Sessa, Luria, Verleger, & Dell'Acqua, 2007; for review see Martens & Wyble, 2010). These studies converge in showing that detected and missed T2s elicit comparable electrophysiological responses at early levels of processing (P1 and N1 components) and that the conscious detection of T2 is reflected by the presence of later N2, P3a and P3b components signaling prolonged maintenance of the stimulus trace and allocation of attentional resources to its processing (Sergent et al., 2005; Sessa et al., 2007). Therefore in the present study

we also recorded T1-and T2-related ERPs, to investigate whether changes in the AB produced by the predictive coding of incoming conscious T2s were matched to specific changes in T1-or T2-related ERPs components.

2. Materials and methods

2.1. Participants

Thirty-five healthy right-handed subjects (age: 18–26 years) participated in the ERPs study. Nineteen participants performed Experiment 1 and sixteen performed Experiment 2. The ERPs study was preceded by a Pilot behavioral study run on a different sample of 28 participants: 14 participants performed Experiment 1 and 14 participants Experiment 2. All participants had normal or corrected-to-normal visual acuity and reported having normal color vision. They were all recruited in the Department of Psychology of the University "La Sapienza" in Rome (Italy) and gave their informed consent to participate in the study. Measures were run at the IRCCS Santa Lucia Foundation, Rome. The independent ethic committee of the IRCCS Santa Lucia approved experimental procedures.

2.2. Apparatus, stimuli and task

Stimuli were presented on a 17-inch color LCD monitor in the Pilot behavioral study and on 21-inch color CRT monitor in the ERPs study. Stimuli presentation and recording of manual responses was performed with E-Prime software. Participants sat with their head on a chin rest at a distance of 57 cm from the monitor. In two separate experimental sessions, each participant performed an AB task. In each trial of the task, a series of random letters was rapidly presented at central fixation (RSVP). In each trial two consecutive targets were interspersed in the series of random letters: the first target (T1) could be a letter "B" or "G", the second target was a letter "X". In each trial, at the end of the letter stream participants pushed the "B" or "G" button of the computer keyboard to indicate whether T1 was a "B" or a "G" and then pushed the "1" or "2" button to indicate, respectively, whether T2 ("X") was presented or not. Random sequences of 7–15 letters preceded T1. After the presentation of T1 another series of 8 letters was presented. In Experiment 1, T2 was presented as the 2nd, 3rd, 4th or 6th letter in the 8 letter sequence that followed T1, corresponding to experimental Lags 2, 3, 4 and 6 respectively (Fig. 1A). In Experiment 2, T2 was presented as the 2nd, 3rd, 4th, 5th, 6th or 7th letter in the 8 letter sequence that followed T1, corresponding to experimental Lags 2, 3, 4, 5, 6 and 7 respectively (Fig. 1B). In each trial, non-target letters were randomly taken from the uppercase version of the 26 letters of the alphabet (excluding, "B", "G" or "X"). No letter was presented twice within the same trial. Each letter was presented for 15 msec with an inter-stimulus interval (ISI) of 75 msec, producing a presentation rate of 11.11 letters/sec. Letters were .82° in height and .60° in width. They were displayed at the center of a uniform grey field (9.1 cd/m^2) that subtended 16.3° × 12.4°. Non-target letters and T2 were presented in black while T1 was presented in white (32.9 cd/m^2). Each trial began with the 180 msec presentation of a small white fixation dot. Participants initiated each trial by pressing the spacebar. Each participant performed the task in a "Frequent" condition in one experimental session and in an "Infrequent" condition in another session (Fig. 1). In both conditions, there were 360 trials in which the same number of T2s was always presented inside the AB at Lag 2 (180 msec after T1, 120 trials), Lag 3 (270 msec after T1, 120 trials) and Lag 4 (360 msec after T1, 120 trials). In both conditions there were also 360 trials in which T2s could be presented or not presented outside the AB. In Experiment 1, all T2s that were presented outside the AB appeared at Lag 6 (540 msec after T1). In Experiment 2, T2s that were presented outside the AB were equally distributed among Lag 5 (450 msec after T1), Lag 6 (540 msec after T1) and Lag 7 (630 msec after T1). In the "Frequent" condition of both Experiments, T2s presented outside the AB appeared on 80% of the 360 trials (thus yielding 72 catch trials with no T2), whereas in the "Infrequent" condition they appeared only on 20% of the same 360 trials (thus yielding 288 catch trials with no T2). In each experiment the order of sessions (Frequent *vs* Infrequent) was counterbalanced across participants. Sessions were separated by a one-week interval. The main difference between Experiment 1 and 2 was that in Experiment 1 T2s presented outside the AB appeared at a fixed time Lag from T1 (i.e., Lag 6: Fig. 1A), whereas in Experiment 2 T2s presented outside the AB appeared at three different Lags from T1 (i.e., Lag 5, 6 or 7; Fig. 1B). Both in the Pilot and ERPs study no information on the frequency of occurrence and the timing of T2s was provided to participants.

2.3. Electrophysiological recording and data processing

The EEG was recorded using a BrainVision system from 64 electrodes placed according to the 10–10 system (Di Russo et al., 2012). All scalp channels were referenced to the Central Cz channel. All channels were initially referenced to the left mastoid (M1), and the ground electrode was located to the CPz. Horizontal eye movements were monitored with a bipolar recording from electrodes at the left and right outer canthi. Blinks and vertical eye movements were recorded with an electrode below the left eye, which was referenced to site Fp1. The EEG from each electrode site was digitized at 250 Hz with a .01–80 Hz bandpass filter, including a 50 Hz notch filter, and was stored for off-line averaging. Computerized artifact rejection was performed prior to signal averaging in order to discard epochs in which transient EEG voltage changes exceeded ±100 μV or relevant eye position changes (i.e., electro-oculogram activity exceeding ±70 μV), blinks or amplifier blocking occurred. Participants showing artifacts in more than 20% of trials were discarded from the ERPs and behavioral analyses. This led to the exclusion of three out of the 19 participants initially enrolled in Exp1. T1-and T2-related ERPs were averaged in epochs that began 200 msec prior to the presentation of T1/T2 and lasted for 700 msec after the presentation of T1/T2. To further reduce high-frequency noise, the averaged ERPs were low-pass filtered at 30 Hz. The 200 msec epoch preceding the appearance of T1/T2 was used as baseline and corrected to 0 μV.

For each ERPs component and each experimental condition, topographical maps of ERPs activity were computed

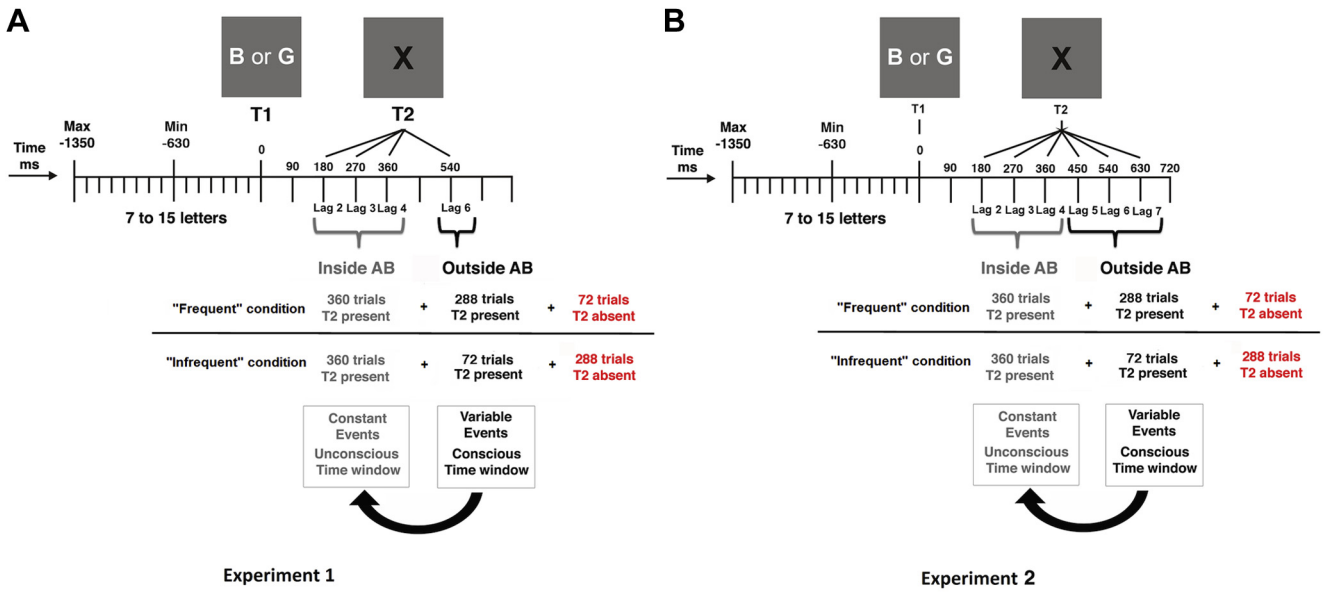

Fig. 1 – Task design. In each trial a rapid visual stream (duration 630–1350 msec) of 7–15 consecutive letters was presented at fixation before a first target letter was presented at time 0 (T1 = B or G). T1 was followed by another series of 8 consecutive letters. One out of these letters was the second target (T2 = X). T2 was presented inside (lag 2 to 4) or outside the Attentional Blink (AB) period (lag 6 in Experiment 1, lags 5 to 7 in experiment 2). Each letter was presented for 15 msec and was separated from the subsequent letter by a 75 msec blank lag. (A) Structure of Experiment 1: in the "Frequent" condition T2 was presented inside the AB on 360 trials (grey text), outside the AB in other 288 trials (black text) at a fixed time lag from T1 (i.e., at lag 6) and was not presented, either inside or outside the AB, in 72 trials (red text). In the "Infrequent" condition T2 was presented inside the AB on 360 trials (grey text), outside the AB in other 72 trials (black text) at a fixed time lag from T1 (i.e., at lag 6) and was not presented, either inside or outside the AB in 288 trials (red text). (B) Structure of Experiment 2: the "Frequent" and "Infrequent" conditions were as in Experiment 1 except that the presentation of T2s outside the AB was equally distributed among three different time lags from T1, i.e., lag 5, 6 and 7. In both Experiment 1 and 2 we studied the influence of variations in probabilistic contingency and the timing of target-events presented within the Conscious time-window outside the AB (black text) on the detection of constant target-events presented within the Unconscious time-window inside the AB (grey text).

using Analyzer software (v. 1.01; BrainVision system). Scalp topographies show voltages recorded at each electrode during time samples of 4 msec. The topographical maps reported in Figs. 7–9 shows the voltages recorded at the time point corresponding to the peak of each component and were obtained averaging EEG activity from Lag 2–3–4 (labelled Inside Blink) and the activity from Lag 6 (labeled Outside Blink). The topographical maps depicting activity from single lags are reported in Supplementary Material (see Supplementary Fig. 1 and 2).

2.3.1. *ERPs related to seen versus unseen T2s*

Trials were included into averaging only if T1 was identified correctly (correct discrimination of T1s ranged between 96.5% and 97%). T2-related ERPs were averaged separately for seen and unseen T2s in each experimental lag (lags 2, 3, 4, 6, in Experiment 1; lags 2, 3, 4, 5, 6 and 7 in Experiment 2). In each participant, the ERPs components that were specifically related to the processing of Seen and Unseen T2s were isolated by subtracting the ERPs recorded in catch-trials in which T2s were absent from the ERPs recorded in trials in which T2s were present (i.e., Seen T2 minus Absent T2, Unseen T2 minus Absent T2). ERPs related to Absent T2s were averaged considering the entire sample of catch trials (i.e., 360) presented in the Fr and InFr experimental conditions. The waveforms resulting from these subtractions are assumed to reflect the selective processing of T2s (Sergent et al., 2005; Kranczioch, Debener, & Engel, 2003). As a supplementary control we also assessed whether the baseline EEG activity recorded during the sessions with Fr and InFr conditions of both experiments were equivalent. To this aim, we run a sample-by-sample *t*-test analysis (performed through Vision Analyzer software version 1.05) comparing the Grand-Averages of EEG activity related to catch-trials. No difference was found between the Fr and InFr sessions.

In line with previous investigations, the amplitudes of the different ERPs components were measured as mean activity values within corresponding component-related time windows (see Inline Supplementary Table 1). These time-windows were defined as follows. First, we individuated groups of at least 8 electrodes showing a significant deviation from the baseline on least ten consecutive 4 msec time samples (total time = 40 msec; Berchicci, Lucci, Pesce, Spinelli & Di Russo, 2012, Lucci, Berchicci, Spinelli, Taddei, & Di Russo, 2013; Sergent et al., 2005). In each 4 msec time sample the significance of deviation from the baseline was evaluated through *t*-test with a criterion of $p < .05$ (Sergent et al., 2005). Statistically defined *t*-maps that highlight scalp sites where ERPs component are significantly present, allows optimizing

the selection of electrodes pools (see Inline Supplementary Table 2). Second, for each component and each lag we established the intervals of significance using a point-by-point analysis according to Guthrie and Buchwald's criteria (see Guthrie & Buchwald, 1991). The latency of each ERPs component was obtained by averaging the individual peak latencies. Individual peaks were estimated by applying an automatic peak-detection algorithm (Vision Analyzer 1.05) and then verified through visual inspection.

The duration of a component corresponded to the time interval comprised between the peak and the offset of the component, i.e., the return of the component potential to the baseline (i.e., mean baseline voltage ±2 SD).

2.3.2. *Dipole localisation*

The estimation of the intracranial sources of ERPs components was carried out using the BESA 2000 system. We used the spatiotemporal source analysis of BESA that estimates location, orientation and time course of multiple equivalent dipolar sources by calculating the scalp distribution obtained for a given model (forward solution). This distribution was then compared to that of the actual ERPs. Interactive changes in sources location and orientation lead to minimization of residual variance between the model and the observed spatiotemporal distribution of the component in investigation. The three-dimensional coordinates of each dipole in the BESA model were determined with respect to the Talairach axes. In these calculations, BESA assumed a realistic approximation of the head (based on the MRI of 24 subjects). The possibility of interacting dipoles was reduced by selecting solutions with relatively low dipole moments with the aid of an "energy" constraint (weighted 20% in the compound cost function, as opposed to 80% for the residual variance). The optimal set of parameters was found in an iterative manner by searching for a minimum in the compound cost function.

3. Results

3.1. *Behavioral*

3.1.1. T1

Individual percentages of correct discrimination of T1s in the Pilot and in the ERPs study were analyzed through separate Experiment (1,2) × Experimental Condition (Fr, InFr) ANOVAs. These ANOVAs were run to compare Experiment 1 with Experiment 2, thus testing the influence of the Frequent (Fr) versus Infrequent (InFr) presentation and the temporal uncertainty of T2s occurring outside the AB on the detection of T1s. No statistical main effect or interaction was found in the Pilot study or in the ERPs study (All $F < 1$). These results show that experimental manipulations had no influence on detection of T1s. Mean percentages of correct T1 discrimination are reported in Table 1. A Study (Pilot, ERPs) × Experiment (1,2) × Experimental Condition (Fr, InFr) ANOVA showed no main effect or interaction for the factor Study, demonstrating that the results of the Pilot and ERPs study were comparable. In both studies accuracy of T1 discrimination was at ceiling.

Table 1 – Percentages of consciously detected T1s in Experiments 1 and 2 in the Pilot, ERPs and Pilot + ERPs study.

	Fr		InFr	
	Pilot	ERPs	Pilot	ERPs
Exp. 1	96.8	97.4	97.1	97.2
Exp. 2	97.3	96.9	97	97.1

3.1.2. *Early T2s presented inside the AB*

Individual percentages in the detection of early T2s that followed correct discrimination of T1s (see Fig. 2), were analyzed in a series of Experiment (1, 2) × Experimental Condition (Fr, InFr) × Lag (Lag 2, Lag 3, Lag 4) ANOVAs. T2s were detected more frequently in the InFr condition [Pilot study: $F(1,26) = 20.8$, $p < .001$; ERPs study: $F(1,30) = 40$, $p < .001$]. This result shows that paucity of late T2s outside the AB prompted redirection of conscious processing towards early T2s inside the AB. Most importantly, significant Experiment × Experimental Condition interactions were found [Pilot study: $F(1,26) = 4.9$, $p < .05$; ERPs study: $F(1,30) = 7.9$, $p < .008$]. These interactions were qualified by planned comparisons showing that compared to the Fr condition of Experiment 1, when the AB was at its highest level, in Experiment 2 detection of T2s inside the AB improved both in the Fr and InFr condition (Pilot study: Fr Exp 1 = 45% *vs* InFr Exp 1 = 65%; Fr Exp 1 = 45% *vs* Fr Exp 2 = 59%; Fr Exp 1 = 45% *vs* InFr Exp 2 = 66%; ERPs study: Fr Exp 1 = 47% *vs* InFr Exp 1 = 68%; Fr Exp 1 = 47% *vs* Fr Exp 2 = 60%; Fr Exp 1 = 47% *vs* InFr Exp 2 = 68%; all comparisons $p < .005$). The same comparisons highlighted no difference in the detection of T2s was present among the InFr condition of Exp1 and the Fr and InFr conditions of Exp 2 (all comparisons, p = n.s.). Finally, a significant main Lag effect was found [Pilot study: $F(2,52) = 91.2$, $p < .0001$; ERPs study: $F(2,60) = 104$, $p < .0001$]: this showed improved detection of T2s at later lags (Pilot study: Lag 2 = 45%, Lag 3 = 60%, Lag 4 = 72.2%; ERPs study: Lag 2 = 47.3%, Lag 3 = 62.6%, Lag 4 = 74.3%, all between-lags comparisons $p < .001$). A Study (Pilot, ERPs) × Experiment (1, 2) × Experimental Condition (Fr, InFr) × Lag (Lag 2, Lag 3, Lag 4) ANOVA showed no main effect or interaction for the factor Study.

3.1.3. *Late T2 presented outside the AB*

Detection of late T2s presented at Lag 6, that was the only Lag shared by Experiment 1 and Experiment 2 outside the AB (see Fig. 2), was analyzed through a series of Experiment (1,2) × Experimental Condition (Fr, InFr) ANOVAs. A significant effect of Experiment was found [Pilot study: $F(1,26) = 32$, $p < .001$; ERPs study: $F(1,30) = 18.4$, $p < .001$]. This shows that compared to Experiment 1, in Experiment 2 temporal uncertainty worsened the detection of late T2s (Pilot study: Exp 1 = 95.9%, Exp 2 = 84.5%; ERPs study: Exp 1 = 96.3%, Exp 2 = 83.5%; Fig. 2A). A Study (Pilot, ERPs) × Experiment (1,2) × Experimental Condition (Fr, InFr) ANOVA showed no effect or interaction for the factor Study. Since in the two experimental conditions the percentages of T2s were calculated from samples of different trials numerosity (i.e., 288

trials in the Fr condition and 72 trials in the InFr one), as a further control we repeated the series of ANOVAs using the *arcsine* transformation of percentage data (Sheskin, 2003). This new series of ANOVAs confirmed the results of previous analyses.

3.1.4. *T2 detection as a function of Lag*

We checked further the results obtained in the previous separate assessments of T2 detection Inside and Outside the AB, by investigating the course of T2 detection as a function of Lag in a series of Experiment (1, 2) × Experimental Condition (Fr, InFr) × Lag (Lag2, Lag3, Lag4, Lag6) ANOVA. A significant Lag effect was found [Pilot study: $F(3,78) = 155.9$, $p < .0001$; ERPs study: $F(3,90) = 126.5$; $p < .0001$]. This showed a progressive improvement in the detection of T2s as a function of Lag length (Pilot study: Lag 2 = 45%; Lag 3 = 60%; Lag 4 = 72.2; Lag 6 = 90.2%; ERPs study: Lag 2 = 47.3%; Lag 3 = 62.6%; Lag 4 = 74.3%; Lag 6 = 89.9%; all between-lags comparisons $p < .001$). Most importantly, significant Experiment × Experimental Condition × Lag interactions were found [Pilot study: $F(3,78) = 2.5$, $p < .05$; ERPs study: $F(3,90) = 4.5$, $p < .01$]. Planned comparisons of the means showed that these interaction were due to worse detection of T2 at Lag 2,3 and 4 in the Fr condition of Experiment 1 when the AB was maximal and worse detection of T2 at Lag 6 in Experiment 2 when the timing of T2s presented outside the AB was uncertain. A control Study (Pilot, ERPs) × an Experiment (1, 2) × Experimental Condition (Fr, InFr) × Lag (Lag2, Lag3, Lag4, Lag6) ANOVA showed that all these results were comparable between the Pilot and ERPs study. The same results were obtained using the *arcsine* transform of percentage data (Sheskin, 2003). In summary, the results of these analyses replicate the main findings obtained through the separate assessment of performance Inside and Outside the AB.

3.2. *Sensitivity and response bias in the detection of T2s*

We used Signal Detection Theory (SDT) to test whether the different rate of T2s presented in the different experimental conditions determined changes in sensitivity and response bias. In fact, one possible explanation for the improvement of the AB in the InFr experimental condition of Exp 1 and 2 is that in this condition the overall rate of T2s was lower than in the Fr condition and participants more likely to respond "T2 present". Although this explanation is directly contradicted by the finding that in Exp 2 the AB equally improved both in the Fr and InFr condition, that is independently from the rate of T2s, it is still important to test whether changes in the AB are systematically linked to changes in detection sensitivity and response bias. To this aim, we compared raw visibility ratings in trials with T2s present (i.e., seen responses = Hits, H) with those observed in catch trials with no T2s present [i.e., seen responses to absent stimuli = False Alarms (FA)] and calculated indexes of detection sensitivity [d' = z(H)−z(FA)] and bias [$B_{ln} = -d'^{*} \frac{z(H)+z(FA)}{2}$] using the SDT. Individual d' and B observed in the Pilot and in the ERPs study were analyzed through a series of Experiment (1, 2) × Experimental Condition (Fr, InFr) × Lag (2,3,4,6) ANOVAs. Individual percentages of H and FA were entered in a series of Experiment (1, 2) × Experimental Condition (Fr, InFr) ANOVAs. The factor

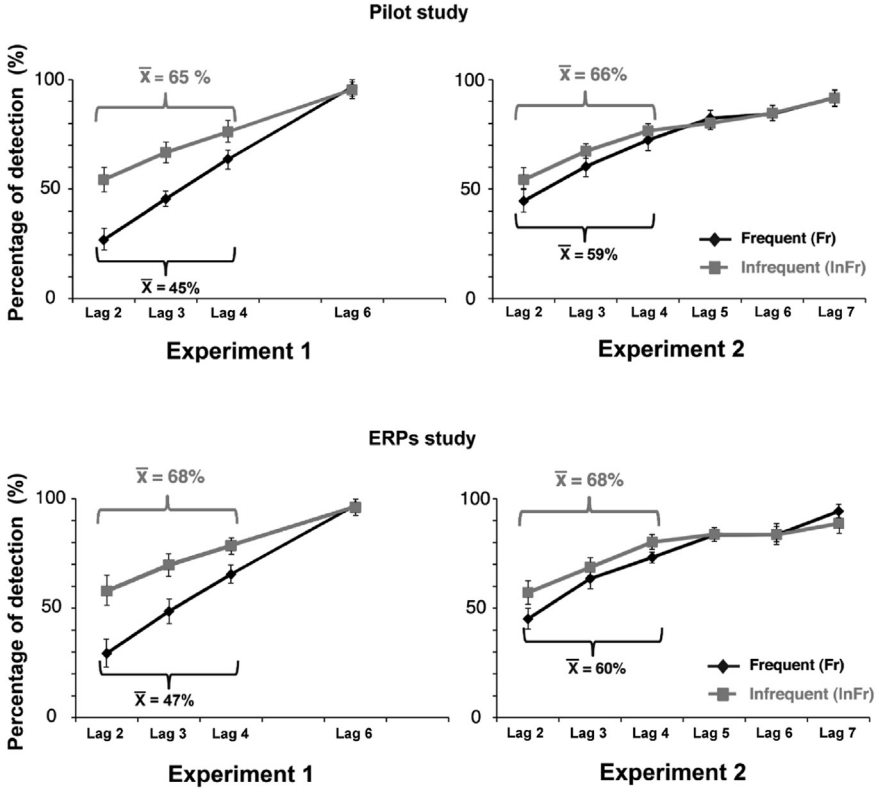

Fig. 2 – Percentages of consciously detected T2s in Experiment 1 and 2 (lags 5 and 7 were not used in Experiment 1) in the Pilot (A), ERPs (B) and Pilot + ERPs (C) study. Error bars = s.e.

Lag was not considered in the analysis of Hits because this would have just replicated the analyses presented for the assessment of T2 detection as a function of Lag. The factor Lag was also not considered in the analysis of FA because FA cannot be assigned to a specific Lag.

3.2.1. *d'*

In the Pilot study (Fig. 3), sensitivity increased as a function of Lag [$F(3,78) = 165.5$, $p < .0001$]. A significant Experiment × Lag interaction [$F(3,78) = 28$, $p < .0001$] was qualified by higher sensitivity outside the AB in Experiment 1 (Lag 6: planned comparison, $p < .001$), when the timing of T2s presented outside the AB was fixed. Finally, a significant Condition × Lag interaction [$F(3,78) = 7.8$, $p < .001$] was qualified by higher sensitivity in the InFr condition inside the AB (Lags 2–4: all planned comparisons $p < .02$).

In the ERPs study (Fig. 3), all these results were replicated ([Main effect of Lag: $F(3,90) = 139.9$, $p < .0001$; Experiment × Lag interaction: $F(3,90) = 22.3$, $p < .0001$; Experimental Condition × Lag interaction: $F(3,90) = 14.8$, $p < .0001$]. In addition a significant Experiment × Experimental Condition × Lag interaction was found [$F(3,90) = 3.6$, $p = .016$]. Planned comparisons showed that this interaction was due to important changes in sensitivity inside and outside the AB. Inside the AB sensitivity was lower in the Fr condition of Exp 1 as compared to all other conditions of both experiments (all planned comparisons $p < .003$ at Lag 2 and $p < .05$ at Lag 3). No equivalent differences in sensitivity were present al Lag 4. Outside the AB, changes in sensitivity were clearly modulated by the combination of probabilistic contingency and temporal predictability of T2s: sensitivity was at its lowest level in the InFr condition of Exp 2 (i.e., when T2s were rare and unpredictable in time), increased in the Fr condition of the same experiment (when T2s were frequent though unpredictable in time), increased further in the InFr condition of Exp 1 (when T2s were infrequent but predictable in time) and reached its maximum level in the Fr condition of Exp 1 (when T2s were both frequent and predictable in time; all planned comparisons $p < .03$).

A control Study (Pilot, ERPs) × Experiment (1, 2) × Experimental Condition (Fr, InFr) × Lag (2,3,4,6) ANOVA that all these results were comparable between the Pilot and ERPs study.

3.2.2. *Bias*

In the Pilot study (Fig. 3) the Bias decreased as a function of Lag [$F(3,78) = 75.3$, $p < .0001$]. Planned comparison showed that this decrease started from Lag 3 onwards (i.e., planned comparisons between Lag 2 and 3: $p =$ n.s.; other comparisons $p < .05$). A significant Experiment × Lag interaction [$F(3,78) = 17.1$; $p < .0001$] was also present. This was qualified by planned comparisons (all $p < .001$) showing that while in Exp 1 participants were generally less conservative, had a bias toward "target absent" responses, outside (Lag 6) than inside the AB (Lags 2,3,4), in Exp 2 they started to be less conservative from Lag 4 onwards (Lag 2 and 3 *vs* Lag 4: $p < .05$; Lag 4 *vs* Lag 6: $p < .01$). The Experimental condition × Lag interaction was also significant [$F(3,78) = 4.7$; $p = .004$]. Planned comparisons showed that at Lag 2 the bias was equivalent between the Fr and InFr condition while at the remaining Lags it was generally higher in the Fr condition (all $p < .001$).

In the ERPs study (Fig. 3) a similar main Lag effect [$F(3,90) = 138$, $p < .0001$] and a similar Experiment × Lag interaction [$F(3,90) = 26.7$, $p < .0001$] were found. In addition, a main effect of Experimental Condition showed that participants were more conservative in the Fr condition [$F(1,30) = 4.6$; $p = .03$; Fr = 2.37, InFr = 1.14].

A Study (Pilot, ERPs) × Experiment (1, 2) × Experimental Condition (Fr, InFr) × Lag (2,3,4,6) ANOVA showed that all results were comparable between the Pilto and ERPs study.

3.2.3. *Hits (H) and FA*

Both in the Pilot and ERPs study the rate of Hits was equivalent across the different Experiments and Experimental conditions (All $F < 2$, $p =$ n.s; Fig. 4). A Study (Pilot, ERPs) × Experiment (1, 2) × Experimental Condition (Fr, InFr) ANOVA showed no main effect or interaction for the factor Study.

As regards with FA a significant "Experiment × Experimental condition" interaction was present in the ERPs [$F(1,30) = 4.3$, $p < .05$] whereas in the Pilot study no equivalent interaction was found [$F(1,22) = .5$, $p =$ n.s.]. Post-hoc comparisons showed that this interaction was accounted by a higher rate of FA in the InFr condition of Experiment 2 (see Fig. 4). This result points at a double dissociation between the rate of FA and the improvement in the AB: the rate of FA was equivalent in the Fr and InFr conditions of Exp 1 when the AB improved in the InFr condition, while a higher rate of FA was present in the InFr condition of Exp 2 when the AB improved both in the Fr and InFr condition. A Study (Pilot, ERPs) × Experiment (1, 2) × Experimental Condition (Fr, InFr) ANOVA showed no significant main effect or interaction for the factor Study.

3.3. *Testing the influence of learning effects on the AB*

In a first series of control analyses we tested whether the order in which the Fr and InFr conditions were administered had an influence on the AB. A series of Experiment (1,2) × Experimental Condition (Fr, InFr) × Session Order (InFr First, Fr First) × Lag (Lag 2, 3, 4, 6) ANOVAs showed no main effect or interaction involving the Session order factor (All $F < 2$). This shows that performance in the Fr and InFr conditions did not depend on the order in which these conditions were administered.

In a second series of analyses we tested whether due to learning effects the AB changed between the first and second half of experimental sessions. Individual percentages of T2s detected inside the AB were entered in a series of Experiment (1,2) × Experimental Condition (Fr, InFr) × Part of Session (First half, Second half) × LAG (Lag 2, 3, 4, 6) ANOVAs. No significant main effect or interaction was found for the factor Part of Session (All $F <$ or $= 1$; Pilot study: First half = 63%, Second half = 62%; ERPs study First half = 66%, Second half = 64%). This shows that both in Experiment 1 and 2, changes in the AB were already set within the first half of the task.

Similarly, we also checked whether detection of late T2s presented outside the AB (Lag 6 in the Fr and InFr condition) changed as a function of the Part of Session. A series of Experiment (1, 2) × Experimental Condition (Fr, InFr) × Part of Session (First half, Second half) ANOVAs showed no

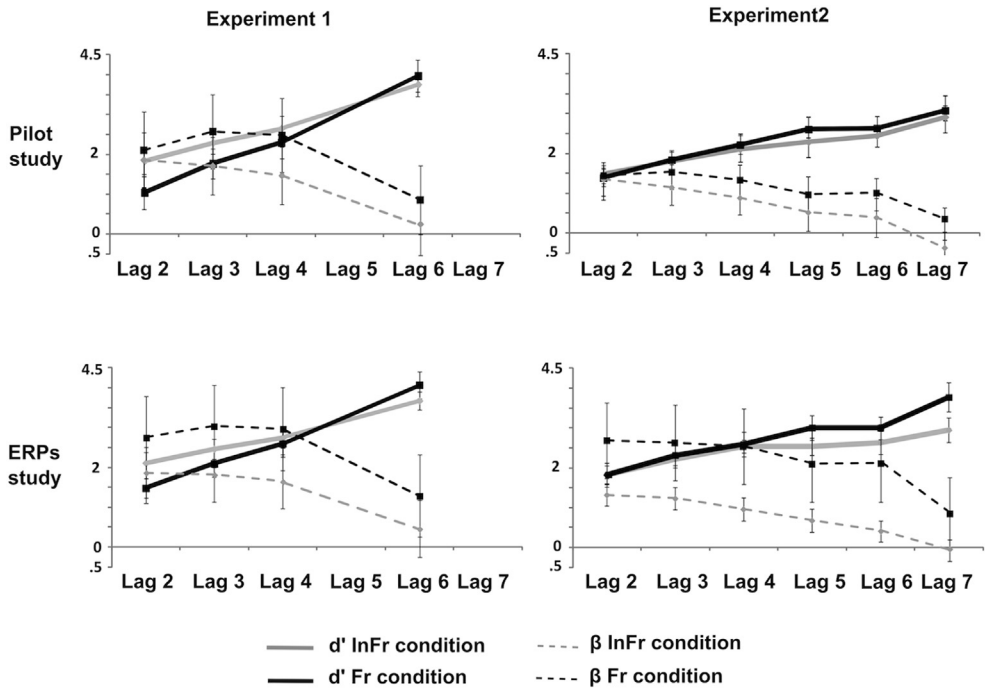

Fig. 3 – d' and Beta (natural log, ln) values observed at the different Lags in the Pilot Study, ERPs Study and Pilot + ERPs Study. Error bars = s.e.

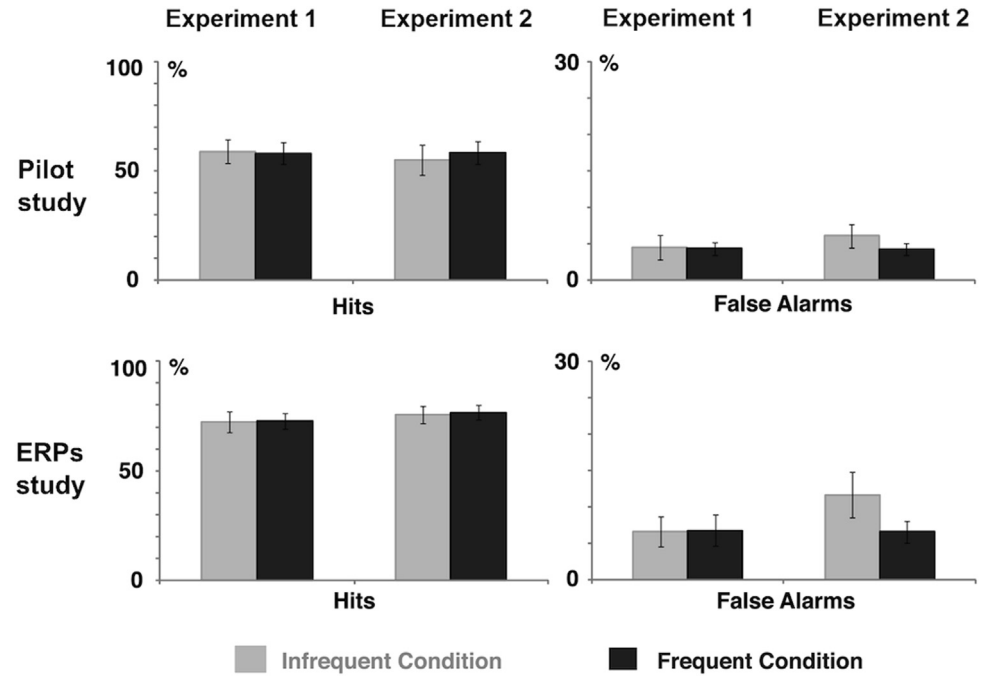

Fig. 4 – Overall Hit (A) and False Alarm (B) rates observed in the two experimental behavioral conditions (Infrequent *vs* Frequent presentation of T2s outside the AB) in the Pilot Study, ERPs Study and Pilot + ERPs Study. Error bars = s.e.

significant effect or significant interaction involving the factor Part of Session (All $F < \text{or} = 1$; Pilot study: First half = 92%, Second half = 91%; ERPs study: First half = 88%, Second half = 87%).

All these ANOVAs were repeated taking also into account the factor Study (Pilot, ERPs): no main effect or interaction was found for this factor. Due to the paucity of trials presented in each half of the AB task, we did not run the same analysis on ERPs data.

4. Electrophysiological

4.1. T1-related ERPs

A series of Experiment (1,2) × Experimental Condition (Fr, InFr) × Electrode Position (Left, Right and Central) ANOVAs were used to evaluate the effects of experimental manipulations on the amplitude and latency of T1-evoked P1, N1, N2, P3a and P3b ERPs components. Due to their the typical scalp topographic distribution, the analysis of the P3a and P3b components was run considering also the anterior versus posterior position of electrode derivations. No significant main effect or interaction was found in the amplitude and latency of all components, showing no effect of experimental manipulations on T1-related ERPs (All $F < 1$).

Importantly, we also investigated whether detection of early T2s inside the AB was linked to modifications in the amplitude and latency of T1-related P1, N1, N2, P3a and P3b ERPs components. To this aim, for each component we ran an Experiment (1,2) × Experimental Condition (Fr, InFr) × Electrode Position (Left, Right and Central) × Detection of Early-T2s (Seen, Unseen) ANOVAs. No main effect or interaction was found (All $F < 1$): this shows that detection of T2s inside the AB was not dependent on changes in the processing of preceding T1s (Tables 2A and 2B).

4.2. T2-related ERPs

4.2.1. Early T2s presented inside the AB

To investigate the neural signatures of the AB, we compared ERPs related to Seen T2s (i.e., Seen T2-minus Absent T2-related ERPs) *vs* Unseen T2s (i.e., Unseen T2-minus Absent T2-related ERPs). We ran a series of Experiment (1,2) × Detection (Seen, Unseen) × Experimental Condition (Fr, InFr) × Lag (Lag 2, Lag 3, Lag 4) × Electrode Position (Left, Right and Central) ANOVAs, on the amplitude and latency of T2s-related P1, N1, N2, P3a and P3b ERPs components. For P3a and P3b components we also considered the anterior versus posterior position of electrodes. No significant difference was found in the amplitude and latency of early P1 and N1 components related to seen versus unseen T2s (All $F < 1$). In contrast, the amplitude of the N2, P3a and P3b components was always larger for seen versus unseen T2s [N2: $F(1,30) = 32.8$, $p < .0001$, seen = −1.25 μV *vs* unseen = −.349 μV; P3a: $F(1,30) = 11.5$, $p < .001$; seen = 2.12 μV *vs* unseen = 1.07 μV; P3b: $F(1,30) = 17.7$, $p < .001$, seen = 2.59 μV *vs* unseen = 1.53 μV, Fig. 5]. These results replicate previous findings by Sergent et al. (2005).

4.2.2. Changes in the AB due to experimental manipulations

The electrophysiological correlates of AB changes induced by manipulation in the probability of occurrence and the timing of T2s presented outside the AB, were explored by analyzing ERPs related to Seen-T2s (i.e., averaged Seen T2-related minus Absent T2-related ERPs), through a series of Experiment (Exp1, Exp2) × Lag (Lag 2, Lag 3, Lag 4), Experimental Condition (Fr, InFr) × Electrode Position (Left, Right and Central) ANOVAs.

4.2.2.1. P1 and N1. No effect or interaction was found for both latency and amplitude of the P1 and N1 components (All $F < 1$).

4.2.2.2. N2. The analysis of the N2 amplitude revealed a significant Experiment (Exp1, Exp2) × Experimental Condition (Fr, InFr) interaction [$F(1,30) = 4.9$, $p = .03$]. This showed that the amplitude of the N2 was lower in the Fr condition of Experiment 1, when the AB was maximal, compared to all other conditions of both experiments (Planned comparisons: Fr Exp 1 = −.7 μV *vs* InFr Exp 1 = −1.49 μV, $p = .02$; Fr Exp 1 = −.7 μV *vs* Fr Exp 2 = −1.50 μV, $p = .02$; Fr Exp 1 = −.7 μV *vs* InFr Exp 2 = −1.26 μV, $p < .05$; see Fig. 6). The amplitude of the N2 was not different between the Fr and InFr conditions of Exp 2 (Fr Exp 2 = −1.50 μV *vs* InFr Exp 2 = −1.26 μV, $p = .44$). No main effect or interaction of the Lag effect was found (All $F < 1$), showing that in all experimental conditions the amplitude of N2 remained constant throughout the AB period. This finding suggests that the N2 does not suffer from the concurrent processing of T1.

The same result was also found for the duration of the N2 component, that was reduced in the Fr condition of Experiment 1 when the AB was maximal [$F(1,30) = 7.4$; $p = .01$; Planned comparisons: Fr Exp 1 = 48.4 msec *vs* InFr Exp 1 = 58.8

Table 2 – (A) Averaged peak latency (msec) and (B) averaged mean amplitude (μV) of T1-related ERPs components preceding Seen and Unseen T2s presented inside the AB in the Frequent and Infrequent experimental conditions.

Exp 1					Exp 2			
	Cond Fr		Cond Infr		Cond Fr		Cond Infr	
	Seen	Unseen	Seen	Unseen	Seen	Unseen	Seen	Unseen
A								
P1	112	101	126	126	118	118.5	121	121
N1	138	145	143	139	143	132	142	145
N2	217	219.5	215	215	218	211	215	214
P3a	330	322.8	323	311	329	333.3	317	321
P3b	425	422	423	422.6	419	420	411	423
B								
P1	1.29	1.11	0.88	0.84	0.66	0.75	0.9	0.82
N1	−0.18	−0.22	−0.5	−0.48	−0.27	−0.32	−0.6	−0.58
N2	−1.19	−0.73	−1.69	−1.4	−1.04	−1.05	−1.35	−1.12
P3a	1.92	2	2.24	1.61	3.06	2.78	2.5	2.66
P3b	1.9	2.06	1.47	1.57	1.94	1.8	1.8	1.58

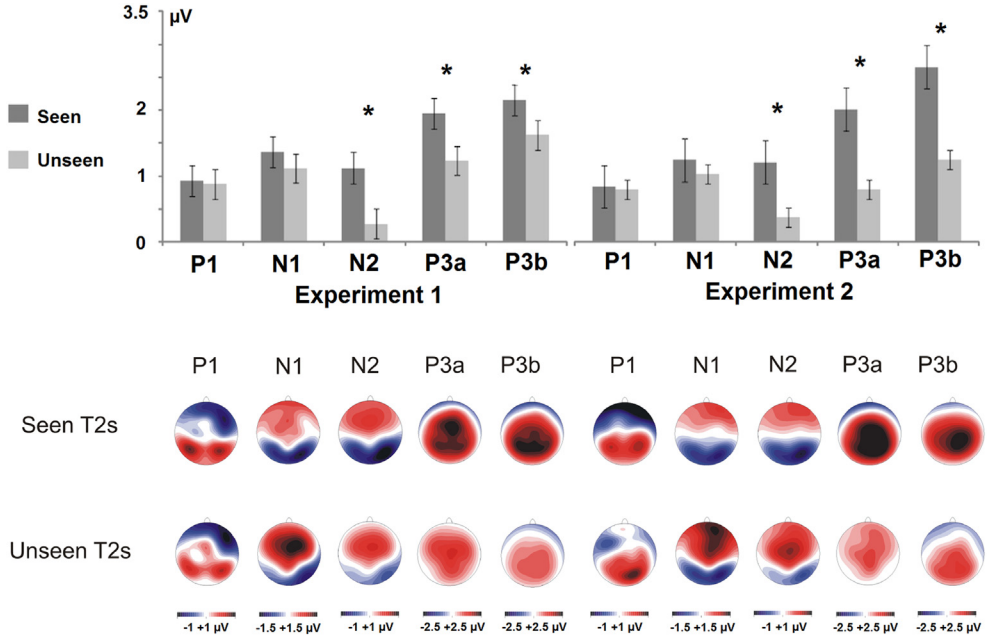

Fig. 5 – (A) Amplitude (μV) of ERPs components related to Seen and Unseen T2 in Experiment 1 and 2. Error bars = s.e. (B) Scalp topographies showing P1, N1, N2, P3a and P3b components related to seen and unseen T2s in Experiment 1 and 2.

msec, $p = .01$; Fr Exp 1 = 48.4 msec *vs* Fr Exp 2 = 66.8 msec, $p < .001$; Fr Exp 1 = 48.4 msec *vs* InFr Exp 2 = 61.5 msec, $p = .003$; See Fig. 7A and Inline Supplementary Fig. 1]. Crucially to the aim of our study, these results show that the basic and earliest electrophysiological correlate of improved detection of T2s inside the AB was an enhancement in the amplitude and duration of the N2 wave signaling pre-conscious storage of visual traces in extra-striate cortex (Sergent et al., 2005). No main effect or interaction was found for the Lag factor (All $F < 1$).

Topographical mapping of the N2 showed a bilateral distribution focusing on lateral occipital areas (Sergent et al., 2005), quite similar in the different experimental conditions (Fig. 6B). Based on the timing and the bilateral distribution the N2, dipole analysis was fit in the 200–250 msec time windows with a symmetrical pair of sources. The analysis localized the origin of the N2 in the fusiform gyrus (Bledowski et al., 2004; Sergent et al., 2005, Fig. 7B–D).

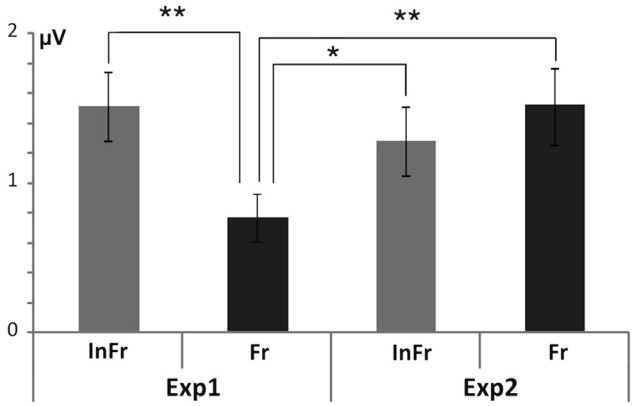

Fig. 6 – Mean amplitude (μV) of the N2 component recorded in the Infrequent and Frequent experimental conditions of Experiment 1 and 2. Error bars = s.e.; $^{**}p = .02$, $^{*}p < .05$.

4.2.2.3. P3a. The augmented amplitude and duration of pre-conscious storage signaled by the N2 wave, increased the number of trials in which the trace of early T2 was still available for conscious processing at the end of T1 processing. In both experiments, this was associated with an increased latency of the ensuing and anteriorly centered P3a wave, signaling access of the sensory trace to the parietal-frontal network modulating conscious processing (Del Cul, Baillet, & Dehaene, 2007; Polich, 2007). In fact, compared to all other experimental conditions, the latency of the P3a component was shorter in the Fr condition of Experiment 1, when the AB was maximal [Experiment (Exp1, Exp2) × Experimental Condition (Fr, InFr) interaction: $F(1,30) = 103.3$, $p < .001$; Planned comparisons: Fr Exp 1 = 424 msec *vs* InFr Exp 1 = 457 msec, $p < .001$; Fr Exp 1 = 424 msec *vs* Fr Exp 2 = 438 msec, $p < .001$; Fr Exp 1 = 424 msec *vs* InFr Exp2 = 434 msec, $p < .001$]. No corresponding amplitude differences were observed. See Fig. 8A and Inline Supplementary Fig. 2A.

The only significant effect revealed by the analysis of the P3a amplitude was its increase across Lags [$F(2,60) = 12.9$, $p < .0001$]. Planned comparisons showed that the amplitude was lower at Lag 2 (1.19 μV) than at Lag 3 (2.3 μV; planned comparison $p < .001$) and Lag 4 (2.87 μV; planned comparison $p < .001$). No difference was found between Lag 3 and Lag 4 (planned comparison p = n.s.). These results highlight a difference between Lag2, when T2 detection was below or at chance level, and Lags 3 and 4 when average T2 detection was above chance. This finding suggests that the T2-related P3a component is affected by competitive conscious processing of T1 and reduced when T2s are presented at lags that are close to T1 (Sergent et al., 2005).

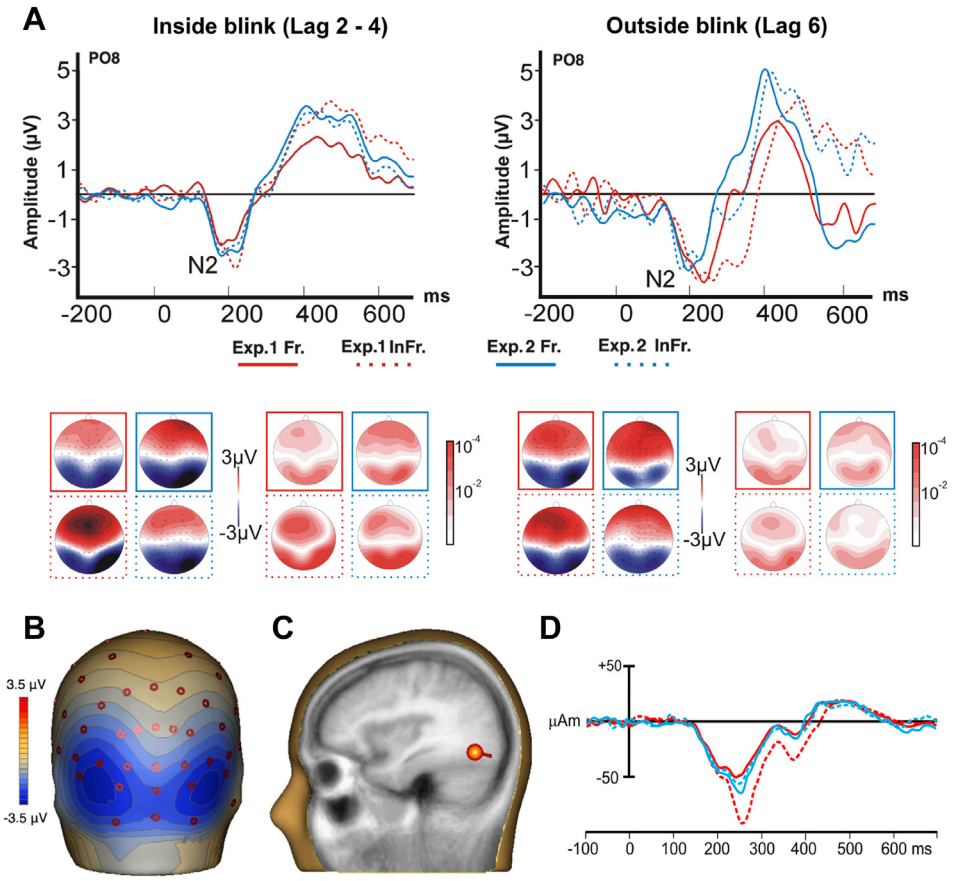

Fig. 7 – (A) T2-related N2 component recorded at different time lags from T1 in Experiment 1 (red lines) and Experiment 2 (blue lines) and corresponding voltage scalp topographies and T probability maps recorded at N2 peak. Inside Blink topographical maps were obtained averaging EEG activity recorded at Lags 2,3 and 4. Outside Blink maps derived from the EEG activity recorded at Lag 6. Continuous lines = Frequent presentation of T2 outside the AB; dashed lines = Infrequent presentation of T2 outside the AB. Inside the AB (lags 1 to 3), N2 and P3b are smaller in the Frequent condition of Experiment 1, where AB is maximal compared to all others experimental conditions. (B) 3D voltage scalp map of the N2 component (C) Dipole origin of the N2 component in the extrastriate cortex-fusyform gyrus (Talairach coordinates: Experiment 1- Frequent condition ±34, −69, −11, Infrequent condition ±32, −66, −9; Experiment 2 – Frequent condition ±38, −64, −10, Infrequent condition ±35, −63, −6). (D) Source time course of N2 generators in the different experimental condition of Experiments 1 and 2.

Topographical mapping of the P3a showed a peak of activity on the frontal-parietal cortex (Fig. 5B; Knight & Scabini, 1998; Polich, 2007; Sergent et al., 2005). Based on the timing and the cortical distribution of the P3a, dipole analysis was fit in the 410–460 msec time window with a symmetrical pair of sources. The analysis localized the origin of the P3a wave at the junction between the pre-central (Ba 6) and the inferior frontal gyrus (Ba 44; Fig. 8B–D; Bledowsy et al., 2004; Sergent et al., 2005).

4.2.2.4. P3b. Similar to the N2 wave, the reduction of the AB (InFr condition Experiment 1, InFr and Fr condition Experiment 2) was matched with enhanced amplitude of the posteriorly centered P3b component, signaling matching of the sensory trace with target representation in working memory, [Experiment (Exp1, Exp2) × Experimental Condition (Fr, InFr) interaction: $F(1,30) = 4.5$, $p = .04$; Planned comparisons: Fr Exp 1 = 1.18 μV *vs* InFr Exp 1 = 3.12 μV, $p = .005$; Fr Exp 1 = 1.18 μV *vs* Fr Exp 2 = 3.05 μV, $p = .007$; Fr Exp 1 = 1.18 μV *vs* InFr Exp 2 = 3.02 μV, $p = .008$; Fig. 9A and Inline Supplementary Fig. 2B]. Interestingly, in the two experiments we found different effects on the latency of the P3b. In Experiment 1, as in the case of P3a, improved detection of T2s inside the AB (InFr condition) was matched with increased latency of the P3b [$F(1,15) = 4.9$, $p = .04$]. In contrast, in Experiment 2, improved detection of T2s inside the AB (InFr and Fr conditions) was matched with a general reduction in the latency of P3b [$F(1,30) = 35.5$, $p < .001$]. An Experiment (Exp1, Exp2) × ERPs Component (P3a, P3b) ANOVA demonstrated that in Experiment 2 the P3b became virtually simultaneous to the P3a (Experiment × ERPs component interaction: $F(1,30) = 25$, $p < .001$; P3a Exp1 = 440 msec *vs* P3b Exp1 = 472 msec, $p < .001$; P3a Exp2 = 436 msec *vs* P3b Exp2 = 436 msec, $p =$ n.s.; Inline Supplementary Fig. 3A and B). This suggests that uncertainty

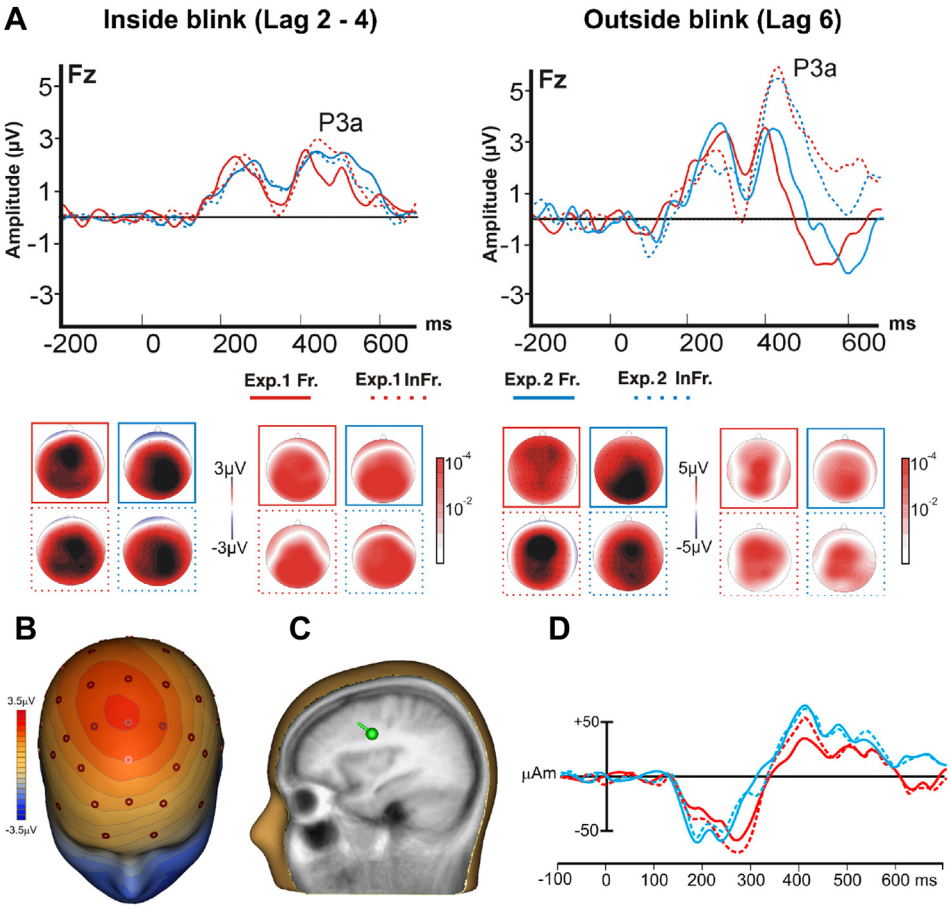

Fig. 8 – (A) ERPs results. T2-related P3a component recorded in Experiment 1 (red lines) and Experiment 2 (blue lines) and corresponding voltage scalp topographies and T probability maps recorded at P3a peak. Inside Blink topographical maps were obtained averaging EEG activity recorded at Lags 2,3 and 4. Outside Blink maps derived from the EEG activity recorded at Lag 6. Inside the AB, P3a latency is smaller when AB is maximal (i.e., continuous red line = Frequent presentation of T2s outside the AB). Outside the AB, P3a is higher for infrequently presented targets (i.e., dashed lines) revealing a "novelty" effect. (B) 3D voltage scalp map of the P3a component (C) Dipole origin of the P3a component in the Precentral-Inferior Frontal Gyrus (Talairach coordinates: +35, −4, 32; −35, −4, 32). (D) Source time course of P3a generators in the different experimental conditions of Experiment 1 and 2.

in the timing of upcoming conscious stimuli promotes synchronization in the activity of the anterior generators of the "novelty"-related P3a component and the posterior generators of the P3b (Knight & Scabini, 1998). No equivalent change was observed in T1-related ERPs.

As for the case of the P3a, the amplitude of the P3b changed across Lags [$F(2,60) = 6,69$, $p < .001$]. The P3b amplitude was lower at Lag 2 (1.87 μV) as compared with Lag 3 [2,75 μV, $p < .01$) and Lag 4 (3,15 μV, $p < .0001$]. No difference was found between Lag 3 and Lag4 (P = n.s). This result can be interpreted along the lines proposed for the P3a.

Topographical mapping of the P3b showed a peak of activity on the occipital-parietal cortex (Fig. 9A; Sergent et al., 2005). Based on the timing and the cortical distribution of the P3b, dipole analysis was fit in the 390–550 msec time windows with a symmetrical pair of sources. The analysis localized the origin of the P3b in the fusiform gyrus (Bledowsky et al., 2004), slightly above the location of the N2 dipole (Fig. 9B, 9C and 9D).

4.2.3. *Late T2s presented outside the AB*

Due to the paucity of unseen T2s at Lag 5, 6, and 7 in both Experiment 1 and 2, corresponding ERPs components were not analyzed. However, we ran a series of Experiment (Exp1, Exp2) × Experimental Condition (Fr, InFr) × Electrode Position (Left, Right and Central) ANOVAs, to study the effects of experimental manipulations on ERPs related to consciously detected T2s outside the AB (i.e., Seen T2-related minus Absent T2-related ERPs). We only considered T2s presented at Lag 6, because this was the only Lag shared by Experiment 1 and 2. The only relevant effect disclosed by this series of ANOVAs, was the enhancement in the amplitude of the P3a component in the InFr condition of both Experiment 1 and 2 [$F(1,30) = 4.59$, $p < .05$; latency: $F(1,30) = 36.9$; $p < .001$; Fig. 8 and

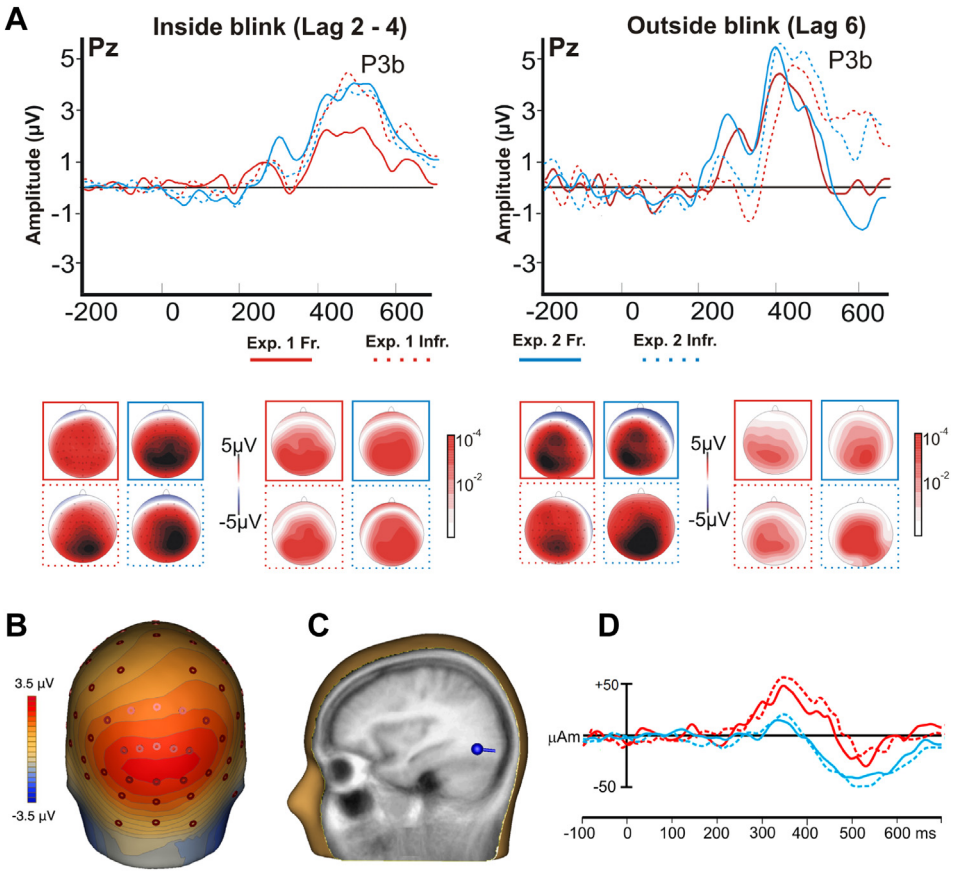

Fig. 9 – (A) T2-related P3b component recorded at different time lags from T1 in Experiment 1 (red lines) and Experiment 2 (blue lines) and corresponding voltage scalp topographies and T probability maps recorded at P3b peak. Inside Blink topographical maps were obtained averaging EEG activity recorded at Lags 2,3 and 4. Outside Blink maps derived from the EEG activity recorded at Lag 6. Continuous lines = Frequent presentation of T2 outside the AB; dashed lines = Infrequent presentation of T2 outside the AB. Inside the AB (lags 1 to 3), N2 and P3b are smaller in the Frequent condition of Experiment 1, where AB is maximal compared to all others experimental conditions. (B) 3D voltage scalp map of the P3b component (C) Dipole origin of the P3b component in the extrastriate cortex-fusyform gyrus (Talairach coordinates: +32, −68, −8; −32, −68, −8). (D) Source time course of P3b generators in the different experimental conditions of Experiment 1 and 2.

Inline Supplementary Fig. 2A]. This effect is explained by the novelty reaction triggered by the rare appearance of T2s in the InFr condition (i.e., 20% of trials).

5. Discussion

5.1. *Behavioral and psychophysical findings*

The results of our investigation show that in observers who are not explicitly informed on the frequency of occurrence and the timing of T2s, the access to awareness of T2s presented inside the AB is relatively improved when T2s occurring outside the AB are infrequent or characterized by uncertain timing and relatively worsened when T2s outside the AB are frequent and predictable in time. This was clearly observed both in a Pilot behavioral study and in an ensuing study, run on different participants, in which behavioral measures were associated with recording of ERPs. By showing that the predictability of T2 occurrence outside the AB improves conscious processing of T2s presented at different time points inside the AB, these results expand on previous evidence demonstrating that cuing the time point of T2s presentation inside the AB improves conscious processing of T2s presented at that time point (Choi et al., 2012; Martens & Johnson, 2005; Shen & Alain, 2011; 2012; Tang et al., 2014; Visser et al., 2014). Importantly, our findings also expand on the results of a previous study (Martens & Johnson, 2005) that, probably due to the limits in the experimental design previously discussed in the introduction, did not highlight the modulation of the AB effect disclosed in our investigation. Along with previous evidence (for review Nobre, Correa, & Coull, 2007), also in our study the above-chance detection of T2s presented outside the AB was higher when these appeared at fixed (Experiment 1) rather than variable timing (Experiment 2).

At first sight the finding that loose timing of late conscious T2s promotes awareness of usually unseen earlier T2s, seems

at odds with evidences showing that timing regularities favor the processing of upcoming stimuli by finely tuning the representation of elapsed time in multimodal and visual areas (Bueti, Bahrami, Walsh, & Rees, 2010; Genovesio, Tsujimoto, & Wise, 2006; Ghose & Maunsell, 2002; Leon & Shadlen, 2003; Nobre et al., 2007; Onoe et al., 2001; Rohenkohl, Cravo, Wyart, & Nobre, 2012). Nonetheless, one should consider that loose timing of upcoming stimuli might strategically broaden the focus of temporal expectation. This would correspond to flattening and enlarging the "hazard function" describing the subjective probability that a stimulus will occur at a specific time point, given that no stimulus has occurred before (Bueti et al., 2010; Leon & Shadlen, 2003; Nobre et al., 2007). Compared to sharp "hazard functions" peaking at a precise time point, broader functions might produce costs for the detection of stimuli presented at that point and benefits in the detection of stimuli presented at adjacent time points. In our study, this was precisely documented by the lower detection rate of T2s presented at lag 6 in Experiment 2, i.e., when outside the AB T2s also occurred at lags 5 and 7, as compared to Experiment 1 when outside the AB T2s were only presented at lag 6. Therefore, the widening of the attentional-temporal focus induced by timing uncertainty of T2s outside the AB might have encompassed T2s presented inside the AB, playing a crucial role in improving their conscious detection.

The results of our study also highlighted a clear functional predominance of predictive knowledge based on the timing of consciously detected T2s over predictive knowledge gathered from their probabilistic occurrence. In Experiment 1, T2s were presented at a fixed time lag outside the AB: in this case improved conscious detection of T2s inside the AB was only observed when T2s outside the AB were infrequent (i.e., Infrequent condition). In contrast, in Experiment 2, T2s were presented at varying and unpredictable time lags outside the AB: in this case detection of T2s inside the AB equally improved both when T2s outside the AB were frequent and infrequent. It is a matter for future studies investigating whether timing and probability of occurrence exert their predictive influence through different or partially shared functional and neural mechanisms.

Can the behavioral results of our study be attributed, more generically, to unmatched demands in responding to T2s between the Fr and InFr experimental condition so that, for example, in the InFr condition participants were less fatigued by responding less frequently and because of this T2s became more salient ? A fundamental objection to this hypotheses is that both in the Fr and InFr condition participants had to detect and respond both to the presence and the absence of T2 targets. This means that the two experimental conditions required equal attentional fatigue and an identical overall number of responses. A number of other findings also do not seem favoring the same hypothesis. First, by comparing the detection of T2s between the first and the second half of the task, we have directly assessed whether learning or fatigue effects affected performance inside and outside the AB: no learning or fatigue effect were found in the Fr and InFr condition both inside and outside the AB. Second, in Exp 1 different percentage detections of T2s were observed inside the AB in the Fr and InFr conditions notwithstanding an identical number of T2s (360 trials) was presented inside the AB in both conditions (see Fig. 2). Viceversa, no difference in the detection of T2s was found outside the AB when T2s were more frequent in the Fr (288 trials) than in the InFr condition (72 trials; see Fig. 2). This double dissociation runs directly against the possibility that the reduction of the AB could be linked to the different overall frequency of T2s in the Fr and InFr condition. This conclusion is supported further by the results of Exp 2 when, all experimental conditions and number of trials being equal to Exp 1, time uncertainty was introduced in the presentation of T2s outside the AB and, because of this, the task putatively required a higher attentional load/fatigue. In this case no difference in the detection of T2s was found between the Fr and InFr conditions both inside and outside the AB (see Fig. 2). It is particularly important to note that in the Fr condition, when participants might have been more fatigued by the frequent detection of T2s, the AB improved and reached the level of the AB observed in the InFr condition in Exp 1 and 2 (see Fig. 2). This proves, rather unequivocally, that the modulation of the AB was not merely linked to the numbers of T2s trials that were presented in the Fr or Infrequent condition. Finally, one could also conservatively consider whether in our experiments ceiling effects precluded the observation of significant differences outside the AB (note that Di Lollo and co-workers emphasised the relevance of this factor for the detection of backward-unmasked T2s presented inside the AB; see Jannati, Spalek, & Di Lollo, 2011). Also in this case our results lend poor support to this possibility because in Exp 2 a significant worsening in the detection of T2s was observed outside the AB as compared to Exp 1 (85% *vs* 95%, respectively; see Fig. 2-Lag 6, i.e., the only Lag shared by Exp 1 and 2). In addition, in Exp 2 percentage detection outside the AB was below ceiling both in the Fr and InFr condition (80% at lag 5 and 85% at Lag 6): this should have made visible the behavioral effects produced by experimental manipulations.

Analyses based on the SDT showed that sensitivity increased while bias decreased as a function of Lag length (for similar results see Charles et al., 2013). Inside the AB sensitivity was lower in the Fr condition of Exp 1, when the AB was at peak, as compared to all other conditions of both Experiments. Outside the AB sensitivity was at the highest level when T2s were frequent and predictable in time and at the lowest level when T2s were rare and unpredictable in time. Participants were more conservative, i.e., they provided "T2 absent" responses more frequently, in the Fr condition: nonetheless the adoption of a more conservative criterion was not linearly correlated to changes in the strength of the AB because in the Fr condition of Experiment 2 the AB was still significantly reduced in comparison to the Fr condition of Experiment 1, when AB reached its peak.

5.2. *Electrophysiological findings*

The conscious perception of a visual stimulus depends both on the strength of the stimulus trace in visual cortex and on the integrated activity of a network of parietal, prefrontal and cingulate areas (Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006; Gross Schmitz, Schnitzler, Kessler, Shapiro, Hommel, and Schnitzler, 2004; Kranczioch, Debener, Schwarzbach, Goebel, & Engel, 2005; Lamme, 2006;

Marcantoni, Lepage, Beaudoin, Bourgouin, & Richer, 2003; Marois, Yi, & Chun, 2004; Nakatani, Ito, Nikolaev, Gong, & van Leeuwen, 2005; Rees et al., 2000; Sergent et al., 2005;). A weak subliminal trace will remain confined to the visual cortex and inaccessible to conscious processing (Lamme, 2003; 2006; Dehaene et al., 2006). A stronger trace will transitorily reverberate in a pre-conscious storage in the extra-striate cortex, and will eventually emerge to consciousness if processing resources in parietal, prefrontal and cingulate areas will be available for re-routing the trace at multiple brain sites ahead of its decay (Chun & Potter, 1995; Sergent et al., 2005). Previous inquiries into the AB effect (Chun & Potter, 1995; Sergent et al., 2005; for review see Dux & Marois, 2009; Martens & Wyble, 2010) pointed out that conscious processing of a stimulus (T1) can run in parallel, along partially different neural pathways, with subliminal and pre-conscious processing of another concurrent stimulus (T2). The results of our study show that when the predicted occurrence of conscious visual stimuli is infrequent (i.e., InFr condition, Exp 1) or characterized by uncertain timing (i.e., Fr and InFr conditions, Exp 2), the brain amplifies the strength and duration of the pre-conscious sensory storage of T2s presented inside the AB. This is signalled by an increase in the amplitude and duration of the N2 wave in the extra-striate cortex. This, in turn, improves the possibility that the pre-conscious traces of stimuli that would have normally remained below the threshold of awareness have access to conscious processing. This result shows that the interaction between conscious and unconscious processing changes flexibly and adaptively as a function of the probabilistic organization of sensory inputs in the environment.

The finding of a link between the strength of pre-conscious processing of early T2s in the extra-striate cortex and their improved conscious detection agrees with data by Sligte, Scholte & Lamme (2008) showing that in humans the level of BOLD response recorded in V4 during the presentation and retention of a visual display, linearly predicts the conscious report of the same display from visual short term memory. According to these authors, V4 acts as an intermediate memory store located between the high-capacity/low-duration iconic store and the low-capacity/high-duration short-term memory one. Thanks to its connections with higher level cortical areas involved in spatial attention (Ungerleider, Galkin, Desimone, & Gattass, 2008), V4 is ideally suited to momentarily host visual information whenever attentional resources cannot immediately deployed to its processing.

The enhancement in amplitude and duration of the N2 wave related to seen T2s inside the AB, was followed by a corresponding increase in the latency of the anteriorly centered P3a component, that marks the transition of the sensory trace to the parietal-frontal network operating its redistribution at multiple brain sites. Variations in the probability of occurrence (Experiment 1) and in the timing (Experiment 2) of T2s presented outside the AB increased the latency of the P3a related to seen T2s inside the AB. This is compatible with data suggesting that transition of T2s traces from the preconscious buffer to the parietal-frontal processing network is only possible after completion of conscious T1 processing (Dell'Acqua et al., 2006; Sergent et al., 2005), so that longer maintenance of T2s' traces in the preconscious buffer, allows and delays, at the same time, their transition to consciousness. At variance with these findings, in the two experiments we have found different effects on the latency of the P3b component that signals the match of the sensory trace with target representation in memory (Polich, 2007). In Experiment 1, improved conscious processing of seen-T2s inside the AB was matched with increased latency of the P3b, whereas in Experiment 2 the latency of the P3b was reduced both inside and outside the AB, so that the P3b became simultaneous to the P3a. This finding might suggests that uncertainty in the timing of upcoming conscious stimuli speeds up the functional connectivity between the anterior generators of P3a and the posterior generators of the P3b (Knight & Scabini, 1998; Polich, 2007). In our study the P3a was sensitive to the novelty of targets, as demonstrated by its enhancement in response to infrequent T2s presented outside the AB (see Fig. 5). This might suggest that the reduction in the latency of the P3b is accountable on the novelty signals conveyed by the P3a. This, however, does not seem to be an entirely satisfactory explanation, because the latency of the P3b was also reduced inside the AB, when T2s were presented on half of the trials and the amplitude of the P3a was comparable to that observed in response to frequent T2s presented outside the AB. Thus, uncertainty in the timing of T2 presented outside the AB seems to exert independent effects on the P3a and P3b related to conscious detection of T2s inside the AB. These observations and hypotheses need to be explored further.

In contrast to the modifications observed in T2-related ERPs, no difference was found between T1-related ERPs preceding seen versus unseen early T2s: this shows that detection of early T2s was not dependent on changes in the neural processing of foregoing T1s (for a review of converging evidence see Craston et al., 2009). This finding points to a sharp functional differentiation between pre-conscious (T2) and conscious (T1) processes running in parallel: preconscious processes can modify their operating mode on the basis of accumulated predictive knowledge whereas conscious processors do not display such an adaptive plasticity. An important aim for future studies is to explore the generality of this functional dichotomy. Several models of the AB that have expanded on the two-stage processing theory by Chun and Potter (1995; for review see Dux & Marois, 2009), have emphasized that conscious processing of a pre-conscious T2 trace requires its access to a capacity-limited second stage of processing, where the trace can be consolidated in working memory. As an example, Bowman and Wyble (2007) identified this second stage with the process of trace "tokenization". This corresponds to the recovery of episodic information that defines the position of the stimulus-trace with respect to other stimuli presented in the RSVP. Tokenization is capacity-limited, so that tokenization of T1 precludes simultaneous tokenization of T2, producing the AB. More recently, Zylberberg, Slezak, Roelfsema, Dehaene, and Sigman (2010) showed that dual-task interference effects observed in the AB task, can be simulated by a network composed of parallel processing modules operating at peripheral sensory levels and a central "router" that flexibly maps parallel sensory processors onto motor outputs defined by the behavioral set.

Flexibility in the chaining of parallel processors and in the recombination of sensory-motor processors, is obtained through inhibition of alternative chaining-recombination options, thus resulting in a "serial" bottleneck precluding simultaneous central sensory-motor mapping of competing parallel processors. Our findings points out that due to their "serial" operating mode and their higher computational complexity, central neural processes that follow preconscious storage and that lead to full subjective awareness hardly adapt their dynamics to changes in the probabilistic structure of behavioral contexts.

In our study the reduction of the AB was not linked to the attentional cuing of a specific time lag inside the AB. At the behavioral level, a reduction of the AB was observed at all lags, i.e., Lag 2, 3 and 4. At the electrophysiological level this was matched with an equivalent enhancement of the N2 wave at all lags inside the AB while the amplitude of the P3a and P3b showed an improvement between Lag 2 and 3, i.e., when T2 detection passed from below to above chance level, but not between Lag 3 and 4 when detection was always above chance. These results seem to point out that our experimental manipulations influenced the competition between T1 and T2 processing, and show that while the preconscious storage signalled by the N2 is not influenced by the temporally contiguous processing of T1, the conscious processing of T2 signalled by the P3a and P3b wave, is reduced when T2s are contiguous to T1. All together these findings suggest that uncued changes in the frequency of occurrence and timing of T2s presented outside the AB influence the capacity-limited mechanisms regulating the course of the parallel conscious processing of T1 and T2 and the strength of the AB (Chun & Potter, 1995; Raymond et al., 1992; Sergent et al., 2005; Shapiro et al., 1994). Nonetheless, this does not exclude that attentional factors might have contributed to the reduction of the AB that was observed in the present investigation. For example, in our study changes in the competitive interaction between the processing of T1s and T2s presented at early lags inside the AB might have been caused by the redirection of attentional resources toward early lags when conscious T2s presented at late lags outside the AB were infrequent or uncertain in time. In summary, our findings suggest the relevance of exploring further the functional interaction between the capacity-limited and the attentional mechanisms that have been demonstrated to influence the presence and magnitude of the AB.

5.3. *Conclusions: expectancy of conscious events and "serendipity"*

The results of our study show that the conscious processing of sensory events that would otherwise escape awareness is improved when the brain guides attention following loose hypotheses on the timing of forthcoming conscious stimuli or with low expectancy on the probability of their occurrence. This finding might offer an insight on the behavioral and neural conditions that predispose an active observer to "serendipity" (Merton & Barber, 2006). The term "serendipity" has a complex semantic and sociological history (Van Andel, 1994; Merton & Barber, 2006; de Rond & Morley, 2010; Eco, 2013). It generally refers to the ability of picking up and appreciating the relevance of incidental observations. According to the physiologist Walter Bradford Cannon (1945), who was among the first to cultivate the term "serendipity" in his reflections on the origin and mechanisms of scientific discovery, "serendipity" is the faculty or chance to find out the proof of an hypothesis in an unexpected way or to discover new objects or relationships without having been explicitly looking for them. This process was later metaphorically defined (Comroe, 1977) as "*looking in a haystack for a needle*", hence with no precise prediction on the location of the needle and poor conviction of finding it, "*and discovering a farmer's daughter*", that is making a "*happy discovery by accident and sagacity*" (Merton & Barber, 2006). Thus, "serendipity" is considered to occur when the attention of an active and "sagacious" observer, as "*… chance favors only the prepared mind* " Pasteur (1854), reported in Peterson, 1954), is not narrowly tied up to an expected outcome (Van Andel, 1994; Merton & Barber, 2006; de Rond & Morley, 2010). The findings of our study show that the combination of an active attentional state with loose probabilistic and temporal expectancies on forthcoming conscious events modifies the interaction between conscious and unconscious processing and favors the emergence to conscious attention of otherwise unnoticed visual events. This likely provides an operational description of the initial mechanisms that trigger the series of cognitive processes that lead to "serendipitous" findings.

Acknowledgments

This work was supported by grants from the University of Rome La Sapienza (Progetti Ateneo 2012) and the Italian Ministery of Health-Fondazione Santa Lucia IRCCS (RF10.091) F.D. We thank two anonymous referees for useful suggestions and Clelia Rossi Arnaud for revising the text of the manuscript. The authors declare no competing financial interests.

Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cortex.2015.05.029.

REFERENCES

Berchicci, M., Lucci, G., Pesce, C., Spinelli, D., & Di Russo, F. (2012). Prefrontal hyperactivity in older people during motor planning. *NeuroImage, 62*(3), 1750–1760.

Bledowski, C., Prvulovic, D., Hoechstetter, K., Scherg, M., Wibral, M., Goebel, R., et al. (2004). Localizing P300 generators in visual target and distractor processing: a combined event-related potential and functional magnetic resonance imaging study. *The Journal of neuroscience, 24*(42), 9353–9360.

Bowman, H., & Wyble, B. (2007). The simultaneous type, serial token model of temporal attention and working memory. *Psychological Review, 114*(1), 38.

Broadbent, D. E., & Broadbent, M. H. (1987). From detection to identification: response to multiple targets in rapid serial visual presentation. *Perception & Psychophysics, 42*(2), 105–113.

Bueti, D., Bahrami, B., Walsh, V., & Rees, G. (2010). Encoding of temporal probabilities in the human brain. *The Journal of Neuroscience, 30*(12), 4343–4352.
Cannon, W. B. (1945). *The way of an investigator: A scientist's experiences in medical research* (p. 100). New York: WW Norton.
Capa, R. L., Bouquet, C. A., Dreher, J. C., & Dufour, A. (2013). Long-lasting effects of performance-contingent unconscious and conscious reward incentives during cued task-switching. *Cortex, 49*(7), 1943–1954.
Charles, L., Van Opstal, F., Marti, S., & Dehaene, S. (2013). Distinct brain mechanisms for conscious versus subliminal error detection. *NeuroImage, 73*, 80–94.
Choi, H., Chang, L. H., Shibata, K., Sasaki, Y., & Watanabe, T. (2012). Resetting capacity limitations revealed by long-lasting elimination of attentional blink through training. *Proceedings of the National Academy of Sciences, 109*(30), 12242–12247.
Chun, M. M., & Potter, M. C. (1995). A two-stage model for multiple target detection in rapid serial visual presentation. *Journal of Experimental Psychology: Human Perception and Performance, 21*(1), 109.
Comroe, J. H. (1977). *Retrospectroscope: Insights into medical discovery* (vol. 2). Menlo Park, CA: Von Gehr Press.
Craston, P., Wyble, B., Chennu, S., & Bowman, H. (2009). The attentional blink reveals serial working memory encoding: evidence from virtual and human event-related potentials. *Journal of Cognitive Neuroscience, 21*(3), 550–566.
De Lange, F. P., Van Gaal, S., Lamme, V. A., & Dehaene, S. (2011). How awareness changes the relative weights of evidence during human decision-making. *PLoS Biology, 9*(11), e1001203.
Dehaene, S., Changeux, J. P., Naccache, L., Sackur, J., & Sergent, C. (2006). Conscious, preconscious, and subliminal processing: a testable taxonomy. *Trends in Cognitive Sciences, 10*(5), 204–211.
Dehaene, S., Naccache, L., Cohen, L., Le Bihan, D., Mangin, J. F., Poline, J. B., et al. (2001). Cerebral mechanisms of word masking and unconscious repetition priming. *Nature Neuroscience, 4*(7), 752–758.
Del Cul, A., Baillet, S., & Dehaene, S. (2007). Brain dynamics underlying the nonlinear threshold for access to consciousness. *PLoS Biology, 5*(10), e260.
Dell'Acqua, R., Sessa, P., Jolicœur, P., & Robitaille, N. (2006). Spatial attention freezes during the attention blink. *Psychophysiology, 43*(4), 394–400.
Di Lollo, V., Kawahara, J. I., Ghorashi, S. S., & Enns, J. T. (2005). The attentional blink: resource depletion or temporary loss of control? *Psychological Research, 69*(3), 191–200.
Di Russo, F., Stella, A., Spitoni, G., Strappini, F., Sdoia, S., Galati, G., et al. (2012). Spatiotemporal brain mapping of spatial attention effects on pattern-reversal ERPs. *Human Brain Mapping, 33*(6), 1334–1351.
Dux, P. E., & Marois, R. (2009). The attentional blink: a review of data and theory. *Attention, Perception, & Psychophysics, 71*(8), 1683–1700.
Eco, U. (2013). *Serendipities: Language and lunacy*. Columbia University Press.
Ferlazzo, F., Fagioli, S., Sdoia, S., & Di Nocera, F. (2008). Goal-completion processes affect the attentional blink. *European Journal of Cognitive Psychology, 20*(4), 697–710.
Ferlazzo, F., Lucido, S., Di Nocera, F., Fagioli, S., & Sdoia, S. (2007). Switching between goals mediates the attentional blink effect. *Experimental Psychology, 54*(2), 89.
Friston, K. (2010). The free-energy principle: a unified brain theory? *Nature Reviews Neuroscience, 11*(2), 127–138.
van Gaal, S., Ridderinkhof, K. R., Fahrenfort, J. J., Scholte, H. S., & Lamme, V. A. (2008). Frontal cortex mediates unconsciously triggered inhibitory control. *The Journal of Neuroscience, 28*(32), 8053–8062.
van Gaal, S., Ridderinkhof, K. R., Scholte, H. S., & Lamme, V. A. (2010). Unconscious activation of the prefrontal no-go network. *The Journal of Neuroscience, 30*(11), 4143–4150.
Genovesio, A., Tsujimoto, S., & Wise, S. P. (2006). Neuronal activity related to elapsed time in prefrontal cortex. *Journal of Neurophysiology, 95*(5), 3281.
Ghose, G. M., & Maunsell, J. H. (2002). Attentional modulation in visual cortex depends on task timing. *Nature, 419*(6907), 616–620.
Gross, J., Schmitz, F., Schnitzler, I., Kessler, K., Shapiro, K., Hommel, B., et al. (2004). Modulation of long-range neural synchrony reflects temporal limitations of visual attention in humans. *Proceedings of the National Academy of Sciences (USA), 101*, 13050–13055.
Guthrie, D., & Buchwald, J. S. (1991). Significance testing of difference potentials. *Psychophysiology, 28*(2), 240–244.
Jannati, A., Spalek, T. M., & Di Lollo, V. (2011). Neither backward masking of T2 nor task switching is necessary for the attentional blink. *Psychonomic Bulletin & Review, 18*(1), 70–75.
Knight, R. T., & Scabini, D. (1998). Anatomic bases of event-related potentials and their relationship to novelty detection in humans. *Journal of Clinical Neurophysiology, 15*(1), 3–13.
Kouider, S., Eger, E., Dolan, R., & Henson, R. N. (2009). Activity in face-responsive brain regions is modulated by invisible, attended faces: evidence from masked priming. *Cerebral Cortex, 19*(1), 13–23.
Kranczioch, C., Debener, S., & Engel, A. K. (2003). Event-related potential correlates of the attentional blink phenomenon. *Cognitive Brain Research, 17*(1), 177–187.
Kranczioch, C., Debener, S., Schwarzbach, J., Goebel, R., & Engel, A. K. (2005). Neural correlates of conscious perception in the attentional blink. *NeuroImage, 24*, 704–714.
Lamme, V. A. (2003). Why visual attention and awareness are different. *Trends in Cognitive Sciences, 7*(1), 12–18.
Lamme, V. A. (2006). Towards a true neural stance on consciousness. *Trends in Cognitive Sciences, 10*(11), 494–501.
Lau, H. C., & Passingham, R. E. (2007). Unconscious activation of the cognitive control system in the human prefrontal cortex. *The Journal of Neuroscience, 27*(21), 5805–5811.
Leon, M. I., & Shadlen, M. N. (2003). Representation of time by neurons in the posterior parietal cortex of the macaque. *Neuron, 38*(2), 317–327.
Lucci, G., Berchicci, M., Spinelli, D., Taddei, F., & Di Russo, F. (2013). The effects of aging on conflict detection. *PloS One, 8*(2), e56566.
Marcantoni, W. S., Lepage, M., Beaudoin, G., Bourgouin, P., & Richer, F. (2003). Neural correlates of dual task interference in rapid visual streams: an fMRI study. *Brain and Cognition, 53*, 318–321.
Marois, R., Yi, D. J., & Chun, M. M. (2004). The neural fate of consciously perceived and missed events in the attentional blink. *Neuron, 41*, 465–472.
Martens, S., & Johnson, A. (2005). Timing attention: cuing target onset interval attenuates the attentional blink. *Memory & Cognition, 33*(2), 234–240.
Martens, S., & Wyble, B. (2010). The attentional blink: past, present, and future of a blind spot in perceptual awareness. *Neuroscience & Biobehavioral Reviews, 34*(6), 947–957.
Melloni, L., Schwiedrzik, C. M., Müller, N., Rodriguez, E., & Singer, W. (2011). Expectations change the signatures and timing of electrophysiological correlates of perceptual awareness. *The Journal of Neuroscience, 31*(4), 1386–1396.
Merton, R. K., & Barber, E. (2006). *The travels and adventures of serendipity: A study in sociological semantics and the sociology of science*. Princeton University Press.
Naccache, L., Blandin, E., & Dehaene, S. (2002). Unconscious masked priming depends on temporal attention. *Psychological Science, 13*(5), 416–424.

Naccache, L., & Dehaene, S. (2001). Unconscious semantic priming extends to novel unseen stimuli. *Cognition, 80*(3), 215–229.
Nakatani, C., Ito, J., Nikolaev, A. R., Gong, P., & van Leeuwen, C. (2005). Phase synchronization analysis of EEG during attentional blink. *Journal of Cognitive Neuroscience, 17*, 1969–1979.
Nieuwenstein, M. R., Chun, M. M., van der Lubbe, R. H., & Hooge, I. T. (2005). Delayed attentional engagement in the attentional blink. *Journal of Experimental Psychology: Human Perception and Performance, 31*(6), 1463.
Nieuwenstein, M. R., & Potter, M. C. (2006). Temporal limits of selection and memory encoding a comparison of whole versus partial report in rapid serial visual presentation. *Psychological Science, 17*(6), 471–475.
Nobre, A. C., Correa, A., & Coull, J. T. (2007). The hazards of time. *Current Opinion in Neurobiology, 17*(4), 465–470.
Olivers, C. N., Van Der Stigchel, S., & Hulleman, J. (2007). Spreading the sparing: against a limited-capacity account of the attentional blink. *Psychological Research, 71*(2), 126–139.
Onoe, H., Komori, M., Onoe, K., Takechi, H., Tsukada, H., & Watanabe, Y. (2001). Cortical networks recruited for time perception: a monkey positron emission tomography (PET) study. *NeuroImage, 13*(1), 37–45.
Pessiglione, M., Schmidt, L., Draganski, B., Kalisch, R., Lau, H., Dolan, R. J., et al. (2007). How the brain translates money into force: a neuroimaging study of subliminal motivation. *Science, 316*(5826), 904–906.
Peterson, H. (1954). *A treasury of the world's great speeches*. New York: Simon and Schuster.
Polich, J. (2007). Updating P300: an integrative theory of P3a and P3b. *Clinical Neurophysiology, 118*(10), 2128–2148.
Potter, M. C., Nieuwenstein, M., & Strohminger, N. (2008). Whole report versus partial report in RSVP sentences. *Journal of Memory and Language, 58*(4), 907–915.
Raymond, J. E., Shapiro, K. L., & Arnell, K. M. (1992). Temporary suppression of visual processing in an RSVP task: an attentional blink? *Journal of Experimental Psychology: Human Perception and Performance, 18*(3), 849.
Rees, G., Wojciulik, E., Clarke, K., Husain, M., Frith, C., & Driver, J. (2000). Unconscious activation of visual cortex in the damaged right hemisphere of a parietal patient with extinction. *Brain, 123*(8), 1624–1633.
Rohenkohl, G., Cravo, A. M., Wyart, V., & Nobre, A. C. (2012). Temporal expectation improves the quality of sensory information. *The Journal of Neuroscience, 32*(24), 8424–8428.
de Rond, M., & Morley, I. (2010). *Serendipity: Fortune and the prepared mind* (vol. 22). Cambridge University Press.
Sdoia, S., & Ferlazzo, F. (2012). An inhibition effect in the temporal constrains of attentional selection: the backward blink. *Acta Psychologica, 139*(3), 501–506.
Sergent, C., Baillet, S., & Dehaene, S. (2005). Timing of the brain events underlying access to consciousness during the attentional blink. *Nature Neuroscience, 8*(10), 1391–1400.
Sessa, P., Luria, R., Verleger, R., & Dell'Acqua, R. (2007). P3 latency shifts in the attentional blink: further evidence for second target processing postponement. *Brain Research, 1137*, 131–139.
Shapiro, K. L., Raymond, J. E., & Arnell, K. M. (1994). Attention to visual pattern information produces the attentional blink in rapid serial visual presentation. *Journal of Experimental Psychology: Human Perception and Performance, 20*(2), 357.
Shen, D., & Alain, C. (2011). Temporal attention facilitates short-term consolidation during a rapid serial auditory presentation task. *Experimental Brain Research, 215*(3–4), 285–292.
Shen, D., & Alain, C. (2012). Implicit temporal expectation attenuates auditory attentional blink. *PloS One, 7*(4), e36031.
Sheskin, D. J. (2003). *Handbook of parametric and nonparametric statistical procedures*. crc Press.
Sligte, I. G., Scholte, H. S., & Lamme, V. A. (2008). Are there multiple visual short-term memory stores? *PLOS One, 3*(2), e1699.
Tang, M. F., Badcock, D. R., & Visser, T. A. (2014). Training and the attentional blink: limits overcome or expectations raised? *Psychonomic Bulletin & Review, 21*(2), 406–411.
Ungerleider, L. G., Galkin, T. W., Desimone, R., & Gattass, R. (2008). Cortical connections of area V4 in the macaque. *Cerebral Cortex, 18*(3), 477–499.
Van Andel, P. (1994). Anatomy of the unsought finding. serendipity: orgin, history, domains, traditions, appearances, patterns and programmability. *The British Journal for the Philosophy of Science, 45*(2), 631–648.
Van den Bussche, E., Notebaert, K., & Reynvoet, B. (2009). Masked primes can be genuinely semantically processed: a picture prime study. *Experimental Psychology, 56*(5), 295.
Visser, T. A., Tang, M. F., Badcock, D. R., & Enns, J. T. (2014). Temporal cues and the attentional blink: a further examination of the role of expectancy in sequential object perception. *Attention, Perception, & Psychophysics, 76*(8), 2212–2220.
Wacongne, C., Labyt, E., van Wassenhove, V., Bekinschtein, T., Naccache, L., & Dehaene, S. (2011). Evidence for a hierarchy of predictions and prediction errors in human cortex. *Proceedings of the National Academy of Sciences, 108*(51), 20754–20759.
Weibel, S., Giersch, A., Dehaene, S., & Huron, C. (2013). Unconscious task set priming with phonological and semantic tasks. *Consciousness and Cognition, 22*(2), 517–527.
Zylberberg, A., Slezak, D. F., Roelfsema, P. R., Dehaene, S., & Sigman, M. (2010). The brain's router: a cortical network model of serial processing in the primate brain. *PLoS Computational Biology, 6*(4), e1000765.