Interplay between supramodal attentional control and capacity limits in the low-level visual processors modulate the tendency to inattention

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Abstract

When engaged in a demanding task, individuals may neglect unexpected visual stimuli presented concomitantly. Here we use a change detection task to show that propensity to inattention is associated with a flexible allocation of attentional resources to filter and represent visual information. This was reflected by N2 posterior contralateral (N2pc) and contralateral delay activity (CDA) respectively, but also during high-order reorienting of attentional resources (known as anterior directing attention negativity, ADAN). Results show that differences in noticing and failing to notice unexpected stimuli/changes are associated with different patterns of brain activity. When processing (N2) and working memory (CDA) capacities are low, resources are mostly allocated to small set-sizes and associated with a tendency to filter information during early low-level processing (N2). When resources are high, saturation is obtained with larger set-sizes. This is also associated to a tendency to select (N2) and reorient resources (ADAN) to maintain extra information (CDA).

Keywords: Flexible Attentional Deployment; Inattentional Blindness; Change Detection; Capacity Limits; Prefrontal control;

1. Introduction

The ability to notice an expected visual stimulus has important implications for human risk assessment that involve safety procedures such as those related to flying aeroplanes (Green, 2003; Harris, 2011; Paries & Amalberti, 1995), air traffic control or for eye witnesses accounts of crimes (Chabris, Weinberger, Fontaine, & Simons, 2011), nuclear industry (Budau, 2011), and surgery (Musson, 2009). Such activities require sustained attention on a demanding task together with an ability to detect potential unexpected changes in the visual scene. In the laboratory, brain activity underlying these processes (i.e., selection

and maintenance of visual stimuli representation in VWM) can be studied using visual search and change detection tasks, and are thought to be crucial for the ability to consciously report the presence/absence of targets/changes.

Three important ERP components have been identified to reflect such mechanisms of attention and memory. First, is the N2pc that has been observed during visual search (Eimer, 1996) and pop-out visual search (Hickey, Di Lollo, & McDonald, 2009; Schubö, Wykowska, & Müller, 2007) tasks, and is thought to be involved in the selection-enhancement and inhibition of visual information (e.g., targets). Next, is the contralateral delay activity (CDA; Drew & Vogel, 2008; Vogel, McCollough, & Machizawa, 2005; Vogel & Machizawa, 2004), which is a sustained contralateral waveform elicited during the retention interval in change detection tasks. Last, more prefrontally, an anterior directing attention negativity (ADAN) may be observed during the signalling control for the reorienting of attention towards the location of upcoming stimuli; this is reflected by a negative deflection occurring between 350 and 500 ms post-stimulus (Drew & Vogel, 2008; Harter, Miller, Price, Lalonde, & Keyes, 1989; Nobre, Sebestyen, & Miniussi, 2000; Simpson et al., 2006). It has been observed to be modulated by a centrally presented spatial cue in anticipation of an upcoming target, although it is not commonly associated with attentional processing *per se*, since it is not sensitive to task demands (Hopf & Mangun, 2000). It is considered a measure (amongst others such as P3 and SPCN; see Eimer & Kiss, 2010; Dell'Acqua et al., 2015) involved in the control of attentional resources, therefore playing an important role in the conscious representation during processing of stimuli.

Furthermore, other studies (Liesefeld, Liesefeld, & Zimmer, 2013; McNab & Klingberg, 2008), have also found an earlier prefrontal component (i.e., 200-300 ms) which has been interpreted as a prefrontal bias signal assumed to reflect active suppression of irrelevant information in a form of attentional weighting which is performed after the initial

scanning process in the parietal areas (N2pc). (See also the discussion on the *Biased Competition Theory*, Desimone & Duncan, 1995; Duncan, Humphreys, & Ward, 1997).

In sum, the N2pc is thought to reflect the selection of items (Eimer, 1996; Luck, Girelli, McDermott, & Ford, 1997; Luck & Hillyard, 1994ab; Woodman, Kang, Rossi, & Schall, 2007; Woodman & Luck, 2003; Hopf et al., 2000) whereas the CDA reflects the storage of the filtered items (McCollough, Machizawa, & Vogel, 2007) after active suppression/selection (prefrontal bias) and in concomitance with supramodal attentional control (ADAN; see Couperus, Alperin, Furlong, & Mott, 2014; Seiss, Gherri, Eardley, & Eimer, 2007).

Although a number of ERPs components reflecting allocation of resources have been identified, the way resources are allocated is still under debate.. According to a flexible allocation of resources view, an undetermined (if not unlimited) number of items can be attended and stored in memory. This implies that the resources allocated to each item decrease as a function of the items *attended* (that can be expectedly or unexpectedly presented on the screen), with the result that the featural information of the attended *n*-th item will not be fully stored (Bays, Catalao, & Husain, 2009). If resources are allocated flexibly, all resources would be deployed irrespective of the number of items processed in a given array of stimuli, whereby a high number of item to attend would result in the loss of some information (i.e., not all the featural information of the stimuli will be processes since resources are diluted across a large number of stimuli). Therefore, one may expect that mean amplitudes in the ERP components underlying processes of visual search (as well as the associated behavioural performance) should be unchanged as a function of set-size until a point (i.e., capacity) where the dilution of the resources across stimuli cause poor processing of each item, therefore starting to affect performance (*appearance* of the capacity limit; see Bays, Catalao, & Husain, 2009). This implies that capacity may correspond to the precision,

that is the number of neurons involved in the encoding of a certain number of items (Dayan & Abbott, 2001; Seung & Sompolinsky, 1993; Vogels, 1990). Therefore, ERPs in the latency of interest (e.g., N2pc, CDA) might show larger mean amplitudes (i.e., more negative) across different individuals when the population employed for storage of a given amount of items is larger. For instance, given the same set-size, an individual with a greater capacity may present more negative mean amplitudes when compared to one with a lower capacity (see for example the overall brain response measure during the N1 latency found in Papera & Richards, 2016, showing that individuals with low levels of inattention may recruit a larger population of neurons during encoding in the N1 latency, therefore potentially allowing the detection of unexpected stimuli).

Flexible resource models propose that the precision at which an item is stored will depend on the number of items to be stored and on the demands of the task (i.e., simpler tasks can be performed well even with high set-sizes requiring a high spread of resources across the items; see: Bays, Catalao, & Husain, 2009; Bays & Husain, 2008; Wilken & Ma, 2004; Zhang & Luck, 2008). The flexible allocation of resources view also asserts an *uneven* spread of resources so that a stimulus may receive more resources at the cost of reducing the resolution of the other stored items (Bays, Catalao, & Husain, 2009; Bays & Husain, 2008). This is particularly relevant in natural scenes, where an uneven distribution of resources may prioritize storage of more salient stimuli (see for instance, Itti & Koch, 2001; Papera, Cooper, & Richards, 2014).

In contrast, a fixed resource view would predict an equal and increasing allocation of resources, that is an *even* spread of resources so that each stimulus receives an equal deployment of resources until all resources have been allocated, leaving any further items not attended (i.e., “quantised” fashion; Barton, Ester, & Awh, 2009; Rouder et al., 2008; Zhang & Luck, 2008). This would reflect in an equally quantised amount of resources until no

resources are left for the processing of further stimuli; ERP components would be modulated as a function of set-size, therefore leading mean amplitudes to saturate when capacity is reached (i.e., more negative mean amplitudes; Vogel & Machizawa, 2004; Jost, Bryck, Vogel, & Mayr, 2010; Luck & Vogel, 1997; Zhang & Luck, 2008; Lee et al., 2010; Rouder et al., 2008; Barton, Ester, & Awh, 2009).

It is well known that resource limits in the low-level visual processors can be associated with a tendency to inattention (Dehaene & Changeux, 2005; Hannon, & Derakshan, 2010; Hannon & Richards, 2010; Mack & Rock, 1998; Most, Scholl, Clifford, & Simons, 2005; Most et al., 2001; Richards, Richards, Hannon, & Vitkovitch, 2010; Simons, 2003). Some researchers argue that failing to notice an unexpected stimulus occurs when early mechanism of exogenous attention and visual working memory (VWM) are predominantly involved in another task, resulting in too few resources remaining for the processing of an unexpected stimulus or change (Papera & Richards, 2016). Other accounts propose that in most IB tasks the unexpected event is not relevant to the primary task, making it susceptible to inhibition and therefore prevented from reaching awareness (Richards, Hannon, Vohra, & Golan, 2014). Furthermore, neural network modelling has argued that intrinsic oscillatory brain activity in high-order brain areas (particularly in the alpha and theta band: Mathewson, Gratton, Fabiani, Beck, & Ro, 2009; Jensen, Bonnefond, & VanRullen, 2012; Papera & Richards, 2016) may prevent low-level processors (i.e., parietal areas) to "ignite" a widespread activation across several regions that are thought to reflect the current conscious content (Dehaene & Changeux, 2005, 2011; Dehaene, Sergen, & Changeux, 2003).

To investigate individual differences in capacity and allocation of resources during selection and maintenance of visual information, an IB task was used (Fig.1A) as an external measure for assessing participants' level of inattention. Research has shown that those who show a high propensity to inattention present a lower working memory capacity (WMC) than

those who are more likely to notice unexpected changes/stimuli (Hannon & Richards, 2010; Richards, Hannon, & Derakshan, 2010; Richards, Hannon, & Vitkovitch, 2010).

Furthermore, their processing capacity during the N2pc is also drastically reduced (Papera & Richards, 2016), and a different brain response pattern may be observed between individuals who show a high or low propensity to inattention, while they are performing a change detection task (see Fig. 1B).

The present study examined differences in the allocation of resources in the posterior regions and supramodal control in the frontal areas into two sub-populations of healthy individuals who show high and low levels of inattention. This allowed us to investigate differences in the brain processing which might lead to a failure in the processing of unexpected visual stimuli/changes, and may explain whether allocation of resources in the brain occur in a flexible or quantised manner.

We hypothesised that although allocation of resources may be flexible, it might be influenced by an individual's capacity, leading to a differential spread of resources depending on the capacity value. Low levels of selection and storage capacity, as estimated respectively during the N2 and CDA latencies, may be associated with prioritizing the allocation of a large proportion of the available resources for small set-sizes. Furthermore, we predict that although resources might be allocated flexibly, they may still be subject to capacity which might influence the way they are flexibly allocated: when capacity limit is low mean amplitudes will saturate quickly for low set-sizes; conversely, a high capacity will allow mean amplitudes to increase more gradually.

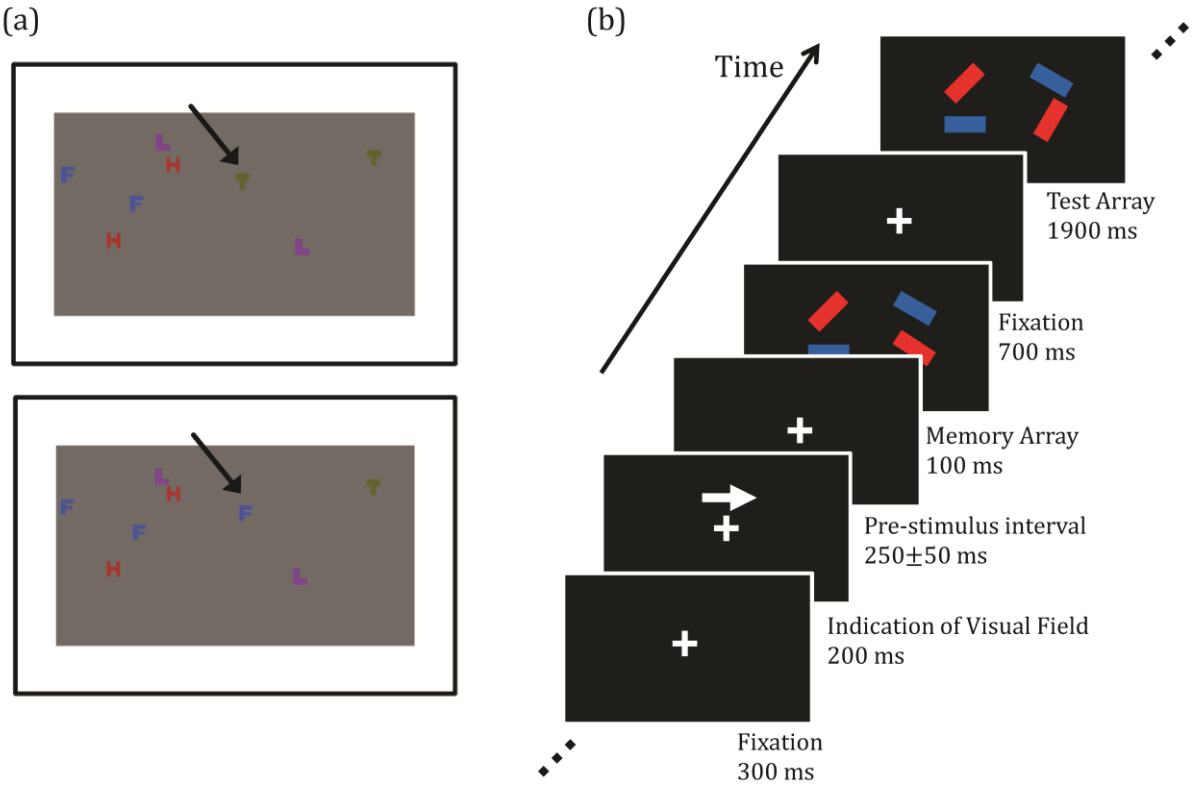

Fig. 1. (a) During the IB task, participants track two blue Fs and two green Ts as they move in a linear but randomly manner around the screen and silently count how many times the Fs and Ts separately hit the frame on the screen but ignore similarly moving distractors (i.e., orange Hs and purple Ls). Several seconds into the task, one target (a green T) unexpectedly turned into another target (a blue F). This was an unexpected, yet task-relevant, change. Participants are asked to report whether they saw the *actual* transition when questioned at the end of the task. Participants were classified as Non-IB (reporting the transition), providing a strong evidence of low level of inattention, or as IB (not reporting the transition) showing a tendency to neglect unexpected (but task-relevant) changes occurring on the screen. (b) Experimental apparatus used for the change detection task: Each trial started with a fixation point of 300 ms followed by an arrow displayed for 250±50 ms indicating the visual field to be attended prior to the presentation of the memory array. Participants were instructed to maintain central fixation whilst they were attending either the left or right side of the screen. The memory array was presented for 100 ms followed by a retention interval of 900 ms (100 ms memory array + 800 ms fixation).

Moreover, since IB participants may be able to hold a smaller number of representations in VWM (i.e., small set-sizes) in a change detection task, this might also have an effect on the ability to select relevant items during the N2 latency: IB individuals may show a higher selection efficiency not as a result of an active process of selection, but as a passive consequence of their capacity limits, hence making them more likely to neglect items in the array. (i.e., a sub-set of items is stored since capacity is low, and this might not include unexpected stimuli). Conversely, Non-IB individuals have been shown to present a higher

capacity, making them more likely to select all the relevant items in the scene, with the possible selection of occurring unexpected (yet relevant) changes/stimuli in a visual scene (at no or little expense in change detection accuracy; see Papera & Richards, 2016). This may be associated with a prefrontal attentional control (i.e., ADAN) to reorient attention towards the extra stimuli. For instance, Dell'Acqua et al. (2015), discuss several frontal components thought to reflect attentional control and found that reduced activity in the frontal areas as reflected by the P3a was associated with a delay in the processing of stimuli in the posterior regions (P3b), suggesting that frontal attentional control may be required to establish a different "mental set" in order to allocate resources for the processing and maintenance in VWM of an unexpected (but relevant) stimulus (see for instance Prada, Barceló, Herrmann, & Escera, 2014). As a result, individuals with a greater frontal control in the deployment of attentional resources (i.e., Non-IB), may be able to allow attention-driven gating of relevant visual information (including unexpected stimuli) in the low-level visual processors (e.g., N2pc). Conversely, individuals with high levels of inattention with low capacity, may not have enough prefrontal control and resources to be allocate to "extra" unexpected stimuli, and therefore prevent this stimuli from entering a level of conscious representation (i.e., SPCN; see Brigadoi et al., 2016; see also Papera & Richards, 2016).

2. Material and Methods

2.1 Participants

Twenty-three healthy individuals were recruited for course credits (four were excluded, N=19, mean age: 25.47±5.68; 7 males; see section 2.3 for the exclusion criteria): Seven were classified as presenting high levels of inattention (IB) and twelve with low levels (Non-IB; see section 2.2 and 2.3 for details about the classification). All participants had normal or sight-corrected and were naïve about the purpose of the experiment. The

experiment was carried out in compliance with institutional guidelines and approval by the departmental ethics committee.

2.2 Stimuli

Inattentional Blindness Task. The IB task was programmed in MatLab™ and based on the work of Richards, Hannon, Vohra, and Golan (2014), where the unexpected event does not involve any addition of new stimuli, but rather an unexpected change to one of the stimuli already present in the visual dynamic scene (Fig. 1A). Since in a standard IB task the status of the unexpected stimulus is ambiguous (see for instance Most et al., 2001; Simons, 2003; see also Supplementary information), this may lead to a bias in that it is not clear whether the best strategy would be to process it or inhibit it due to a lack of relevancy (Richards et al., 2014). Our IB task instead would yield a sharper cut-off between people who are more or less likely to spot an unexpected yet relevant change/stimulus appearing in their visual field.

Participants performed two inattentional blindness tasks – one where there was a change to a target and one where there was a change to a distractor. Since the order in which the two videos were performed did not influence the incidence of IB ($\chi^2(1,N=19)<1.84$, $p>.17$), IB status was determined solely on the basis of performance on the target change video with performance on the distractor-change video being irrelevant to the current experiment, and therefore performance on the distractor change video will not be discussed further.

The relevant-change video comprised a series of targets (two blue Fs and two green Ts) and distractors (two red Hs and two purple Ls) moving linearly around the screen frequently bouncing off the edge of the black frame. The video began with a still frame for 4 s to show the starting position of the 8 items and then the video began and lasted for 30 s. Fifteen seconds into the video, one of the target stimuli undergoes an unexpected change that

was directly relevant to the goal of the task, in which one target (i.e., a green T), turned into another type of target (i.e., a blue F; see Fig. 1A). Participants were required to count the number of bounces *separately* for two green Ts and two blue Fs and report, at the end of the video, how many hits there were for the two target types. There were a total of 7 and 4 counts respectively for the F and T targets. Participants who reported seeing the *actual* target transition (i.e., from a green T to a blue F) showed a low level of inattention and therefore were classified as being Non-IB. Conversely, since the unexpected change is relevant to the primary task, participants who did not notice the transition were classified as IB, showing high levels of inattention.

Change detection Task. We used a change detection task (Phillips, 1974; Vogel, McCollough, & Machizawa, 2005) that allowed us to obtain estimates of VWM from both objective performance and ERP recordings as well as measures of selection efficiency (see next section). Participants were presented with an array of coloured rectangles of varying orientations (radiants: 0°, 45°, 90°, 135°) in both left and right visual fields, and told to remember the orientations of only the red items on either the left or right, as indicated by an arrow presented at the beginning of each trial (see Fig. 1B).

A preliminary study was carried out to assess whether a set-size of 4 items may lead to reach the asymptotic VWM capacity for the whole sample but particularly for the IB subjects. Results showed that set-size 4 had equal mean amplitudes to set-size 2, particularly for IB participants (see Supplementary information); therefore, to assess if the capacity limit was between set-size 2 and 3 (for a justification see Vogel & Machizawa, 2004), smaller set sizes were used: 1 (1T0D), 2 (2T0D) and 3 (3T0D) instead of 2 and 4 only. At set-size 1 only one red rectangle was displayed on both the display areas, whereas set-size 3 presented three red rectangles. Observing no difference between set size 2 and 3 would be an indication that (processing and memory) capacity may have reached. For set-size 2 we had two different

qualitative conditions analogous: one with two target items and one comprising one target item and one distractor (1T1D). Although the overall workload was reduced compared to the pilot study, propensity to filter irrelevant information is still measurable. There was a total of 960 trials (240 trials per condition with 50% of them reporting a single change in orientation for one of the items), divided into 5 blocks of 192 trials each. The task also involved a short practice block to familiarise participants. Participants were instructed to fixate centrally at all times at the beginning of the Randmorph Task. EEG activity was inspected online during the task and participants were given verbal feedback whenever loss of fixation occurred during the familiarisation block and at the end of each experimental block.

The Automated Operation Span (AOSPAN) Task. The AOSPAN (Unsworth, Heitz, Schrock, & Engle, 2005) is a computerized version of the OSPAN task (Turner & Engle, 1989) that estimates WMC of an individual (scores between 0 and 75). The AOSPAN was used to provide an external measure of WMC and attentional executive control (for examples see Papera, Cooper, & Richards, 2014; see also Papera & Richards, 2016); observing associations between this measure and other capacity estimates using a change detection task (see for example: Cowan *et al.*, 2005; Cowan, Fristoe, Elliott, Brunner, & Saults 2006) reinforces the idea of a general difference in attentional control between individual with low and high levels of inattention.

The AOSPAN task comprises series of math problems and letters with each trial containing between 3 and 7 math problems/letters. After each problem has been completed, a letter is displayed that has to be retained until the end of that trial. At the end of each trial a grid appears and the participant has to click the series of letters that had been displayed in the same order as they appeared on the screen. There are two familiarisations prior to the experimental session; first participants perform series of letter and series of math problems separately. Afterwards a second short training is provided with the two separate tasks

combined together in series of math problems and letters. The time limit for completing each problem was determined for each participant during the familiarization phase. The task takes approximately 20 minutes to complete.

2.3 Data acquisition and Analysis

Electrophysiological recordings. ERPs were recorded using silver electrodes mounted in an elastic cap (Easy-Cap) with 23 locations according to the 10-20 system (FP1, FP2, F3, Fz, F4, F7, F8, FC1, FCz, FC2, FC5, FC6, C3, Cz, C4, CP5, CP6, P3, P4, P7, P8, O1, O2) referenced online to an averaged linked-earlobe and digitised at a sampling rate of 500Hz using a SynAmps amplifier (Neuroscan) and later down sampled to 250Hz. The bandpass of the amplifier was set on a range of 0.01-100Hz. The EEG signal was filtered between 0.1 and 40 Hz (Luck, 2005). Horizontal electrooculagram (HEOG) was measured from 2 locations placed 1 cm to the right and left of the outer canthi of both eyes and impedances of all the electrodes were kept below 5KΩ. The continuous EEG was epoched into 1050 ms windows starting 100 ms before the onset of the memory array and covering the entire retention interval (900 ms). A 100 ms baseline prior the onset of the memory array was used. Participants' response was collected from 50 ms after the onset of the second array.

For the ERP recordings we used the following criteria to control the direction of gaze: horizontal: 30μV ~2°, and vertical: 60 μV~4°. Epochs with amplifier saturation above 100 μV were excluded from further analysis. Participants with more than 40% trial rejected were not entered in the analysis. Seven participants were excluded due to excessive artefacts. These criteria resulted in the following number of accepted trials: 210±30, 187±32, 161±27 respectively for set-size 1-2-3, and 199±30 for set-size 1 with distractors. Three participants were excluded for excessive artefacts. All the participants had more than 109 trials per

condition. Only correct trials were included in the analyses for both ERPs and calculations of behavioural estimates.

For the IB task the number of counts for the T and L targets were collated and participants who did not reach at least 54% overall accuracy (i.e., 6 counts) were excluded from further analysis. One participant was excluded since all parts of the IB task were not performed appropriately.

Estimation of capacity scores. VWM capacity was estimated both on the basis of participants' behavioural performance and from brain activity during the retention interval (CDA). For the behaviourally based estimates, we used a standard formula that corrects for guessing to estimate the number of items being stored in VWM (see Cowan, 2001; Owens, Koster, & Derakshan, 2011; Pashler 1988; Vogel & Machizawa 2004):

$$\mathrm{k} = \mathrm{S}(\mathrm{H} - \mathrm{FA}) \quad \text{Equation 1}$$

The formula assumes that the item that changed should be one of the *k* items stored in participant's memory, thus leading to change detection on k/S trials (see Supplementary information for further details).

ERP mean amplitudes during the latency of the CDA (351-900 ms) were used to estimate VWM capacity by measuring the mean increase in amplitude between the array of only target items with the lowest set-size and the one with the highest (in this study set-size one to three; for a justification see Vogel & Machizawa, 2004). The same approach was used for the latency of the N2pc (225-350 ms) to estimate processing capacity and for the prefrontal bias (230-280 ms). However, the former is thought to reflect the reorienting of posterior resources (which are subject to capacity limits) in order to suppress/select information (see results); therefore, this contrast will be mentioned as 1T0D-to-3T0D mean

amplitude increase. (Note: for simplicity, physiological scores were multiplied by -1, thus positive values would indicate a higher capacity).

Estimation of selection and storage efficiency. By comparing brain activity for set size 2 (1 target, 1 distractor) where relevant from irrelevant items should be discriminated with that for set size 2 (2 targets) condition where all items are relevant, it is possible to estimate participants' tendency to select (N2pc) to prevent unnecessary storage of irrelevant items (storage efficiency) in VWM (CDA). Thus, selection and storage were estimated using the following formula:

$$\frac{\mathbf{2T0D-1T1D}}{\mathbf{3T0D-1T0D}} \quad \text{Equation 2}$$

Where 1T0D, 2T0D, and 3T0D are the mean amplitudes for the condition set-size 1, 2 and 3 (both with targets only) respectively; whereas, 1T1D the mean amplitude for the condition set-size 2 with distractor (for other accounts see Owens, Koster, & Derakshan, 2011; Vogel, McCollough, & Machizawa, 2005). During the N2pc latency, negative scores indicate poor efficiency (i.e., $1T1D \cong 2T0D$ in Equation 2), whereas positive values show an increasingly tendency to filter irrelevant information (i.e., $1T1D \cong 1T0D$ in Equation 2). Conversely, in the CDA latency values around zero are an indication of a stable representation during the retention interval. For both estimates, participants with unrealistic extreme values above +13 or below -13 were excluded (N=1 excluded). This may happen when $2T0D > 3T0D$, $1T1T < 2T0D$, or $2T0D \cong 3T0D$, showing that capacity may have been exceeded, or that, for instance, participants with low VWM capacity (e.g. less than two items) attend the condition with distractors as it was a 2 target item condition, resulting in a biased estimation of efficiency. For the ADAN, since the component is thought to reorient resources and not subject to capacity, we calculated a distractor-presence contrast between

1T1D and 2T0D to assess any reorienting effects attributable to the presence of "extra" stimuli (i.e., distractors; for a justification see Liesefeld, Liesefeld, & Zimmer, 2013).

Analysis. The ERP recordings were analysed using the EEGLAB plugin (http://sccn.ucsd.edu/eeglab/), and custom-made MaTLab™ code. Statistical tests were performed using the Statistical Package for the Social Sciences (SPSS) 20.0. Signal detection analysis (response bias and *d*') was performed on the accuracy data.

Hierarchical regressions were also used to assess whether capacity scores (AOSPAN, CDA, N2pc, and behaviourally estimated capacity) were predictive of the tendency to filter distractors during the N2pc latency. Factors were included in the following order: capacity score, interaction capacity × IB status, IB status.

Efficiency and capacity scores based on ERP mean amplitudes were used in logistic and linear regressional analyses to assess their discriminatory power to predict the level of inattention. For the logistic regressions AOSPAN scores, behavioural capacity as estimated from the change detection task and capacity in Mv (increase from set size 1 to set size 3 during the CDA and N2 latencies) were used as explanatory variable to predict the outcome to the IB task. Furthermore, for the linear regression storage efficiency scores during the N2 latency were regressed on the same explanatory variables and also the participants' status (Non-IB was the baseline category). Logistic regressions were also assessed to investigate the mean amplitude increase from set size 2T0D to 1T1D and see whether prefrontal processing was indicative of the level of inattention in the electrode pair F3/4. This allowed us to assess the processing during the presentation of distractors and controlling for the number of items presented. Because the set-size is equal, any difference between the two conditions must be the result of distractor processing (note: this contrast was not normalised by using the difference 3T0D − 1T0D at the denominator of Equation 2, since high-order reorienting of

attentional resources should not be susceptible to capacity, but instead, provide signalling that control operations in the low-level visual processors (i.e., posterior regions; see for instance Edin, 2007).

Since capacity scores predicted the level of inattention, we performed a follow-up mixed ANOVAs to assess differences between the two groups for reaction times, response bias (*C*), *d'* and ERP mean amplitudes, where IB status (IB, non-IB) and set-size (1T0D, 2T0D, 1T1D, and 3T0D) were used respectively as between- and within-subject factors. Greenhouse–Geisser correction was used when appropriate.

For the ERP recordings, activity was assessed on the basis of the regions with the largest magnitude of modulation (for a justification Rutman, Clapp, Chadick, & Gazzaley, 2010). Posterior and prefrontal regions were analysed using respectively the electrode pairs O1/2 and F3/4. Mean amplitudes for the contralateral waveforms in the latency of the N2pc (225-350 ms), CDA (351-900 ms), prefrontal bias (230-280 ms), and ADAN (420-500 ms) were calculated by averaging the activity at right hemisphere electrodes when subjects were instructed to attend the left visual field with the activity observed from the left electrodes when instructed to attend the right visual field. Waveforms were then obtained by subtracting the contralateral activity from the one observed ipsilaterally. Waveforms in the prefrontal regions may not be subject to lateralisation effects (particularly for the prefrontal bias signal), in that representation of visual stimuli should not occur (see for instance Liesefeld, Liesefeld & Zimmer, 2013). However, the ADAN is known to be a lateralised component (Seiss, Gherri, Eardley, & Eimer, 2007) and the same logic as for the N2pc and CDA may apply. Therefore, waveforms in the pair F3/4 were also analysed by averaging between left and right recording sites after effects on lateralisation were ruled out.

2.4 General experimental procedure

Participants first performed the AOSPAN test followed by the IB task. Finally, the change detection task was administered. Fig. 1B depicts the experimental procedure used for the change detection task. Both memory and test arrays were displayed within two display areas of 4.15°×7.41 at 80 cm viewing distance, and 1° away from the centre of the screen for both the right and left side. The size of the rectangles was 1.15° × 0.64° both for red and blue items. Stimuli arrays were matched for the level of luminance between a black background and the foreground targets and distractors. Participants were told use a response box to indicate whether or not the test array contained a change.

3. Results

Low-level-processing ERPs: Selection and storage. Capacity scores were submitted to logistic regressions to assess their power to predict the level of inattention. Processing capacity scores ($e^{\beta_{N2pc}}$) did not predict the level of inattention (p=.14); the regressional model was only marginally significant ($\chi^2(1) = 2.72$, p=.09; Nagelkerke $R^2_{N2pc} = .18$), suggesting no capacity differences during selection among the two groups, suggesting that the difficulty of the change detection task allowed the IB participants to select items in a comparable fashion to the Non-IB participants (see Fig. 2A-B). However, capacity scores estimated during the CDA latency significantly predict the level of inattention ($\chi^2(1) = 4.22$, p<.05; Nagelkerke $R^2_{CDA} = .27$), although the regressor $e^{\beta_{CDA}}$ did not reach statistical significance (p=.07), suggesting that even if both groups are able to select 1 or 3 target items during selection (i.e., N2pc latency), IB participants may be unable to maintain an on-going target representation during the retention interval when arrays of set-size 3 are presented.

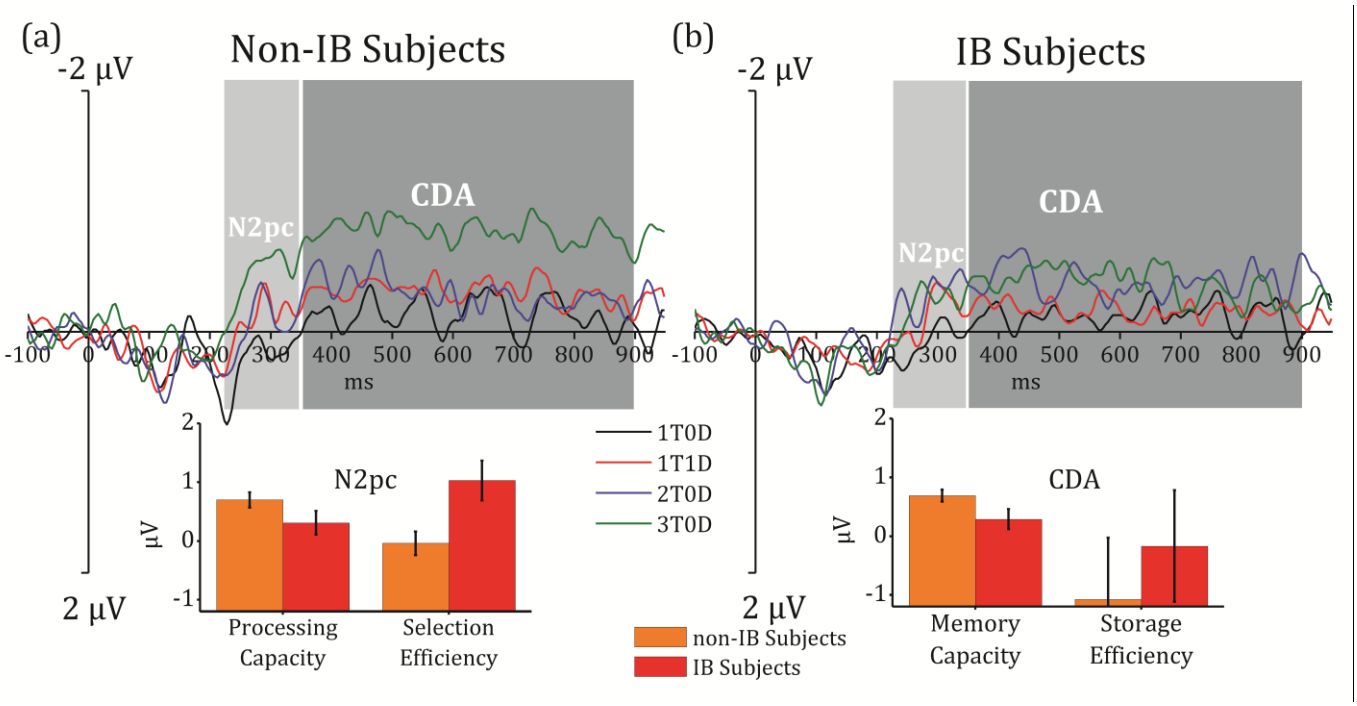

Fig. 2. Plot of the grand averaged ERP difference waves for the contralateral minus ipisilateral activity time-locked to the presentation of the memory array for the electrode pair O1-2 and divided between the two experimental groups: Non-IB (part a) and IB subject (part b). Inset graphs: differences across groups for the four assessed estimates based on the mean amplitude in the latencies of interest (shaded in the ERP plots).

In order to assess whether IB participants reached their memory capacity limit, mean amplitudes for set size 2 without distractors and set size 3 were submitted to a mixed ANOVA with the IB status as the between-subject factor. Results showed a main effect of set size and a significant interaction with IB status ($Fs(1,17) > 11.04$, $ps < .005$, $\eta_p^2 = .39$ and $\eta_p^2 = .48$ respectively for the main effect and interaction) with no main effect of the group ($F(1,17) = .17$, $p = .68$, $\eta_p^2 = .01$). Post hoc t-tests were carried out, showing that mean amplitudes in the IB group between set size 2 and 3 are not significantly different ($\bar{x}_{IB} = -.15$, $SE_{IB} = .08$; $t(6) = -1.81$, $p = .06$, one-tailed) when compared to Non-IB participants ($\bar{x}_{NIB} = .42$, $SE_{NIB} = .09$; $t(11) = 4.34$, $p < .0005$, one-tailed), suggesting –consistently with the preliminary study (see Supplementary information), that IB participants may have reached their VWM capacity limit. IB individuals saturate their resources on a smaller number of items (2T0D), whereas non-IBs do so with a higher number of targets (3T0D), suggesting a flexible dilution

of resources which depends on the capacity limits: for the processing of 2T0D set size IB individuals deploy all their capacity allowance, while non-IB individuals appear to present more resources left when arrays of three target items are displayed, suggesting that although resources are deployed flexibly depending on the capacity, they are not all allocated at any given time as for the flexible allocation model view, but are gradually deployed in an unequal quantised manner, suggesting an hybrid model of resource allocation (see Introduction and Discussion).

High-level processing ERPs: Active suppression and supramodal attentional control. Following Liesefeld, Liesefeld, and Zimmer (2013), we assessed the effect of distractors on active suppression (i.e., prefrontal bias, see Liesefeld et al. 2013) and later reorienting of attention during the presence of distractors (ADAN) in the frontal region (pair F3/4; see Fig. 3). For the prefrontal bias, averaged activity across left and right frontal recording sites was analysed. We compared the set-size two with distractor from the set-size without distractor, so that the effect of the number of items could be controlled for, and therefore any difference should be attributable to the processing of distractors. We evaluated whether this distractor-presence increase was predictive of the level of inattention. No differences were found for the prefrontal bias (*p*s>.94). To exclude a possible lateralisation effect during this latency the same analysis was also carried out on the contralateral waveforms but differences were not significant (*p*s>.47). However, when averaged waveforms were used to assess the increase in mean amplitudes from set-size 1 to set-size 3 (target-presence only), a significant increase was found predictive of the level of inattention ($\chi^2(1) = 7.45, p <$.007, Nagelkerke $R^2 = 0.44$), $e^{\beta_{1T0D\ to\ 3T0D}} = 3.16, \mathrm{W}(1) = 4.95,\ p < .03, \mathrm{CI}_{95} = 1.14,\ 8.73$), suggesting that this component may not only be associated with active suppression of distractors, but also susceptible to cognitive load (no lateralisation effect were found, *p*s>.74; see Fig. 4), with the IB participants showing a poorer modulation. Conversely, non-IBs appear to have a stronger

prefrontal signalling that may produce a facilitation during selection (i.e., less active suppression) and storage (of distractors) in the posterior regions (i.e., N2pc and CDA respectively).

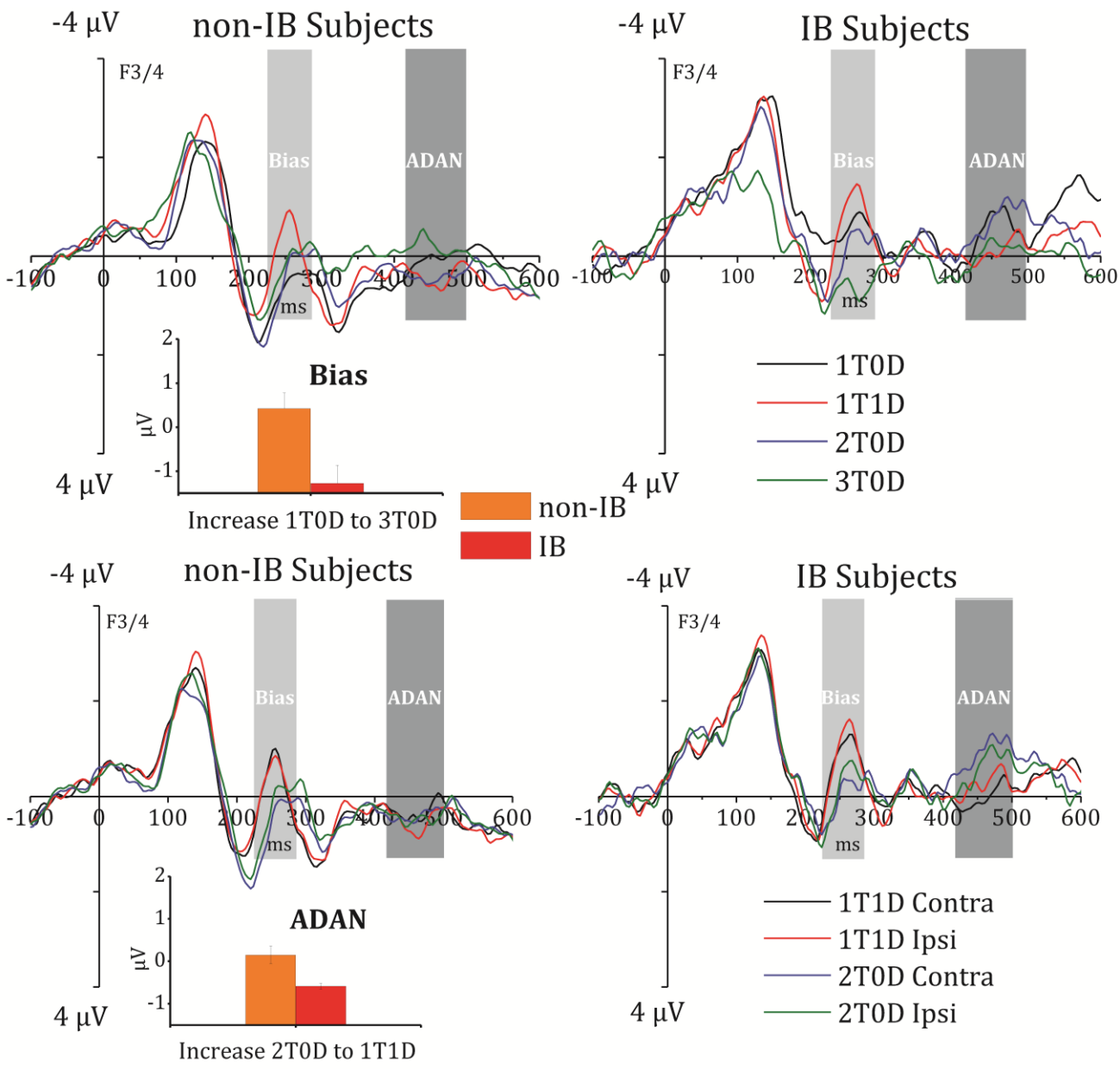

Fig. 3. ERPs waveforms time-locked to the presentation of the memory and between the two experimental groups for the electrode pair F3/4: Non-IB (left) and IB subjects (right).Top panel: Plot of the grand average ERP waves averaged across left and right frontal recording sites (F3/4) to extract the prefrontal bias signal and ADAN components. Inset graph: bias differences across groups based on the mean amplitudes in the latencies of interest (shaded in the ERP plots). Bottom panel: Plot of the grand average ERP difference for the contralateral minus ipisilateral waves. Inset graph: ADAN differences across groups based on the mean amplitudes in the latencies of interest (shaded in the ERP plots).

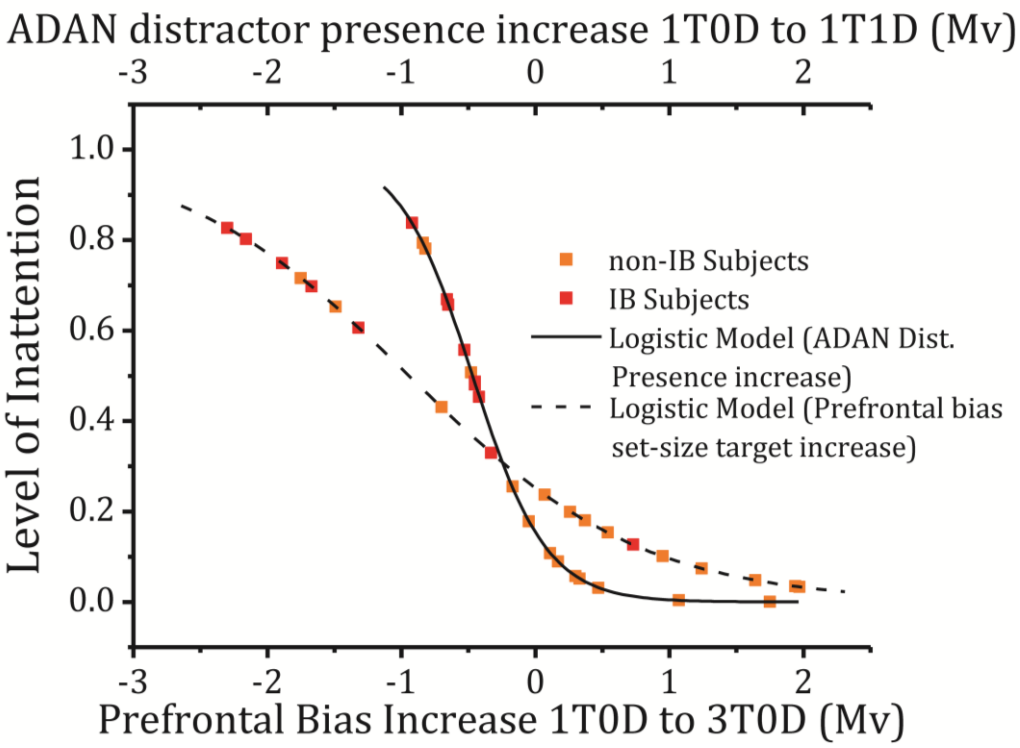

Fig. 4. Predicted probabilities regressing the level of inattention (tendency to neglect the transition change at the IB task) on the prefrontal bias (set-size effect: increase in *Mv* from 1T0D to 3T0D) and ADAN latency (distractor-presence effect: increase in *Mv* from 1T0D to 1T1D).

Differently, the mean amplitude increase for the distractor-presence contrast showed a difference during the ADAN latency, with non-IB subjects resulting with more negative mean amplitudes than IBs ($\chi^2(1) = 8.05, p <.006$, Nagelkerke $R^2 = 0.47$), $e^{\beta_{2T0D\ to\ 1T1D}} = 38.97, \mathrm{W}(1) = 3.89,\ p < .05, \mathrm{CI}_{95} = 1.02,\ 1479.98$), suggesting that, consistently with preliminary selection during the N2pc, non-IB individuals appear to orient their attentional resources towards the distractors in concomitance with higher *d'* scores and a lower response bias (*C*; see behavioural performance). This effect is also visible when averaged waveforms were assessed during the same ADAN latency (for a justification see Couperus, Alperin, Furlong, & Mott 2014), with IB participants allocating fewer resources than non-IBs during the set-size 1 with distractors compared to set size 2; however this effect did not reach statistical significance (*ps*>.12). In sum, ADAN lateralisation of resources during the presentation of distractors may have the effect of decreasing the level of inattention for

unexpected stimuli. No significant lateralisation difference was found for the target-presence contrast (i.e., mean amplitude increase from set-size 1 to 3; *p*s>.84). These results suggest that the tendency to present high/low levels of inattention do not appear to modulate the early processing of distractors in high-level brain processors (F3/4); however, in non-IB subjects, the presence of more targets (i.e., higher set-sizes) appears to be associated with a heavier processing during the prefrontal early component when compared to IBs (latency 230-280 ms). Although the frontal initiation of selection is not different among the two groups, the later ADAN component appears to be differentially modulated across the two groups when distractors are presented, suggesting that non-IB participants allocate resources to "extra" (qualitatively different) visual stimuli, which may be relevant such as the one in the IB task, or alternatively irrelevant as the distractors in the change detection task. However, processing these extra stimuli appears not to impact the performance in non-IB individuals (probably because of the presence of a resource surplus; see next section).

Measures of association and behavioural performance. To evaluate whether capacity scores (AOSPAN, CDA, N2pc and VWM values as estimated from the performance at the change detection task) were predictive of the tendency to filter distractors (i.e., selection efficiency) during the N2pc latency, hierarchical regressions were performed. AOSPAN scores predicted selection efficiency during the N2pc and an interaction was also found with IB status. Furthermore, WMC scores were predictive of the selection efficiency and an interaction with the IB status was found (Fs(2,16) >4.32, *p*<.04; Model 1: AOSPAN scores, AOSPAN scores × IB Status: R^2 = 0.51; Model 2: behavioural capacity, behavioural capacity × IB Status: R^2 =0.35). Regressors for AOSPAN scores and behavioural capacity (Equation 1), as well as their interaction term with IB status were also significant (all *p*s<.05; see Fig. 5A). In summary, selection efficiency was predicted by behavioural estimates of WMC

(AOSPAN) and VWM capacity (Equation 1), reinforcing the idea that capacity limits influence the allocation of resources across a visual array.

The model predicting selection efficiency (N2pc) as a function of the VWM capacity (CDA) was only marginally significant (F(1,17) = 3.94, *p*=.06), and the inclusion of the interaction term CDA capacity × IB status did not increase the explained variance ($\Delta R^2 = .06, F(1,16) = 1.49$, *p*=.23). Processing capacity scores (N2pc) did not predict selection efficiency, and no interaction or main effect of the IB status were found (*p*s>.07). However, a logistic model using selection efficiency as an explanatory variable was predictive of the IB status ($\chi^2(1) = 7.59$, *p*<.007; Nagelkerke $R^2 = .45$), although its regressor was marginal ($e^{\beta_{Sel.\ Eff.}} = 8.33, CI_{95} = .91,76.21, p = .06$), showing that every unit increase in selection efficiency the level of inattention may increase by 8.33 times (see Fig. 5B). Since the effect of the predictor capacity scores (CDA) was only marginal, these results suggest that the storage efficiency in VWM during the retention interval (351-900 ms) may depend on the items that are filtered/not-filtered during the earlier selection and enhancement of stimuli

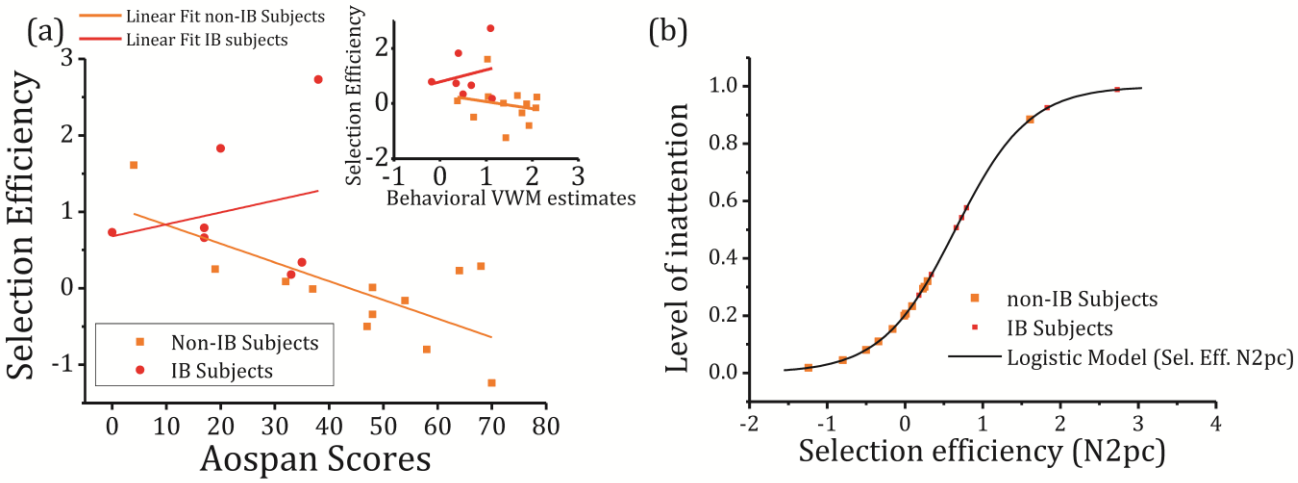

Fig. 5. (a) Scatterplot showing the correlation between AOSPAN and the selection efficiency scores based on the change detection task ERP recordings. Inset graph: correlation between selection efficiency and the behavioural estimate of the WM capacity based on the change detection task objective performance. Linear fit lines are also plotted. (b) Predicted probabilities regressing the level of inattention (tendency to neglect the transition change at the IB task) on the selection efficiency.

in the N2pc latency (225-350), rather than during the retention interval *per se*, as proposed by Vogel, McCollough and Machizawa (2005). A logistic model predicting the IB status as a function of the efficiency storage scores (i.e., Equation 2) was not significant (*p*s>.51). Furthermore, IB and Non-IB individuals appeared to present a reversed pattern when selection efficiency (N2pc) and VWM capacity (CDA) scores are cross-compared. Non-IB individuals appear to select and enhance not only target items but also irrelevant distractors during the N2pc latency (i.e., low selection efficiency), whilst presenting higher WM capacity scores. Conversely, IB participants appear to select only the relevant information during the N2pc latency, whilst they present low VWM capacity scores.

AOSPAN scores, counts during the IB task and estimates of VWM based on the change detection task were submitted to logistic regressions to assess their ability to predict the IB status of the participants. Results showed that AOSPAN and VWM scores behaviourally estimated can reliably predict the tendency to inattention, showing that high levels of inattention (i.e., IB individuals) are associated with both lower AOSPAN scores and VWM estimates ($\chi^2(1) > 6.38$, *p*<.02; Nagelkerke $R^2_{AOSPAN} = .39, R^2_{VWM} = .55$; $e^{\beta_{AOSPAN}} = .92, CI_{95} = .86, .99$; $e^{\beta_{VWM}} = .03, CI_{95} = .002, .67$; *ps*<.04; see Fig. 6A). This suggests that the amount of information that can be stored in VWM is associated with different levels of inattention in a complex dynamic scene; a unit decrease in VWM heightens by 33 times ($1/e^{\beta_{VWM}}$) the level of inattention.

Performance at the primary task in the IB task was also assessed. IB status predicted the number of counts, showing that a higher number of counts at the primary task *decreases* the level of inattention ($\chi^2(1) > 15.44$, *p*<.001; Nagelkerke $R^2_{Count} = .76$); the predictor

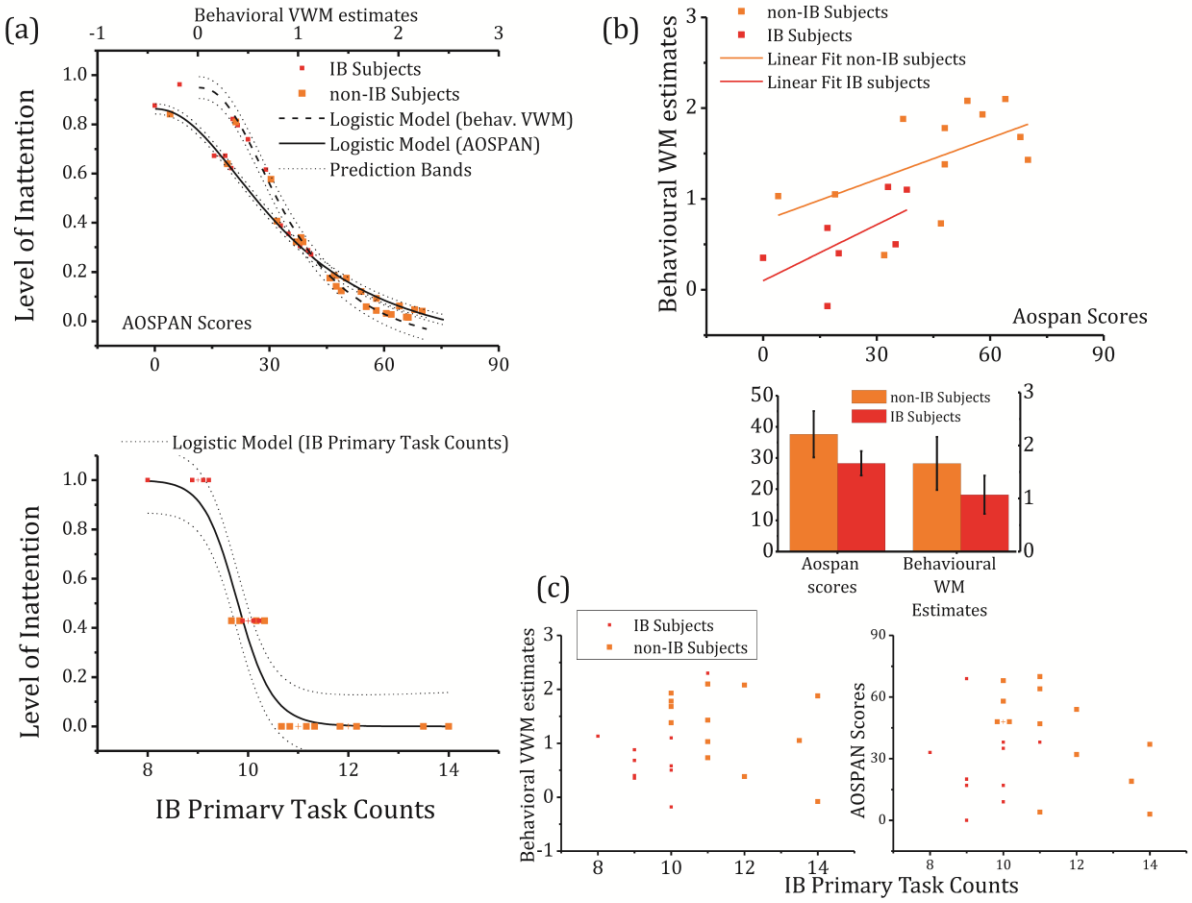

Fig. 6. (a) Predicted probabilities regressing the level of inattention (tendency to neglect the transition change at the IB task) on the AOSPAN and VWM scores (top panel), and IB primary task counts (bottom panel). Note: data points depict the empirical classification as obtained from the IB task (see legend). Plus signs in the plots indicate overlapped *y*-value offset plotting for the same *x*-value. Prediction bands are depicted as dashed lines. (b) Top panel: Scatterplot showing the relationship between AOSPAN scores and the behavioural estimate of the working memory capacity based on behavioural performance in the change detection task; linear fits are plotted to aid visual inspection. Bottom panel: Bar charts showing the overall difference between the low and high inattention groups (error bars depict standard error). (c) Correlations between IB primary task counts and behavioural estimate of WM and VWM capacity.

$e^{\beta_{Counts}}$, although contributing to the model, did not reach statistical significance (p=.99). Interestingly, IB participants failed to notice the unexpected change even though they were poorer at counting, whereas Non-IB subjects noticed it whilst they were performing better than the IB group, suggesting a direct link between capacity limits and inattention (i.e., low capacity impairs both primary task and tendency to notice, extra, unexpected visual stimuli).

Furthermore, AOSPAN scores and estimates of VWM (Equation 1) based on the change detection task are highly correlated ($r(17) = .71$; $p<.0006$; one-tailed; see Fig. 6B),

but both were not found to be significantly correlated with the number of counts (p>.09; one-tailed) at the IB task; however, a clear pattern was still observed between the two groups (see Fig. 6C). Overall, these results reinforce the idea that limits in working memory capacity drive a tendency to attend extra unexpected visual stimuli.

Behavioural performance (i.e., accuracy) was assessed by submitting estimates of *d*' and criterion (*C*) to a mixed ANOVA to assess differential sensitivity and response bias differences across the different set-sizes (set-size 1, set-size 2 with and without distractor, and set-size 3). Main effects of set-size and IB-status were found for both *d*' and *C* (F(3,51) >4.37, p < .01; *d*' size effects: set-size η_p^2=.72, IB group, η_p^2=.21; *C* criterion size effects: set-size η_p^2=.20, IB group, η_p^2=.33; Greenhouse-Geisser correction was used for *C* criterion). Overall, both groups show a lower sensitivity and a more conservative criterion with higher set-sizes; however, when IB are compared to non-IB individuals, IB individuals show a lower level of sensitivity and they tend to be more biased (i.e., conservative –saying more frequently that there is no change) than Non-IB participants (see Fig. 7A-B). Set-size did not interact with IB group for both *d*' and *C* (F(3,51) <.60, p > .61; *d*': η_p^2=.03; *C* criterion:

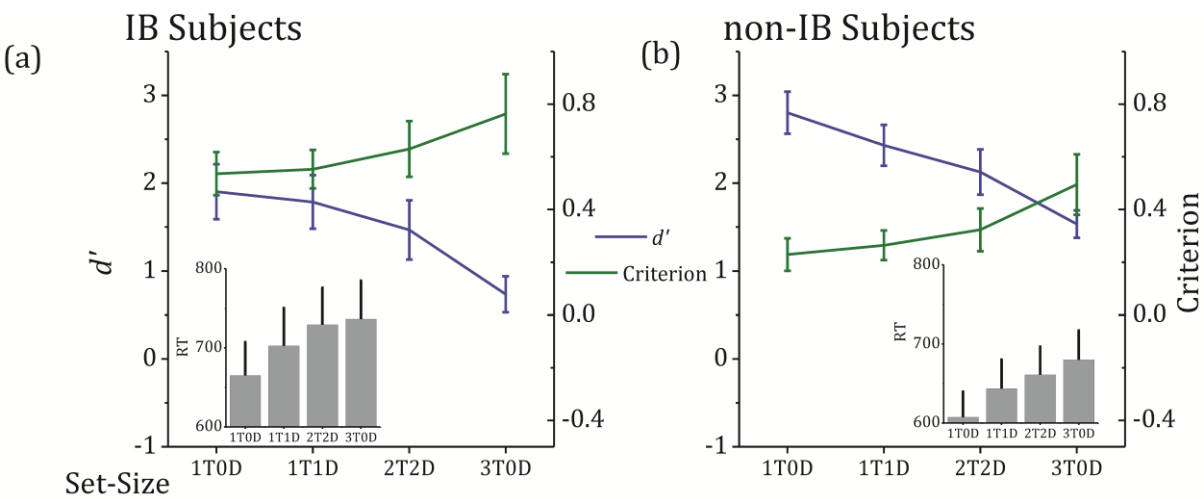

Fig. 7. Estimates of *d'* and *C*riterion as a function of the four experimental conditions for IB (left) and Non-IB participants (right): 1 target (1T0D), 1 target and 1distractors, (1T1D), 2 targets (2T0D) and 3 targets (3T0D). Inset graphs: bar chart depicting reaction time differences for the experimental conditions.

η_p^2<.01), suggesting that differences in *d*' and *C* criterion are attributable to intrinsic differences amongst the two groups in terms of differential allocation of attentional resources or even lower resolution in the low-level visual processors (i.e., participants with limited working memory resources are less sensitive to detect changes and more conservative to make decisions; see for example the explanation in Papera & Richards, 2016). In sum, capacity limits not only are associated with different levels of inattention, but also with differential sensitivity and bias to produce responses.

Furthermore, following Papera, Cooper, and Richards (2014), and Papera and Richards (2016), who showed that IB individuals tend to respond more slowly than non-IB individuals, a mixed-effect ANOVA was carried out on RTs. This analysis showed a significant effect of set-size (F(3,51) =14.44, $p < .001$, η_p^2=.45; Greenhouse–Geisser correction was applied) with RTs increasing as set-size increased. Although IB participants were ~50 ms slower to provide a correct decision (i.e., presence/absence of a change) than Non-IB participants (see inset graphs in Fig. 7A-B) this was not significant (F(1,17) =1.15, p= .29, η_p^2=.06). No differential effects between the set-size and the experimental groups were found (F(1,17) =.10, p= .95, η_p^2<.01). A post-hoc t-test was carried out between the set-size conditions with and without distractor to evaluate whether the inclusion of the distractor had influence on the responsiveness of the participants to make decisions but no differences were found (t(18) =1.62, p=.06; one-tailed).

A ROC curve analysis was performed on the *d'* and *C* estimates. Values of *d'* prime above 2.76 were found to be predictive of the tendency to inattention during the presentation of set-size 3 arrays (AUC=.83, $\mathrm{CI}_{95} = .64, 1;\ \ \mathrm{z} = 3.66, p < 0.02$; effect for lower set-sizes were not significant: p>.07), increasing the likelihood to present low levels of inattention by 4.71 times (LR_+) confirming that differences in VWM capacity scores as estimated from the

change detection task (i.e., Equation 1) may be reliably used to predict propensity to inattention (for instance in the absence of EEG equipment). Conversely, the criterion adopted by the participants could be used as a predictor for the propensity to inattention for set-size 1 and 2 with and without distractor (AUC>.79, lowest bounds: $\mathrm{CI}_{95} = .58, 1;\ \ \mathrm{z} > 2.9, p < 0.04$). *C* values above .38 ($\mathrm{LR}_{+} = 5.43$) for set-size 1, and .46 and .62 for set-size 2 respectively with/without distractor ($\mathrm{LR}_{+} = 4.43$ equal), are associate to a more conservative criterion, therefore making participants more likely to be inattentive towards unexpected stimuli/changes (i.e, participants would tend to say they have not noticed any stimulus/change). However, *C* values for set-size 3 did not reach statistical significance (*p*>.15), suggesting both groups tend to utilise a more conservative criterion for higher set-sizes, leading to a poor discriminatory power and confirming the appearance of an upper capacity limit. Overall these findings are consistent with previous studies showing differences in visual search associated with a tendency to inattention (see for example Papera, Cooper, & Richards, 2014; Papera & Richards, 2016).

4. Discussion

Our results indicate that high levels of inattention are more likely associated with a low WMC, making individuals more susceptible to neglect visual information whether it is pertinent (i.e., a relevant but unexpected change) or not pertinent to the goals of the primary task (i.e., a blue rectangle distractor). Capacity limits as estimated from three different measures can reliably predict the propensity of individuals to neglect unexpected changes in a visual scene: AOSPAN (for a general measure of memory capacity and resource allocation), behaviourally estimated VWM and ERP based WMC scores (CDA). Furthermore, not only capacity limits appear to modulate the level of inattention, but do also drive different perceptual strategies. IB individuals appear to ignore irrelevant distractors (i.e., expected

irrelevant information), in that they may try to ensure that the few resources available to them are used to represent only the target items given their low VWM capacity; this may also apply to unexpected (yet relevant) changes (e.g., IB task). In contrast, Non-IB individuals present a higher VWM capacity and do not present a tendency to filter irrelevant/relevant information; this may be due to their high capacity to represent stimuli during the retention interval in the change detection task, making this *surplus* (i.e., spare capacity left over) of resources the presumed cause for why they present a low level of inattention when inspecting a complex visual scene such as the IB task. Finally, our study suggests that allocation of resources may occur in a quantised and flexible manner. The amount of resources allocated in arrays of increasing set-size varies flexibly depending on the capacity. When capacity is low (e.g., IB individuals), most of the resources available are used for small set-size arrays, leaving few available for processing of further items or higher set-sizes. However, when capacity is high (e.g., non-IB individuals), only a portion of resources are deployed during the presentation of small set-sizes. This suggests that resources might be all allocated (as a flexible model would predict) only when individual's capacity is very low (e.g., IB individuals). Conversely, although resources appear to be allocated in a quantised manner, when capacity is higher increasingly set-sizes receive an increasingly larger chunk of the resources available (see for example the difference in waves between 2T0D and 3T0D in Fig. 2 when capacity is high, e.g., non-IBs), until saturation is obtained (i.e., appearance of capacity limit). This is in contrast with a fixed-resource model, which would predict an equal distribution of resources (i.e., each item receives the same amount of resources, regardless of its complexity; see for instance Barton, Ester, & Awh, 2009), suggesting a hybrid weighting mechanism –flexible and discrete, whose weighting depends on (1) its capacity limits and (2) the number of item presented (i.e., larger chunks of resources are deployed as the system approaches its limit). Given the same set-size (e.g., 2) individuals whose capacity is larger

tend to allocate a smaller population of neurons (more positive mean amplitudes) than those with a small capacity, whose mean amplitudes tend to be more negative (i.e., more resources are required for encoding and representation).

Although flexible models propose that allocation of resources should be larger when the complexity of the items is high, Barton, Ester and Awh (2009) reported that participants' performance remain unchanged even when the number of items in the array remains constant but with substantial changes in the complexity of the items, suggesting again the presence of a discrete mechanism. A discrete on-going WM resource allocation where the VWM sub-component is thought to maintain the representation of 4 ± 1 chunks (Cowan, 2001; Drew & Vogel, 2008; Fukuda, Awh, & Vogel, 2007; Vogel & Machizawa, 2004). The idea of a "new magical number" for the VWM compared to the 7 ± 2 number for the Short Term Memory or WM (Miller, 1956; see also Baddeley & Hitch, 1974) is supported by several findings that report a sustained performance drop in change detection paradigms with set-sizes of more than 4-5 items. This would occur irrespective of the complexity of the array: an array of items with more than one feature per item does not significantly affect the memory capacity when is compared with an array of one stand-alone feature items (Luck & Vogel, 1997).

Even though in our study item complexity was not manipulated, results showed that differences in the allocation of resources in more complex array of items such as those with distractors appear to be influenced by individual differences in VWM capacity and secondarily by the number of items in the array, leading to differential perceptual strategies (i.e., filtering distractors and prevent them from being maintained in VWM, or selecting them and keep their representation). Future research may address this matter by using simpler and complex items (in a fashion similar to Barton, Ester, & Awh, 2009) and see whether this affects the amount of resources allocated to stimuli.

However, our results cannot tell us what is the proportion of resources that are allocated to each of the items *within* the display array. Future research could evaluate a reconfiguration of the change detection task that might enable the issue of processing of targets and distractors to be examined directly during the N2 latency, since the N2pc appear to be the summation of two subcomponents (Feldmann-Wüstefeld & Schubö, 2013): a P_D (distractor positivity) component that mirrors direct suppression of the cortical representation of distractors, and a N_T component thought to enhance the representation of relevant stimuli such as targets. By positioning the distractors in the periphery of the array with targets displayed centrally would enable a possible contralateral waveform to be detected that would reflect the representation of the distractors in memory. Conversely, reversing the display for, such that targets were presented in the periphery with the distractors centrally presented would give a measure of the representation of targets in memory.

During the N2pc latency, processing capacity scores did not predict the level of inattention; however, a difference in the use of the available resources during this latency was observed. This tendency to filter information appears to be the result of intrinsic limits in the amount of resources available to maintain an on-going representation of visual stimuli during the retention interval (CDA latency). Although VWM capacity scores (CDA) were not sufficiently predictive (i.e., marginal effect, p=.06) of the selection efficiency (N2pc), IB participants with low VWM capacity (CDA latency) were observed not to attend irrelevant information during the N2pc period since representing distractor in visual working memory (CDA latency) may impair their ability to maintain the representation of the relevant target items.

One possibility might be that the low capacity observed for IB participants drives a tendency to actively filter irrelevant information, but may also be explained by a passive process where items are ignored/not attended as a result of a lack of resources. This may also

apply to non-IB individuals when set-sizes near their capacity limit are used. Future research should address this question further to clarify the nature of this mechanism. The former mechanism appears to be consistent with data that come from eyetracking studies, showing that IB individuals fixate irrelevant distractors more frequently than do Non-IBs, perhaps in an attempt to rapidly select and filter them (Richards, Hannon, & Vitkovitch, 2012). Moreover, electrophysiological findings show that rapid distractor suppression during the latency of the N2 can be observed during the presentation of salient but irrelevant visual information (Kiss, Grubert, Petersen, & Eimer, 2012).

It is still unclear if the CDA is purely a measure of visual working memory or if it reflects a common mechanism of resource allocation control and storage of information (working memory). Some researchers (Sanada, Ikeda, Kimura, & Hasegawa, 2013) have resolved this ambiguity by referring to the CDA or to sustained posterior contralateral negativity (SPCN) on the basis of the task, with the CDA being observed during working memory tasks (i.e., memory mechanism), and the SPCN elicited in non-working memory tasks, such as target identification (Papera & Richards, 2016; Jolicoeur, Brisson, & Robitaille, 2008; Mazza, Turatto, Umiltà, & Eimer, 2007), since they involve on-going maintenance of visual search stimuli (i.e., attentional resources).

The CDA has been observed in change detection tasks requiring the maintenance of target items and has been interpreted as reflecting the number of items retained in visual working memory (Drew & Vogel, 2008; Ikkai, McCollough, & Vogel, 2010; McCollough, Machizawa, & Vogel, 2007; Vogel, McCollough, & Machizawa, 2005; Vogel & Machizawa, 2004). However, its interpretation is controversial since other studies appear to provide evidence that the CDA does not reflect a memory maintenance mechanism *per se* but a more general measure of resource allocation more consistent with the notion of working memory (WM; Todd & Marois, 2004; Van Dijk, Van der Werf, Mazaheri, Mendendorp, & Jensen,

2010; Xu & Chun, 2006). This is also been brought to attention by recent studies showing that a reduction in CDA amplitudes does not necessarily imply that memory storage may be reduced, but it might be associated with a specific deficit in the allocation of attentional resources during encoding and retention of visual stimuli (see for example Berggren & Eimer, 2016).

Differences in capacity limits in VWM (CDA) also appear to modulate the levels of inattention and also differences in item selection during the N2pc, suggesting a strong coupling between selection and storage (see also McCollough, Machizawa, & Vogel, 2007). Participants can select and then maintain a given number of items in their VWM, but when memory capacity is exceeded mean amplitudes in the CDA latency are significantly diminished; this may support the idea of a discrete mechanism for the maintenance of a limited number of items (e.g. 2-3 chunks of information in accordance with the discrete resources view). However, our results show a relationship between a discrete and flexible allocation of resources making the two not necessarily mutually exclusive.

In our study, IB participants appear to saturate their resources much earlier with lower set sizes (i.e., set size 1-2) than Non-IB participants, leaving few or no resources available for higher set sizes. Both high and low level of inattention individuals showed a comparable processing capacity (i.e., N2pc, scores do not predict the inattention level); however, during the CDA latency, when set size 2 without distractors is presented, IB participants allocate most of the available resources to maintain the representation of the two target items. This leaves insufficient resources for array of set size 3, suggesting that capacity in VWM may have been exceeded. No differences were found between set size 2 without distractors and set size 3 in IB participants. This was opposed to Non-IB participants who showed an increase for set-size 3, suggesting more availability of resources to represent further items.

Capacity limits are associated with different levels of inattention; therefore, we followed up these differences in order to assess whether they are linked to a differential supramodal attentional control. An increase in mean amplitudes from set-size 1-to-3 was found during the latency of the prefrontal bias between low and high level of inattention individuals. In contrast to Liesefeld, Liesefeld and Zimmer (2013), our findings show that this component may not only reflect a process of active suppression (i.e., no differences were found for the distractor-presence contrast between non-IBs and IBs), but also subject to cognitive demands (if extra resources are available), since mean amplitudes significantly increased for the 1-to-3 set-size for non-IBs compared to IB participants. Next, we found evidence of lateralisation effects during the ADAN latency, suggesting that prefrontal cortex in individuals with high capacity (i.e., N2pc/CDA) *and* low levels on inattention (compared to those with low capacity and high levels of inattention), may signal the necessity to allocate more resources for the maintenance of the distractor; this implies that extra resources for the processing of the distractors must be available in VWM. However, the reason why distractors are attended is still unknown. Some studies have proposed a link between the tendency to present low level of inattention and ADHD (see for example Arcos-Burgos et al., 2010; Grossman, Hoffman, Berger, & Zivotofsky, 2015; Martinez, Muenke, & Arcos-Burgos, 2011; Papera & Richards, 2016; Ribasés et al., 2010). Although still controversial, since a number of studies discuss an impairment during visual search in ADHD subjects (Fallgatter et al., 2013; Maccari et al., 2013), ADHD individuals may present an alternative perceptual style which is less equipped to deal with detection of repeated stimuli, but more adapted to reorient/allocate visual-spatial attention towards unexpected stimuli (Couperus, Alperin, Furlong, & Mott, 2014; Grossman et al., 2015). This also appears to receive support from genetic studies, which showed that nucleotide polymorphism variants for the LPHN3 that confer ADHD susceptibility are older than the LPHN3 allelic variant that protects against

ADHD (Ribasés et al., 2010; Arcos-Burgos et al., 2010; Martinez et al., 2011). Therefore, it may be conceivable that this type of scene exploration (anticipation of extra stimuli) may have provided some advantage in evolutionary terms. For instance, it may have allowed the detection of an unexpected prey (or a predator) more readily (Hartmann & Ratey, 1995). In our study, non-IB participants were able to notice the unexpected (and relevant) stimulus in the IB task, but also distractors during the change detection task (which are expected although participants do not know when they are displayed), suggesting that these individuals may have a pure tendency to notice unexpected changes in the visual scene (regardless of their relevancy). This explanation also appears to be consistent with studies that investigate prefrontal alpha synchronization, which is thought to reflect top-down inhibition of the frontal areas in order to avoid these areas becoming involved in distracting new activities while a task is performed (see for instance Sauseng et al., 2005 ; Dehaene & Changeux, 2011; see also Papera & Richards, 2016, for associations between theta power and ERPs during early visual processing between low and high level of inattention individuals). In this sense, non-IB individuals may present a weaker feedback modulation toward the posterior areas to prevent the processing of unexpected incoming stimuli, therefore making them more easily "distracted" (i.e., less prefrontal inhibition) by incoming unexpected stimuli. Future research should investigate further the existence of tight prefrontal ERP-ERSPs associations to reorient attention during preselection (bias) and storage (ADAN).

In contrast with Vogel, McCollough, and Machizawa, (2005; see also McCollough, Machizawa, & Vogel, 2007) we found that although non-IB participants have a higher capacity than IB subjects (and therefore, following their findings, should be able to filter irrelevant distractors; see Vogel *et al.*, 2005), they appeared to select and maintain the representation of distractor items along with the targets, suggesting that participants that present high memory capacity *and* low levels of inattention maybe not directly equal to

participants with high memory capacity only (there is no assessment of the level of inattention in Vogel *et al.*, 2005). As noted, high capacity and low levels of inattention may confer an advantage in visual search behaviour (e.g., noticing unexpected stimuli may be useful) when this does not come at the expense of the primary task performance. For instance, an individual with both low levels of inattention and capacity may not have such advantage. Our results have shown that participants with high levels of inattention appear to neglect unexpected visual stimuli/changes more likely because of a tendency to filter ambiguous (e.g., red-cross, see Supplementary information), relevant (e.g., target letter change), and irrelevant (e.g., distractors) stimuli, and that this appears to be the result of their capacity constraints. Future research should evaluate the level of inattention for those participants that present both high capacity and high tendency to filter information/high level of inattention (if observable), and why they may not present the advantage of noticing unexpected stimuli. One possible concern is that is the possibility that our results may have been distorted by the choice to subtract 1T1D from 2T0D as an index of filtering efficiency, rather than, for instance, 2T1D from 3T0D might have provided a more sensitive measure. However, since the pilot study showed that individuals with low and high level of inattention may present a relatively low capacity (when compared to subjects with normal levels of inattention; see for example the k levels in Fukuda, Awh, & Vogel, 2010; Vogel, McCollough, & Machizawa, 2005), using a contrast with a higher set-size might have produced a ceiling effect (i.e., mean amplitudes saturates very quickly, preventing the observation of difference between the groups; this was shown in our pilot study; see Supplementary information).

Despite flexible models offering an explanation for the processing and storage of visual information, the type of resource allocation they proposed is challenged by those findings that support the notion of a discrete storage of the information (i.e., a given number

of chunks or items). Vogel and Machizawa (2004) found that during the retention interval the CDA amplitude was enhanced when the number of items was higher (e.g. for example from 1 item to 4 items), showing an asymptotic drop between 3 and 4 items (see also Fukuda, Awh, & Vogel, 2010; Vogel, McCollough, & Machizawa, 2005). In contrast, flexible models propose that neural activity associated with storage of items should continue even for set size of 5 or more items. However, previous research outlined above support the notion that storage is limited to a few number of items in VWM; this was also found in our study, where IB participants clearly show a drop in their mean amplitudes between set-size 2 vs. 3. Moreover, *d*' and *C* estimates in our study showed that accuracy decreases concomitantly with an increase of the conservatism in the participants' decisions, favouring the idea that a memory limit can be expected at relatively low set-sizes.

4.1 Conclusions

Taken together, these results suggest that further developments in visual processing modelling should take into account the capacity limits during both selection and maintenance of stimuli in VWM, since individual differences in such limits determine a differential allocation of resources (i.e., both quantise and flexible) for when individuals have to attend low or high set-sizes. Furthermore, the complexity of the array appears to be resolved by the participants depending on their availability of resources: irrelevant items are only selected if the available resources for participants are enough to perform a visual search task and a surplus of resources is available for processing them. High capacity limits and tendency to process extra stimuli (which may be relevant) appears to be associated with low levels of inattention when engaged in a demanding multi-object task. A crucial question for future research is whether this allocation of extra resources is not a correlative measure but indeed the direct cause of the neglect of unexpected visual stimuli.

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7. References

Arcos-Burgos, M., Jain, M., Acosta, M.T., Shively, S., Stanescu, H., Wallis, D., *et al*. (2010). A common variant of the latrophilin 3 gene, LPHN3, confers susceptibility to ADHD and predicts effectiveness of stimulant medication. *Molecular Psychiatry*, 11, 1053-1066. DOI: 10.1038/mp.2010.6

Baddeley, A.D., & Hitch, G. (1974). Working memory. In G.H. Bower (Ed.), *The psychology of learning and motivation: Advances in research and theory* (Vol. 8, pp. 47–89). New York: Academic Press.

Barton, B. B., Ester, E. F., & Awh, E. (2009). Discrete resource allocation in visual working memory. *Journal of Experimental Psychology: Human Perception and Performance*, 35, 1359-1367. Doi: 10.1037/a0015792

Bays, P. M., & Husain, M. (2008). Dynamic shifts of limited working memory resources in human vision. *Science*, 321, 851-854. Doi: 10.1126/science.1158023

Bays, P. M., Catalao, R. F. G., & Husain, M. (2009). The precision of visual working memory is set by allocation of a shared resource. *Journal of Vision*, 9, 1-11. Doi:10.1167/9.10.7

Berggren, N., & Eimer, M. (2016). Does Contralateral Delay Activity Reflect Working Memory Storage or the Current Focus of Spatial Attention within Visual Working Memory? *Journal of Cognitive Neuroscience*, 28(12):2003-2020. Doi: 10.1162/jocn_a_01019

Brigadoi, S., Cutini, S., Meconi, F., Castellaro, M., Sessa, P., Marangon, M., ... Dell'Acqua, R. (2016). On the Role of the Inferior Intraparietal Sulcus in Visual Working Memory for Lateralized Single-feature Objects. *Journal of Cognitive Neuroscience*, 14, 1-15. Doi: 10.1162/jocn_a_01042

Budau, J. (2011). Inattentional blindness: present knowledge, recent research and implications for the nuclear industry. *32nd Annual Canadian Nuclear Society conference and 35th CNS/CNA student conference* 45(18). DOI: not available

Chabris, C. F., Weinberger, A., Fontaine, M., & Simons, D. J. (2011). You do not talk about Fight Club if you do not notice Fight Club: Inattentional blindness for a simulated real-world assault. *I-Perception*, 2(2), 150–153. Doi:10.1068/i0436

Couperus, J., Alperin, B., Furlong, D., & Mott, K. (2014). Visual Selective Attention in Adults with ADHD: Electrophysiological Evidence of Facilitation and Suppression. *Journal of Behavioral and Brain Science*, 4, 129-140. doi: 10.4236/jbbs.2014.43017.

Cowan, N. (2001). The magical number 4 in short-term memory: a reconsideration of mental storage capacity. *Behavioural and brain sciences*, 24, 87-185. Doi: 10.1017/S0140525X01003922

Cowan, N., Elliott, E. M., Saults, J. S., Morey, C. C., Mattox, S., Hismjatullina, A., & Conway, A. R. A. (2005). On the Capacity of Attention: Its Estimation and Its Role in Working Memory and Cognitive Aptitudes. *Cognitive Psychology*, 51(1), 42–100. Doi:10.1016/j.cogpsych.2004.12.001

Cowan, N., Fristoe, N. M., Elliott, E. M., Brunner, R. P., & Saults, J. S. (2006). Scope of Attention, Control of Attention, and Intelligence in Children and Adults. *Memory & Cognition*, 34(8), 1754–1768.

Cowan, N., Fristoe, N.M., Elliott, E.M., Brunner, R.P., & Saults, J.S. (2006). Scope of attention, control of attention, and intelligence in children and adults. *Memory and Cognition*, 34(8), 1754-1768. Doi: 10.3758/BF03195936

Dayan, P., & Abbott, L. F. (2001). *Theoretical neuroscience: Computational and mathematical modelling of neural systems*. Cambridge, MA: MIT Press.

Dehaene, S., & Changeux, J. P. (2005). Ongoing Spontaneous Activity Controls Access to Consciousness: A Neuronal Model for Inattentional Blindness. *PLOS Biology*, 3(5): e141. Doi:10.1371/journal.pbio.0030141

Dehaene, S., Changeux, J.P. (2011). Experimental and theoretical approaches to conscious processing. *Neuron,* 70(2), 200-227. Doi: 10.1016/j.neuron.2011.03.018

Dehaene, S., Sergen, C., & Changeux, J.P. (2003).A neuronal network model linking subjective reports and objective physiological data during conscious perception. Proceedings of the National Academy of Science of the United States of America 100(14), 8520-8525. Doi: 10.1073/pnas.1332574100

Dell'Acqua, R., Dux, P.E., Wyble, B., Doro, M., Sessa, P., Meconi, F., & Jolicœur, P. (2015). The attentional blink impairs detection and delays encoding of visual information:

evidence from human electrophysiology. *Journal of Cognitive Neuroscience*, 27(4),720-35. Doi: 10.1162/jocn_a_00752.

Desimone,. R., & Duncan, J. (1995). Neural Mechanisms of Selective Visual Attention. *Annual Review of Neuroscience*, 18: 193-222. Doi: 10.1146/annurev.ne.18.030195.001205

Drew, T., & Vogel, E. K. (2008). Neural measures of individual differences in selecting and tracking multiple moving objects. *Journal of Neuroscience*, 28, 4183-4191. Doi: 10.1523/JNEUROSCI.0556-08.2008

Duncan, J., Humphreys, G., & Ward, R. (1997). Competitive brain activity in visual attention. *Current Opinion in Neurobiology*, 7(2):255-61. Doi: http://dx.doi.org/10.1016/S0959-4388(97)80014-1

Echambadi, R., & Hess, J.D. (2007). Mean-Centering Does Not Alleviate Collinearity Problems in Moderated Multiple Regression Models. *Marketing Science*, 26(3), 438-445. DOI: http://dx.doi.org/10.1287/mksc.1060.0263

Edin, F. (2007). *Neural Mechanisms Determining Visuospatial Working Memory Tasks: Biophysical Modeling, Functional MRI and EEG*. Doctoral Thesis, KTH Royal Institure of Tecnology, University of Stockholm.

Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity. *Electroencephalograpy and Clinical Neurophysiology*, 99, 225-234. Doi: 10.1016/0013-4694(96)95711-9

Eimer, M., & Kiss, M. (2010). The top-down control of visual selection and how it is linked to the N2pc component. *Acta Psychologica*, 135(2):100-2. Doi: https://dx.doi.org/10.1016/j.actpsy.2010.04.010

Fallgatter, A. J., Ehlis, A.-C., Dresler, T., Reif, A., Jacob, C. P., Arcos-Burgos, M., … Lesch, K.-P. (2013). Influence of a Latrophilin 3 (LPHN3) risk haplotype on event-related potential measures of cognitive response control in attention-deficit hyperactivity disorder (ADHD). *European Neuropsychopharmacology : The Journal of the European College of Neuropsychopharmacology*, 23(6), 458–468. http://doi.org/10.1016/j.euroneuro.2012.11.001

Feldmann-Wüstefeld, T., & Schubö, A. (2013).Context homogeneity facilitates both distractor inhibition and target enhancement. *Journal of vision* 13(3): 11, 1–12. Doi: 10.1167/13.3.11

Fukuda, K., Awh, E., & Vogel, E. K. (2010). Discrete capacity limits in visual working memory. *Current Opinion in Neurobiology*, 20, 177-182. Doi: 10.1016/j.conb.2010.03.005

Green, G. (2003). Inattentional blindness and conspicuity. http://www.visualexpert.com/Resources/.

Grossman, E.S., Hoffman, Y.S., Berger, I., & Zivotofsky, A.Z. (2015). Beating their chests: University students with ADHD demonstrate greater attentional abilities on an nattentional blindness paradigm. *Neuropsychology*, Mar 2, 2015, No Pagination Specified (ahead of print). DOI: http://dx.doi.org/10.1037/neu0000189

Hannon, E. M., & Richards, A. (2010). Is inattentional blindness related to individual differences in visual working memory capacity or executive control functioning? *Perception*, 39, 309–319. Doi:10.1068/p6379

Harris, D. (2011). *Human Performance on the Flight Deck*. Aldershot: Ashgate.

Harter, M.R., Miller, S.L., Price, N.J., Lalonde, M.E., & Keyes, A.L. (1989). Neural processes involved in directing attention. Journal of Cognitive Neuroscience;1, 223–237. Doi: 10.1162/jocn.1989.1.3.223.

Hartmann, T., & Ratey, J. J. (1995). *ADD success stories: A guide to fulfillment for families with attention deficit disorder: Maps, guidebooks, and travelogues for hunters in this farmer's world*. Grass Valley, CA: Underwood Books.

Hickey, C., Di Lollo, V., & McDonald, J.J. (2009). Electrophysiological indices of target and distractor processing in visual search. *Journal of Cognitive Neuroscience*, 21(4),760-775. Doi: 10.1162/jocn.2009.21039.

Hopf, J.M., & Mangun, G.R. (2000). Shifting visual attention in space: an electrophysiological analysis using high spatial resolution mapping. *Clinical Neurophysiology*, 111(7):1241-57. Doi: http://dx.doi.org/10.1016/S1388-2457(00)00313-8

Ikkai, A., McCollough, A. W., & Vogel, E. K. (2010). Contralateral delay activity provides a neural measure of the number of representations in visual working memory. *Journal of Neurophysiology*, 103, 1963-1968. Doi: 10.1152/jn.00978.2009

Itti, L., & Koch, C. (2001). Computational modelling of visual attention. *Nature Reviews Neuroscience*, 2(3), 194–203. Doi:10.1038/35058500

Jensen, O., Bonnefond, M., & VanRullen, R. (2012).An oscillatory mechanism for prioritizing salient unattended stimuli. *Trends in Cognitive Sciences,* 16(4), 1364-66. DOI:10.1016/j.tics.2012.03.002

Jolicoeur, P., Brisson, B., & Robitaille, N. (2008). Dissociation of the N2pc and sustained posterior contralateral negativity in a choice response task. *Brain Research*, 1215, 160–172. Doi: 10.1016/j.brainres.2008.03.059

Jost, K., Bryck, R.L., Vogel, E.K., & Mayr, U., (2010). Are old adults just like low working wemory young adults? Filtering efficiency and age differences in visual working memory. *Cerebral Cortex,* 21, 1147-1154. Doi:10.1093/cercor/bhq185

Kiss, M., Grubert, A., Petersen, A., & Eimer, M. (2012). Attentional Capture by Salient Distractors during Visual Search Is Determined by Temporal Task Demands. *Journal of Cognitive Neuroscience*, 243, 749–759. Doi: 10.1162/jocn_a_00127.

Lee, E. Y., Cowan, N., Vogel, E. K., Rolan, T., Valle-Incla, F., & Hackley, S. A. (2010). Visual working memory deficits in patients with Parkinson's disease are due to both reduced storage capacity and impaired ability to filter out irrelevant information. *Brain*, 133, 2677-2689. Doi: 10.1093/brain/awq197

Liesefeld, A.M., Liesefeld, H.R., & Zimmer, H.D. (2013). Intercommunication Between Prefrontal and Posterior Brain Regions for Protecting Visual Working Memory From Distractor Interference. Psychological Science, 25(2), 325-333. Doi: 10.1177/0956797613501170

Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature*, 390, 279-281. Doi:10.1038/36846

Luck, S.J. (2005). *An Introduction to the Event-Related Potential Technique*. The MIT Press: Cambridge, Massachusetts.

Luck, S.J., & Hillyard, S.A. (1994a). Electrophysiological correlates of feature analysis during visual search. *Psychophysiology*, 31, 291–308. Doi: 10.1111/j.1469-8986.1994.tb02218.x

Luck, S.J., & Hillyard, SA. (1994b). Spatial filtering during visual search: evidence from human electrophysiology. *Journal of Experimental Psychology: Human Perception and Performance*, 20, 1000–1014. Doi: 10.1037/0096-1523.20.5.1000

Luck, S.J., Girelli, M., McDermott, M.T., & Ford, M.A. (1997). Bridging the gap between monkey neurophysiology and human perception: An ambiguity resolution theory of visual selective attention. *Cognitive Psychology*, 33, 64–87. Doi:10.1006/cogp.1997.0660

Maccari, L., Casagrande, M., Martella, D., Anolfo, M., Rosa, C., Fuentes, L.J.,et al. (2013). Change blindness in children with ADHD: a selective impairment in visual search?. *Journal of Attention Disorders*, 17(7), 620-7. DOI: 10.1177/1087054711433294

Mack, A., & Rock, I. (1998) *Inattentional Blindness*. MIT Press.

Martinez, A. F., Muenke, M., & Arcos-Burgos, M. (2011). From the black widow spider to human behavior: Latrophilins, a relatively unknown class of G protein-coupled receptors, are implicated in psychiatric disorders. *American Journal of Medical Genetics B Neuropsychiatric Genetics*, 156(1), 1-10. DOI: 10.1002/ajmg.b.31137

Mathewson, K.E., Gratton, G., Fabiani, M., Beck, D.M., & Ro, T. (2009). To see or not to see: prestimulus alpha phase predicts visual awareness. *Journal of Neuroscience*, 29, 2725–2732. DOI: 10.1523/JNEUROSCI.3963-08.2009

Mazza, V., Turatto, M., Umiltà, C., & Eimer, M. (2007). Attentional selection and identification of visual objects are reflected by distinct electrophysiological responses. *Experimental Brain Research*, 181, 531–536. Doi: 10.1007/s00221-007-1002-4

McCollough, A.W., Machizawa, M.G., Vogel, E.K. (2007). Electrophysiological measures of maintaining representations in visual working memory. *Cortex*, 43, 77–94. Doi: 10.1016/S0010-9452(08)70447-7

McNab, F., & Klingberg, T. (2008). Prefrontal cortex and basal ganglia control access to working memory, Nature Neuroscience, 11 103-107. Doi: 10.1038/nn2024

Miller, G. A. (1956). The magical number seven, plus or minus two: Some limits on our capacity for processing information. *Psychological Review* 63:81–97. Doi: 10.1037//0033-295X.101.2.343

Most, S. B., Simons, D. J., Scholl, B. J., Jimenez, R., Clifford, E., & Chabris, C. F. (2001). How not to be seen: The contribution of similarity and selective ignoring to sustained inattentional blindness. *Psychological Science*, 12, 9–17. Doi: 10.1111/1467-9280.00303

Most, S.B., Scholl, B.J., Clifford, E.R., & Simons, D.J. (2005). What you see is what you set: sustained inattentional blindness and the capture of awareness. *Psychological Review,* 112(1), 217–242. Doi: 10.1037/0033-295X.112.1.217

Musson, D. (2009). Putting behavioural markers to work. Developing and evaluating safety training in healthcare settings. In R. Filn & L. Mitchell (Eds). *Safer surgery: Analysing behaviour in the operating theatre* (p. 423-435). Aldershot: Ashgate.

Nobre, A.C., Sebestyen, G.N., Miniussi, C. (2000). The dynmamics of shifting visuospatial attention revealed by event-related potentials. Neuropsychologia,38, 964–974. Doi: http://dx.doi.org/10.1016/S0028-3932(00)00015-4

Owens, M., Koster, E.H.W., & Derakshan, N. (2011). Impaired filtering of irrelevant information in dysphoria: an ERP study. *Social cognitive and affective neuroscience*, 7 (7), 752-763. Doi: 10.1093/scan/nsr050

Papera, M., & Richards, A. (2016). Attentional Gain and Processing Capacity Limits Predict the Propensity to Neglect Unexpected Visual Stimuli. *Psychophysiology*, 5, 634-649. Doi: 10.1111/psyp.12614

Papera, M., Cooper, P.C., & Richards, A. (2014). Artificially created stimuli produced by a genetic algorithm using a saliency model as its fitness function show that Inattentional Blindness modulates performance in a pop-out visual search paradigm. *Vision Research*, 97, 31-44. DOI: 10.1016/j.visres.2014.01.013

Paries, J., & Amalberti, R. (1995). Recent trends in aviation safety: From individuals to organisational resources management training. *Risøe National Laboratory Systems Analysis Department Technical Report*. Series l (pp. 216-228). Roskilde, Denmark: Risøe National Laboratory.

Pashler, H. (1988). Familiarity and visual change detection. *Perception and Psychophysics*, 44, 369-378. Doi: 10.3758/BF03210419

Phillips, W. A. (1974). On the distinction between sensory storage and short-term visual memory. *Perception & Psychophysics*, 16, 283-290.

Prada, L., Barceló, F., Herrmann, C. S., & Escera, C. (2014). EEG delta oscillations index inhibitory control of contextual novelty to both irrelevant distracters and relevant task-switch cues. *Psychophysiology*, 51, 658–672. Doi: 10.1162/jocn_a_00752

Ribasés, M., Ramos-Quiroga, J.A., Sánchez-Mora, C., Bosch, R., Richarte, V., Palomar, G., *et al.* (2010). Contribution of LPHN3 to the genetic susceptibility to ADHD in adulthood: A replication study. *Genes, Brain and Behavior*, 10(2), 149-157. DOI: 10.1111/j.1601-183X.2010.00649.x.

Richards, A., Hannon, E., & Derakshan, N. (2010). Predicting and manipulating the incidence of inattentional Blindness. *Psychological Research Psychologische Forschung*, 74, 513–523. Doi: 10.1007/s00426-009-0273-8

Richards, A., Hannon, E., & Vitkovitch, M. (2012). Distracted by distractors: Eye movements in a dynamic inattentional blindness task. *Consciousness and Cognition*, 21, 170–176. Doi: 10.1016/j.concog.2011.09.013

Richards, A., Hannon, E., Vohra, S. I., & Golan, J. (2014). Tales of the unexpected: attentional awareness; goal-relevance and prior exposure to an unexpected change. *Psychology of Consciousness: Theory, Research, and Practice*, 1(3), 284-291. Doi: http://dx.doi.org/10.1037/cns0000021

Rouder, J. N., Morey, R. D., Cowan, N., Zwilling, C. E., Morey, C. C., & Pratte, M. S. (2008). An assessment of fixed-capacity models of visual working memory. *Proceedings ofthe National Academy of Sciences*, 105, 5975-5979. Doi: 10.1073/pnas.0711295105

Rutman, A.M., Clapp, W.C., Chadick, J.Z. & Gazzaley, A. (2010). Early top-down control of visual processing predicts working memory performance. *Journal of cognitive neuroscience* 22, 1224–1234. Doi: 10.1162/jocn.2009.21257

Sanada, M., Ikeda, K., Kimura, K., & Hasegawa., T. (2013). Motivation enhances visual working memory capacity through the modulation of central cognitive processes. *Psychophysiology*, 50(9), 864-71. Doi: 10.1111/psyp.12077

Sauseng, P., Klimesch, W., Stadler, W., Schabus, M., Doppelmayr, M., Hanslmayr, S., … Lamme, V. A. F. (2005). A shift of visual spatial attention is selectively associated with human EEG alpha activity. *European Journal of Neuroscience*, *22*, 2917–2926. doi: 10.1111/j.1460-9568.2005.04482.x

Schubö, A., Wykowska, A., Müller, H. J. (2007). Detecting pop-out targets in contexts of varying homogeneity: Investigating homogeneity coding with event-related brain potentials (ERPs). *Brain Research*, 1138, 136-147. DOI: 10.1016/j.brainres.2006.12.059

Seiss, E., Gherri, E., Eardley, A. F., & Eimer, M. (2007). Do ERP components triggered during attentional orienting represent supramodal attentional control?: (Brief report). *Psychophysiology*, 44(6), 987–990. http://doi.org/10.1111/j.1469-8986.2007.00591.x

Seung, H., & Sompolinsky, H. (1993). Simple models for reading neuronal population codes. *Proceedings of the National Academy of Sciences of the United States of America*, 90, 10749–10753.

Simons, D. J. (2003). *Surprising studies of visual awareness* (DVD). Champaign, IL: Viscog Productions. <http://www.viscog.com>.

Simpson, G.V., Dale, C.L., Luks, T.L., Miller, W.L., Ritter, W., Foxe, J.J.(2006). Rapid targeting followed by sustained deployment of visual spatial attention. Neuroreport, 17, 1595–1599. Doi: 10.1097/01.wnr.0000236858.78339.52

Todd, J. J., & Marois, R. (2004). Capacity limit of visual short-term memory in posterior parietal cortex. *Nature*, 428, 751-754. Doi:10.1038/nature02466

Turner, M.L., & Engle, R.W., (1989). Is working memory capacity task dependent? *Journal of Memory and Language*, 28(2): 127-154. Doi: http://dx.doi.org/10.1016/0749-596X(89)90040-5

Unsworth, N., Heitz, R.P., Schrock, J.C., & Engle, R.W. (2005). An automated version of the operation span task. *Behavior Research Methods*, 37, 498-505. DOI: 10.3758/BF03192720

Van Dijk, H., Van der Werf, J., Mazaheri, A., Medendorp, W. P., & Jensen, O. (2010). Modulations in oscillatory activity with amplitude asymmetry can produce cognitively relevant event-related responses. *Proceedings of the National Academy of Sciences*, USA, 107, 900-905. Doi: 10.1073/pnas.0908821107

Vogel, E. K., & Machizawa, M. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature*, 428, 748-751. Doi: 10.1038/nature02447

Vogel, E. K., McCollough, A. W., & Machizawa, M. G. (2005). Neural measures reveal individual differences in controlling access to working memory. *Nature*, 438, 500-503. Doi: 10.1038/nature04171

Vogel, E. K., Woodman, G. F., & Luck, S. J. (2006). The time course of consolidation in visual working memory. *Journal of Experimental Psychology: Human Perception and Performance*, 32, 1436–1451. Doi: http://psycnet.apa.org/doi/10.1037/0096-1523.32.6.1436

Vogels, R. (1990). Population coding of stimulus orientation by striate cortical cells. *Biological Cybernetics*, 64, 25–31.

Wilken, P., & Ma, W. J. (2004). A detection theory account of change detection. *Journal of Vision*, 4, 1120-1135. Doi:10.1167/4.12.11

Woodman, G.F., & Luck, S.J. (2003). Serial deployment of attention during visual search. *Journal of Experimental Psychology-Human Perception and Performance*, 29, 121–138. Doi: 10.1037/0096-1523.29.1.121

Woodman, G.F., Kang, M.S., Rossi, A.F., & Schall, J.D. (2007) Nonhuman primate event-related potentials indexing covert shifts of attention. *Proceedings of the National Academy of Sciences of the United States of America*, 104(38), 15111-6. Doi: 10.1073/pnas.0703477104

Xu, Y., & Chun, M. M. (2009). Selecting and perceiving multiple objects. *Trends in Cognitive Sciences*, 13,167-174. Doi: 10.1016/j.tics.2009.01.008

Zhang, W., & Luck, S. J. (2008). Discrete fixed-resolution representations in visual working memory. *Nature*, 453, 233-235. Doi:10.1038/nature06860

Figure and Table Captions