REVIEW ARTICLE

THE JOURNAL OF
NEUROBEHAVIORAL
SCIENCES
NÖRODAVRANIŞ BİLİMLERİ DERGİSİ

Year : 2015
Volume : 2
Issue Number : 1
Doi Number : 10.5455/JNBS.1429716677

Article history:
Received 29 April2015
Received in revised form 05 May 2015
Accepted 06 April 2015

ATTENTIONAL GUIDANCE BY THE CONTENTS OF WORKING MEMORY AND THE N2PC COMPONENT

DİKKATİN ÇALIŞAN BELLEK İÇERİĞİ TARAFINDAN TAHSİS EDİLMESİ VE N2PC BİLEŞENİ

Fatma Keskin Krzan[*1]

Abstract

The Biased Competition Model suggests that stimuli matching the contents of working memory increase the likelihood that memory-matching items will be attended. According to this account, the representations in working memory create an involuntary capture of attention toward memory-matching items in the visual field. This influential assumption proposed by the biased competition model has been explored in a number of studies, showing that the contents of working memory exert an automatic bias in favor of memory matching items. These studies showed that active maintenance of objects in working memory automatically shift attention toward the memory matching-object and produce a negative early lateralized event related potential (ERP), the N2pc, toward the side of visual field where the memorized item appeared. This component, the N2pc is an important tool to investigate the allocation of attention by working memory representations, especially for the activity the activity that is specific to the hemisphere which is contralateral with respect to the hemifield containing e.g. the to-be-remembered items could be measured. This characteristic of the N2pc facilitates measuring the general direction of attention with fine-grained temporal resolution. Therefore, the N2pc could be used as an index to describe the lateralization effect of memorized items on attention related studies.

Keywords: Attention, Working Memory, The N2pc, Lateralization

Özet

Yanlı Rekabet Modeli çalışan bellek içeriği ile eşleşen uyaranların, hafıza ile uyumlu olan uyaranların dikkat olasılığını arttıracağını ileri sürer. Bu açıklamaya göre, çalışan bellek içindeki temsiller, görsel alan içerisindeki temsillerle eşleşen uyaranlara doğru istemdışı bir dikkat oluşturur. Yanlı Rekabet Modeli tarafından önerilen bu etkili varsayım, çalışma belleğinin içeriğinin bellekle eşleşen öğeler lehine otomatik önyargı oluşturduğunu gösteren bir dizi çalışmada araştırılmıştır. Bu çalışmalar, çalışan bellekte sürdürülen nesnelerin, bellekle eşleşen öğelere yönelik otomatik bir dikkat oluşturup, bellek temsilinin oluştuğu görsel alanda erken negatif lateral olaya ilişkin potansiyelini (N2pc) ortaya çıkardığını göstermiştir. Bu bileşen, N2pc, dikkatin çalışan bellekteki temsiller tarafından tahsis edilmesini araştırmak için önemli bir araçtır ve bu bileşenin özellikle hatırlanan nesnelere kontralateral hemisfere özgü aktiviteyi ölçmektedir. N2pc bileşeninin bu özelliği dikkatin genel yönünü detaylı bir şekilde ölçmeyi kolaylaştırmaktadır. Bu nedenle, N2pc bileşeni dikkat ilgili çalışmalarda hafızada korunan öğelerin yanallaşma etkisini açıklamak için bir indeks olarak kullanılabilir.

Anahtar Kelimeler: *Dikkat, Çalışma Belleği, N2pc, Lateralizasyon*

1. Introduction

For our adaptive control of actions, we have to selectively process and store relevant information from among distractor stimuli in the environment. Attention enables observers to focus on a subset of the information present in a complex visual scene (Bundesen, 1990; Desimone & Duncan, 1995; Hopfinger, Woldorff, Fletcher, & Mangun, 2001; Wilson, Woldorff, & Mangun, 2005). Working memory is crucial in guiding attention to form a link between controlled action and perception that provides limited and temporary access to maintain recently encountered information in mind (Desimone & Duncan, 1995). In the course of this complex visual processing, the neural representations of objects in a visual scene compete to gain access to higher level of processing (Desimone, 1996; Soto, Hodsoll, Rotshtein, & Humpreys, 2008). During this competition, working memory guides shifts of attention in favour of the information matching the items recently maintained in working memory (Duncan & Humphreys 1989; Desimone & Duncan 1995; Desimone, 1996; Soto, Heinke, Humphreys, & Blanco, 2005; Olivers, Meijer, & Theeuwes, 2006; for a review, see Soto et al., 2008). As a result, the content of working memory often determines the winner of the competitions, and thus determines which stimulus is attended (Desimone, 1996). For instance, when we search

---

[1] Üsküdar University, Faculty of Humanity and Social Sciences, Department of Psychology

[*] Address for Correspondance: Cognitive Neuroscientist, Department of Psychology, Üsküdar University, Altunizade Mh. Haluk Türksoy Sk. No:14 İstanbul, Türkiye 34662. Tel: +902164002222 Fax: +902164741256 E-mail: fatma.keskinkrzan@uskudar.edu.tr

for something in a crowded place (e.g., looking for a red shirt in a full of clothes), stimuli stored in our working memory (e.g. the red shirt) can guide the deployment of attention to visually matching item (e.g., a red sweater) in the environment. In this example, the deployment of attention is determined by an active mechanism in which the stronger attentional capture is controlled through the voluntary and goal-oriented guidance of working memory (Desimone & Duncan, 1995; Bundensen, 1990). However, this memory-driven guidance by items stored in working memory can also automatically influence visual selection even when those items are task-irrelevant and while observers' attention is focused on another demanding visual monitoring task (Soto et al., 2005; Downing, 2000; Eimer & Kiss., 2007). For example, driving a car near a forest area requires scanning our visual field for animals that may suddenly leap into the road. Holding a representation of an animal in working memory will automatically guide our attention to any animal-like objects while driving in a forest zone, even without the goal of looking for the animal per se. This example shows how the information stored in working memory (e.g. the animal) guides attention in an involuntary manner, even though it is irrelevant to the current task (e.g. maintaining the presentation of the animal while driving the car).

Recent studies have used a variety of techniques to explore the mechanism involved in memory-driven guidance of visual selection. Behavioral studies (Soto et al., 2005; Downing, 2000), electrophysiological (ERPs) and imagining studies (fMRI) in human (Mazza et al., 2011; Eimer & Kiss., 2010; Kumar et al., 2009; Dell'Acqua et al., 2009; Soto, Humphreys, & Rotshtein, 2007; Lepsien, Griffin, Devlin, & Nobre, 2005) and in monkeys (Chelazzi, Duncan, Miller, & Desimone,1998; Soto, Greene, Chaudhary, & Rotshtein, 2012) have shed light on some aspects of the role of working memory in guiding visual attention. Compared with other techniques, the event related potential technique (ERP) has been widely used in these attention related studies because of its high and precise temporal resolution measures of cognitive processing (Kumar et al., 2009; Awh, Anllo-Vento, & Hillyard, 2000; Kuo et al., 2009; McCollough, Machizawa Maro, Edwar, & Vogel, 2007; Carlisle, Geoffrey. & Woodman, 2011; Mazza et al., 2011).

Specifically, a specific ERP response, called N2pc component, reflecting the orienting of selective attention to targets or relevant locations in the visual field, has been intensively used to measure observers' attention across visual space (Woodman, Arita, & Luck, 2009; McCollough et al., 2007; Mazza et al., 2011). This lateralized ERP component reflects a direct measure of attentional process, acting differentially in the hemisphere contralateral to visual targets/relevant locations compared with the hemisphere ipsilateral to the targets/relevant locations (Luck & Hillyard, 1994; McCollough et al., 2007; Robitaille, & Jolicœur, 2006). Most experiments measured the N2pc component during visual search tasks in which stimuli were presented either to the left or right of a central fixation point (bilateral visual search displays) to produce stimulus-driven responses equally from both left/right visual fields. This bilateral presentation of the search array was thought to provide balanced perceptual stimulation to both hemispheres and allow measuring the activity that is specific to the hemisphere which is contralateral with respect to the hemifield containing e.g. the to-be-remembered items (McCollough et al., 2007; Kuo et al., 2009; Kumar et al., 2009; Mazza et al., 2011; Kiss et al., 2008; Dell'Acqua et al., 2009). The N2pc component can be isolated at posterior electrode sites as the difference in mean amplitude between the contralateral and ipsilateral waveforms with a latency of 180-300 ms post-stimulus interval (Woodman & Luck, 1999). Results showed that active maintenance of an object in working memory automatically shifts attention toward the memory matching-object and produces the N2pc component to the side of visual field where the matching item appeared (Kumar et al., 2009; Mazza et al., 2011; Kuo et al., 2009; Kiss et al., 2008; Dell'Acqua et al., 2009). More recently, the N2pc has been also observed in an ERP study investigation memory-driven attentional capture with no lateralized stimuli presentation. A recent ERP study (Astle et al., 2010) found a lateralized brain activity (e.g. the N2pc) after a single test object presentation at the center of visual field, toward the original location of those test object-matching items in a preceding memory array. Namely, when the test object appeared at the fixation point, participants' attention was automatically allocated to the original (lateralized) location of an item in the preceding memory array that matched the test object (Astle et al., 2010; Kuo et al., 2009; McCollough et al., 2007). This N2pc activity found by Astle et al. (2010) is unusual for the reason that the N2pc component has been typically measured during lateralized visual targets. Therefore, (hypothetically) there should be no N2pc activity, if there are no lateralized stimuli in a visual display. However, despite non-lateralized stimuli presentation, maintaining an item in working memory biased visual selection automatically to its original location whenever a match occurred between the memory item and the central object matching the memory contents (Astle et al., 2010). Astel et al.'s study provides novel evidence that the lateralized spatial bias of memory content is so powerful that it can also occur even with a central item, presented at the fixation point (and even when it is presented subliminally).

Several dominant theories of visual attention propose that the contents of working memory automatically guide attention toward memory-matching objects (Bundesen, 1990; Desimone & Duncan, 1995; Duncan & Humphreys, 1989). This claim was at the basis of one of the most influential models on attention: the "Biased Competition Model". According to this model, stimuli compete with each other in the visual field for processing capacity, and the stronger sensory input becomes the focus of attention (Desimone & Duncan, 1995). This competition can be biased by an attentional template that preserves short-term description of information recently held in memory and is prioritized in the visual cortex (Desimone & Duncan, 1995). If one searches for a particular item (e.g., a yellow car), information matching the internal representation (attentional template) of that item will be pre-activated and therefore gaining a competitive advantage over other sensory inputs (e.g. a red car). This sustained neural

activity derives from neural circuits mediating working memory, especially in the prefrontal cortex and provides an automatic competitive advantage for matching sensory inputs (Desimone & Duncan, 1995). Within this framework, the deployment of attention is automatically determined by an active mechanism in which the stronger attentional capture is explained through the voluntary and goal-oriented guidance of working memory (Desimone & Duncan, 1995).

2. Review of the Literature:

2.1. Attentional Guidance by the Contents of Working Memory

Several dominant theories of visual attention propose that the contents of working memory automatically guide attention toward memory-matching objects (Bundesen, 1990; Desimone & Duncan, 1995; Duncan & Humphreys, 1989). This claim was at the basis of one of the most influential models on attention: the "Biased Competition Model". According to this model, stimuli compete with each other in the visual field for processing capacity, and the stronger sensory input becomes the focus of attention (Desimone & Duncan, 1995). This competition can be biased by an attentional template that preserves short-term description of information recently held in memory and is prioritized in the visual cortex (Desimone & Duncan, 1995). If one searches for a particular item (e.g., a yellow car), information matching the internal representation (attentional template) of that item will be pre-activated and therefore gaining a competitive advantage over other sensory inputs (e.g. a red car). This sustained neural activity derives from neural circuits mediating working memory, especially in the prefrontal cortex and provides an automatic competitive advantage for matching sensory inputs (Desimone & Duncan, 1995). Within this framework, the deployment of attention is automatically determined by an active mechanism in which the stronger attentional capture is explained through the voluntary and goal-oriented guidance of working memory (Desimone & Duncan, 1995).

2.2. Single Unit Recordings

Chelazzi and colleagues (1998) provided evidence for the Bias Competition Model in a study on monkey neurophysiology during memory-guided visual search task. Chelazzi et al., (1998) examined the role of attention in temporal cortex of monkeys, using single cell recordings. Each trial began with a fixation stimulus. While the monkeys maintained fixation, a target object (e.g. a flower) at the center of the display was presented for 300 ms and they were trained to hold that object in memory (Figure 1). After 1500 ms, a visual search display with two test objects was presented simultaneously for 600 ms. On target-present trials, one of the objects matched the previous object (the other object was novel) and the monkeys were rewarded for responding to the object matching the cue. On target-absent trials, neither of the two objects matched the previous object. In the search display, the monkey's task was to direct its gaze to the memory-matched object.

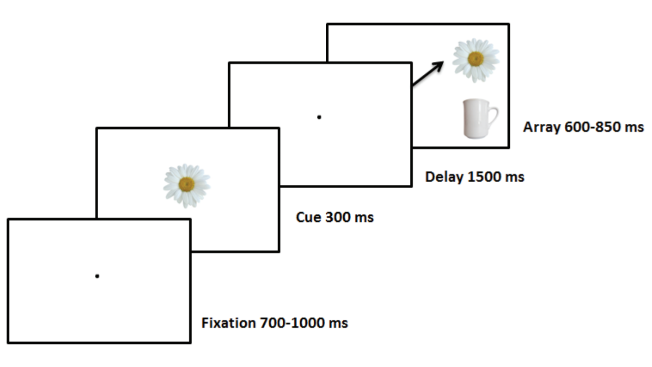

Figure 1: An illustration of a trial sequence. Data were obtained while the monkeys performed a task in which they were briefly presented with a target object at the center of their visual fields and were required to remember it (flower). After a blank, a visual search display with multiple objects was presented, one of which would be the same as the remembered object (flower) and other one was novel (a cup). The task was to make an eye movement to the object matching the memorized object. Adapted from Chelazzi et al. (1998).

Behavioral data showed that, when the search array was presented, object matching the cue appeared to dominate the response (Chelazzi et al., 1998). Namely, the monkeys made significantly greater responses (eye movements) to the object that matched the memorized item (the flower) relative to non-matching stimuli (the cup). Single-cell recording results also showed that cells in the inferior temporal cortex contralateral to the object matching the cue had a higher firing rate relative to non-matching object.

2.3. Behavioral Studies

In line with bias competition model, many studies demonstrated that the activation of object representations in working memory biases associated representations making them automatically more attractive to bias attention (for a review, see Olivers, 2008). More recently, a number of behavioral studies demonstrated that working memory can bias the deployment of attention automatically towards to items that match the contents of working memory even when they are irrelevant for the current task (Olivers, Meijer, & Theeuwes, 2006; Soto et al., 2005; Downing, 2000). For example, Soto et al. (2005) investigated the effect of irrelevant contents of working memory on attention while participants were required to hold an object cue in working memory followed by a search task for a titled line. On some trials the cue could contain either the search target (valid trials) or a distractor (invalid trials) in the following search array. Namely, the target could appear inside a surrounding object that either matched or did not match the memorized item. Behavioral data showed that the participants were faster when the target appeared within the objects that matched the memory item (Soto et al., 2005). Other evidence for irrelevant working memory content on attention has been demonstrated by Downing (2000) in a visual memory task, in which observers were asked to memorize a central face. During a delay period, the simultaneous representations of two faces were shown on either side of the fixation point, only one of which matched the one held in working memory. After a delay, the subjects were required to perform an orientation discrimination task on a small bracket oriented left or right that appeared at the location of one of the two faces. When the small bracket appeared at the location of the face that matched the one in working memory, reaction times to the small bracket were faster than when it appeared over the non-matched face (Downing, 2000). A similar paradigm was used to test a group of patients with visual extinction with difficulty detecting the presence of a contralesional stimulus when ipsilesional items appeared simultaneously (Soto, Humphreys, & Heinke, 2006; for a review, see Soto et al., 2008). The patients showed enhanced awareness for contralesional targets when the visual search array contained the item held in working memory. However, no such effect was found when the initial items were merely identified or viewed passively (Soto et al., 2006).

2.4. fMRI Studies

Further evidence that underline the effect of irrelevant working memory content on orienting attention comes from functional brain imaging (fMRI). Recently, Soto et al. (2007) reported fMRI evidence showing that maintenance of an object in working memory is accompanied by increased neural signal in occipital and frontal regions (see also, Woodman & Luck, 2007). Neuronal correlates were measured when subjects were presented with an initial cue and subsequently required to search for a target presented at the center of a surrounding either cued or non-cued object (Figure 2). With the reappearance of the stimulus held in working memory, they found an enhanced activity in a network of areas, including the superior frontal gyrus, parahippocampal gyrus and lingual gyrus. In the working memory condition where subjects had to hold the cue in their working memory, an enhanced neuronal signal in the areas that encode the prior occurrence of stimuli (superior frontal gyrus, midtemporal, and occipital regions) was found to drive attention to locations where the item reappeared (Soto et al., 2007). In contrast, when the cue reappeared in the repetition condition where the subjects were required to identify and compare two cues, reduced neuronal signal was observed in the same areas. These results suggest that there is neuronal dissociation on visual selection between the working memory and priming effects when the search target matched the content of working memory.

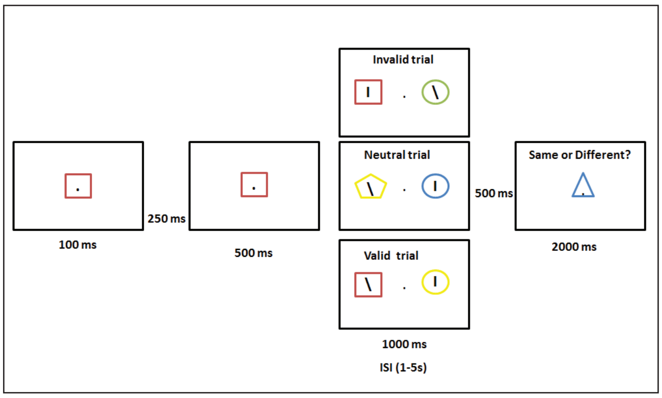

Figure 2: An Illustration of the experimental stimuli used in Soto et al.'s study (2007). Each trial began with a cue and participants were required either hold the cue in working memory or merely identify. Subsequently, they were asked search for a target (tilted line) that could appear surrounded by either a cued (red square, valid trials) or non-cued item (green circle, invalid trials). At the end of the trial, an object was presented and the participants were asked to decide whether it was the same or different with the memorized object shown at the beginning of the trial. Adapted from Soto et al. (2007).

Awh and colleagues (Awh, Jonides, Smith, Buxton, Frank, Love, Wong, & Gmeindl, 1999) have also measured fMRI activation to provide sensitive measure of the direction of attention in a spatial working memory task. They asked participants to perform a spatial memory task in which they were required to remember the locations of the memory cues. After presentation of a flickering grid, a memory probe was shown either right or left side of the fixation point and the participants were asked to indicate whether it was in the same location as any of those locations shown in the beginning of the trial. They found enhanced fMRI activation in the early visual areas contralateral to attended locations that are being held in working memory relative to irrelevant locations.

2.5. Event Related Potential (ERP) Studies

More recently, these behavioral and fMRI methods were supported by event-related brain potentials (ERPs) in order to provide information concerning the time-course of neuronal mechanisms underlying the effects of orienting attention to the internal representations held in working memory. Specifically, studies have focused on a specific ERP response, called N2pc component reflecting direction of attention (Woodman & Luck, 1999; McCollough et al., 2007; see also Luck, 2005). For instance, several ERP studies demonstrated that task-irrelevant working memory representations guide attention toward memory-matching items in visual search displays and elicit the N2pc activity at posterior electrode sites over the hemisphere contralateral to the visual field of these memory-matching items (Kumar et al., 2009; Astle et al., 2009; Eimer & Kiss, 2010). Additionally, when a search target was presented in the same side of an item matching the content of working memory (e.g. a task irrelevant distractor) the amplitude of the N2pc component was larger relative to other conditions where the spatial position of the target and the memory-matching item was different (Mazza et al., 2011; Kumar et al., 2009; Kuo et al., 2009).

2.6. Event Related Potential (ERP)

Event-related potentials (ERPs) reflect brain activities associated with the operation of information processing in preparation for or in response to discrete events such as encoding, selecting, and memorizing (Fabiani, Gratton,

JNBS 2015 Published by Üsküdar University www.jnbs.org

& Federmeier, 2007; Luck & Hillyard, 1994; Luck, 2005; Hillyard & Kutas, 1983). ERPs provide online measures of cognitive processing with fine-grained temporal resolutions and allow for examination of informational processing by means of noninvasive electrical recordings from the intact scalp (Hillyard & Picton 1987; McCollough et al., 2007; Luck, 2005; Hillyard & Kutas, 1983). ERP waveforms are scalp-recorded voltage changes related to a particular psychological or neural process, and consist of a series of positive and negative voltage deflections which are called components (Hillyard & Kutas, 1983).

The N2pc is one of the well-studied ERP components in attention-related studies. This is a negativity typically elicited 180-300 ms following the onset of a search array and can be defined as a difference between the contralateral and ipsilateral sites with respect to the target or relevant locations in the visual field (Luck, Chelazzi, Hillyard, & Desimone 1997; Mazza et al., 2011; Luck, 2005; Luck & Hillyard, 1994). The N denotes a negative polarity, 2 describes its latency in the waveform (i.e. it is second negative deflection, around 200ms), and pc refers "posterior-contralateral" as it appears over posterior (p) electrode sites contralateral (c) to the target side (Luck, 2005; Fabiani et al., 2007; Luck & Hillyard, 1994). This negative deflection can be examined clearly by measuring the difference in amplitude between the activities generated in contralateral and ipsilateral electrode sites relative to the position of the target in a visual search array. Woodman and Luck (1999) demonstrated that when the participants shift their attention from the left visual field to the right visual field, the N2pc component also shifts from the right hemisphere to the left hemisphere, enabling millisecond-by-millisecond measurement of the attentional orienting (See also Luck et al., 2005). As illustrated in Figure 3, two distinctively colored items were presented in one hemifield, making it possible to examine the ERPs elicited by identical stimuli with differing spatial directions of attention (Luck, 2005). When participants attended to the left side of the visual display, the voltage was more negative for right-hemifield (contralateral to the side of the left-hemifield targets) than for the left-hemifield targets (ipsilateral to the side of the left targets) (Luck, 2005).

Traditionally, the N2pc component is regarded as an indicator of the spatially selective attentional processing of target versus distractor items in visual search (Kiss et al., 2008). Dell'Acqua et al., (2009) measured the N2pc activity when observers were searching for a target held in visual short-term memory and when they searched for a target in visually presented displays. Perceptual search consisted of a target (pre-cue) followed by a search array. The task was to decide whether or not the pre-cue was present in the search array. In the visual short-term memory search, a post-cue was preceded by a visual search task, and the task was to decide whether the post-cue was present in the previously displayed search array. They found similar scalp distribution of the lateralized ERP response (the N2pc) in short-term memory and perceptual search trials. More importantly, a lateralized ERP response was elicited by the central post-cue target (e.g., colored square) when observers were searching the array held in visual short-term memory which was similar to the N2pc activity observed in pre-cued trials. Notably, this modulation of the N2pc as a function of location was thought to indicate that some of the intrinsic spatial configuration of the original perceptual array is preserved together with the remembered items (Dell'Acqua et al., 2009; See also Kuo et al., 2009; Gratton, 1998; Jiang, Makovski, & Shim, 2009; Desimone & Duncan, 1995).

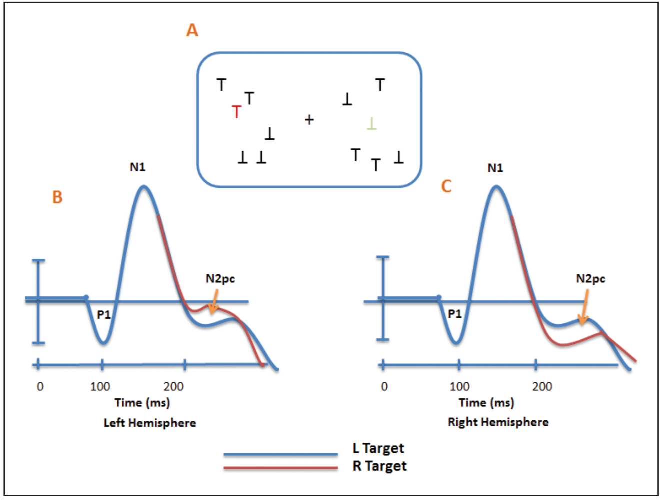

Figure 3: An illustration of a typical paradigm for eliciting an N2pc component. (A) At the beginning of each trial, the participants are required to attend to one color and to indicate the orientation of the item drawn in color (e.g. upright T or inverted T). ERP activity was recorded from electrodes over right and left posterior visual areas (B) The activity at posterior left scalp sites is more negative (grey shaded areas) when the target (colored T) was presented in the right hemifield than when it appeared in the left hemifield. (C) On contrary, the activity is more negative when the target was in the left hemisphere than when the target appeared in the right hemisphere. Adapted from Luck (2005).

The link between the N2pc component and shifts of attention by irrelevant memory content was also explored in a combined working memory - attention task. Kumar et al. (2009) provided ERP evidence that irrelevant contents of working memory can bias visual selection and produce the N2pc component during a visual search task where search target was surrounded by a memory matching-distractor. At the beginning of each trial, participants were presented with a memory prime to perform a match-to-sample task at the end of some trials. Subsequently, they were presented with a search task in which four lines were located at the center of surrounding shapes (square, circle, triangle, and hexagon) appearing at one of eight possible locations in visual search. The task was to report the orientation of a tilted line presented among three other vertical lines (Figure 4). Each of the stimuli surrounding the lines was unique in color and shape, and in some trials, one of these shapes matched the memory item (matching distractor). There were three conditions in which the locations of the matching distractor and the search display varied. In ipsilateral invalid cueing trials, the matching distractor appeared on the same side of the fixation point as the target; in contralateral invalid cueing trials, the matching distractor appeared on the side of the fixation point opposite the target. In neutral trials, the matching distractor did not appear in the search display.

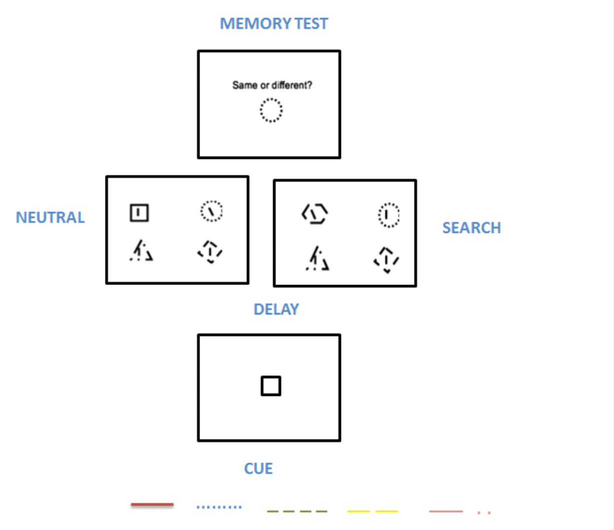

Figure 4: An illustration of the trial sequence used In Kumar et al.'s study. The observers were shown a cue appeared either for 133 ms or for 500 ms in the beginning of each trial. After 800 ms, the subjects were presented a search display containing four lines located in the center of surrounding shapes (square, circle, triangle, and hexagon). In the working memory condition, participants were required to memorize the cue for the memory test shown at the end of the trial. In the priming condition, they were asked to compare the two presentations of cues and refrain from responding to the search display if the second presentation of the cue differed from the first one in either color or shape. Adapted from Kumar et al., 2009.

Behavioral results showed that visual searches were significantly affected by the presence of a distractor matching the one held in memory (matching distractor), but not when the prime was merely identified and not held in memory (Kumar et al., 2009). More importantly, in ipsilateral invalid cueing trials, the N2pc was more pronounced relative to the contralateral invalid cueing and neutral trials. Kumar et al. proposed that involuntary effects of the working memory content can determine the efficiency of target selection (i.e., at early stage) and this effect is reflected in the measures of the N2pc activity (2009).

Astle et al. (2010) found that when an item (test object) matching the content of working memory appeared at the fixation point, participants' attention was automatically allocated to the original (lateralized) location of items in the preceding memory array that matched the test object (Figure 5). Namely, after a single test object presentation appearing at the center of visual field (i.e., there are no lateralized stimuli only a single item at the fixation), they found a lateralized brain activity (e.g. the N2pc) at electrode sites contralateral to the original location of those object-matching items in the preceding visual display.

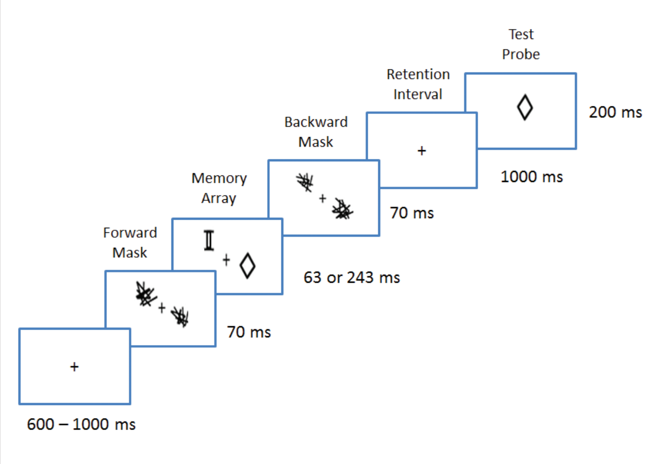

Figure 5: An illustration of the trial sequence used in Astle et al.' study (2010). Each trial started with a fixation cross (duration: 600-1000 ms). A memory array of two items was presented either subliminally for 63 ms or supraliminally for 243 ms before and after two pattern mask comprising a lateralized visual noise. After a further delay of 800-1000 ms, a central test object was presented for 200 ms at fixation point.

In their study, the electrophysiological sessions started and concluded with an explicit memory task: at the beginning of each trial participants were either subliminally (63 ms) or supraliminally (243 ms) presented with a memory array of two items interspersed between two masking displays. The memory array was followed by the presentation of an item (test object) appearing at the fixation point at the end of the trial. The task was to decide whether the test probe had been present in the original memory array and only on half of the trials the test probe appeared in the preceding memory array. During EEG session, the participants were asked to perform a perceptual judgment task: to judge the symmetry along the vertical midline of the centrally presented test probe. This task was unrelated the contents of the memory array and was designed to explore whether maintaining the information of the memory array shape influences the processing of the test object in a spatially specific way (i.e., having seen that item before at a particular location).

In certain trials the test object was the same as the one in the memory array (probe-present trials), and in other trials the memory array did not contain the test object (probe-absent trials). When the participants were presented with the display including a centrally located test object matching the memory array item, they observed an N2pc toward the original location of the probe-matching item in the memory array in both subliminal and supraliminal conditions. They also found a behavioral facilitation (faster reaction times and higher accuracy in congruent relative to incongruent trials) when the shape in the memory array matched the test object. They concluded that information stored in memory leaves a trace that contains the original spatial layout of the items in the memory array (Dell'Acqua et al., 2009; See also Gratton, 1998; Kuo et al., 2009; Jiang, Olson,

JNBS 2015 Published by Üsküdar University www.jnbs.org

& Chun, 2000; Desimone & Duncan, 1995), and that this trace captures attention automatically whenever a match occurs with currently perceived item (i.e., a match between the items in the preceding memory array and the test object) (Astle et al., 2010).

One of the most significant findings emerging from that study is that although the task was unrelated to the contents of the memory array (e.g. judging the symmetry along the vertical midline of the test object), the spatially specific biasing of mnemonic information held in working memory still survived and captured the participants' attention and to its original location and yet produced the N2pc when there was a match between the memory matching item and the upcoming stimulus (test object) (Figure 5). Interestingly, the results also indicate that although the participants failed to perceive previously presented stimuli in memory array (e.g. in a subliminal condition) and failed to recognize them subsequently, the participants' attention was captured by the lateralized items (in memory array) due to the original spatial layout of the memory array that is preserved in working memory. Namely, the participants were unintentionally storing the items with their spatial configuration although they were irrelevant to the content of working memory and consciously undetectable (Astle et al., 2011; Kuo et al., 2009).

3. Conclusion

Research reviewed here highlights the few characteristics of the N2pc component that appear to play a role in attention and display properties that enable to evaluate the direction of attention. Studies of visual spatial attention showed that active maintenance of objects in working memory automatically shift attention toward the memory matching-object and produce an N2pc toward the side of visual field where the memorized item appeared (Kumar et al., 2009; Mazza et al., 2011; Kuo et al., 2009; Kiss et al., 2008; Dell'Acqua et al., 2009). In these studies, the N2pc component was typically measured under conditions in which the items were presented on each side of the fixation (bilateral visual search displays) (McCollough et al., 2007; Robitaille & Jolicoeur, 2006). Due to bilateral presentation of the search array, which provides balanced perceptual stimulation to both hemispheres and allows for measure of activity specific to the contralateral hemifield containing the to-be-remembered item, this characteristic of the N2pc facilitates measuring the general direction of a person's attention with fine-grained temporal resolution.

Despite further research will need to evaluate and assess this aspect more deeply, recent findings may still provide important insights regarding the nature of automatic capture of attention and spatial bias by the content of working memory. For instance, many previous studies also proposed that visual working memory contains the spatial information of the object (Kuo et al., 2009; Astle et al., 2010; Dell'Acqua et al., 2009; See also Gratton, 1998; Jiang et al., 2000; Desimone & Duncan, 1995; Astle et al., 2009; Lepsien, 2005; Olson & Marshuetz, 2005). Additionally, studies, linking spatial attention and spatial working memory by demonstrating considerable overlap between brain areas that are active during attention task and those active during spatial working memory tasks (Awh & Hillyard, 2000; for a review, see Awh & Jonides, 2001) are convincing reason for a linkage between the spatial information and the working memory. Therefore, exciting directions for future research, providing new insights into the effects of the N2pc on spatial attention by the content of working memory may also intensify our understanding how attention and memory link together. This phenomenon can be also found in everyday life experiences. For instance, when we look for something, we typically start to search at the initial location of the previously seen object. Particularly, reconsidering the first example mentioned in the introduction part (e.g. driving a car near a forest area), if one were to see an animal at particular location while driving to work (e.g. on the left side of the road), then on a way back home, having seen the animal at that particular location would bias the observers' attention automatically to the same location, whenever there is any evocative information related to the presence of an animal in the environment (e.g. a traffic sign containing animal figure). However, further investigation will be required to explore this important issue more intensively.

References

Astle, D.E., Scerif G., Kuo B.C., Nobre A.C. (2009). Spatial selection of features within perceived and remembered objects. Front Hum Neurosci 3:6.

Awh, E., Anllo-Vento L., & Hillyard S.A. (2000). The Role of Spatial Selective Attention in Working Memory for Locations: Evidence from Event-Related Potentials. Journal of Cognitive Neuroscience 12:5, pp. 840–847.

Awh, E., Jonides J., Smith E.E., Buxton R.B., Frank L.R., Love T., Wong E.C., & Gmeindl L. (1999). Rehearsal in spatial working memory: Evidence from neuroimaging. Psychol Sci 10(5):443–437.

Awh, E., & Jonides, J. (2001). Overlapping mechanisms of attention and spatial working memory. TRENDS in Cognitive Sciences Vol.5 No.3.

Bundesen, C. (1990). A theory of visual attention. Psychological Review, 97, 523–547.

Carlisle, N.B., & Woodman, G.F. (2011). Automatic and strategic effects in the guidance of attention by working memory representations, Acta Psychologica 137, 217–225.

Chelazzi, L., Duncan, J., Miller, E.K., & Desimone, R. J. (1998). Responses of Neurons in Inferior Temporal Cortex During Memory-Guided Visual Search. J Neurophysiol. 80:2918-2940, 1998.

Dell'Acqua, R., Sessa, P., Toffanin, P., Luria, R., & Jolicoeur, P. (2009) Orienting attention to objects in visual short-term memory. Neuropsychologia 48:419–428.

Desimone, R. (1996). Neural mechanisms for visual memory and their role in attention. Proc. Natl. Acad. Sci. USA. Vol. 93, pp. 13494–13499. Colloquium Paper.

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. Annual Review of Neuroscience, 18, 193–222.

Downing, P.E. (2000). Interactions between visual working memory and selective attention. Psychological Science, 11, 467–473.

Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. Psychological Review, 96, 433–458.

Eimer, M., & Kiss, M. (2007). Attentional capture by task-irrelevant fearful faces is revealed by the N2pc component. Biol Psychol 74:5.

Eimer, M., & Kiss, M. (2010). An electrophysiological measure of access to representations in visual working memory. Psychophysiology 47:197–200.

Fabiani, M., Gratton, G., & Federmeier, K.D. (2007) : "Event-Related Brain Potentials: Methods, Theory, and Applications". In Handbook of Psychophysiology, ed. by John T. Cacioppo, Louis G. Tassinary, and Gary G. Berntson. 3rd. ed. Cambridge: Cambridge University Press. ISBN 978-0-521-84471-0. pp. 85–119.

Gratton, G. (1998) The contralateral organization of visual memory: A theoretical concept and a research tool. Psychophysiology, 35. 638–647.

Hillyard, S.A., & Kutas, M. (1983). Electrophysiology of Cognitive Processing. Annu Rev Psychol. 34:33-61.

Hillyard, S.A., & Picton, T.W. (1987). Electrophysiology of cognition. In Plum F (Ed), Handbook of Physiology: Section 1. The Nervous System: Volume 5. Higher Functions of the Brain, Part 2. Bethesda: Waverly Press.

Hopfinger, J.B., Woldorff, M.G., Fletcher, E.M., Mangun, G.R., (2001). Dissociating top-down attentional control from selective perception and action. Neuropsychologia 39, 1277–1291.

Hutchinson, J. B., & Turk-Browne, N. B. (2012). Memory-guided attention: Control from multiple memory systems. Trends in Cognitive Sciences, 16, 576-579.

Jiang, Y., Olson, I. R., Chun, M. M. (2000). Organization of visual short-term memory. Journal of Experimental Psychology: Learning, Memory, and Cognition, 26, 683-702.

Jiang, Y.V., Makovski, T., & Shim, W.M. (2009). Visual memory for features, conjunctions, objects, and locations. In J.R. Brockmole (Eds.), The Visual World in Memory. (pp. 33-65). Psychology Press.

Kiss, M., Van Velzen, J., & Eimer, M. (2008). The N2pc component and its links to attention shifts and spatially selective visual processing. Psychophysiology, 45, 240-249.

Kumar, S., Soto, D., & Humphreys, G. W. (2009). Electrophysiological evidence for attentional guidance by the contents of working memory. European Journal of Neuroscience, 30, 307–317.

Kuo, B.C., Rao A, Lepsien J, Nobre AC (2009). Searching for targets within the spatial layout of visual short-term memory. J Neurosci 29:8032– 8038.

Lepsien, J., Griffin, I. C., Devlin, J. T., & Nobre, A. C. (2005). Directing spatial attention in mental representations: Interactions between attentional orienting and working-memory load. NeuroImage, 26(3), 733–743.

Luck, S.J., & Hillyard S.A. (1994). Spatial filtering during visual search: evidence from human electrophysiology. J Exp Psychol Hum Percept Perform 20:1000 –1014.

Luck, S.J., Chelazzi L., Hillyard S.A., & Desimone R., (1997). Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. J Neurophysiology, 77:24–42.

Luck, S.J. (2005). An introduction to the event-related potentials and their neural origins. In S.J. Luck, An Introduction to the Event-Related Potential Technique. (pp. 1-50). Cambridge, MA: MIT Press. Pay particular attention to pages 3-34.

Luck, S.J. (2005). The operation of attentiondmillisecond by milliseconddover the first half second. In Ogmen H, & Breitmeyer, B.G. (Eds),The First Half Second: The Microgenesis and Temporal Dynamics of Unconscious and Conscious Visual Processes. Cambridge, MA: MIT Press.

Mazza, V., Dallabona M., Chelazzi L., Turatto M. (2011) Cooperative and opposing effects of strategic and involuntary attention. Journal of Cognitive Neuroscience, 23:10, 2838-2851.

McCollough, A.W., Machizawa, M.G., & Vogel, E.K. (2007). Electrophysiological measures of maintaining representations in visual working memory, Cortex, 43(1):77-94.

Olivers, C. N., Meijer, L. F., & Theeuwes, J. (2006). Featurebased memory-driven attentional capture: Visual working memory content affects visual attention. Journal of Experimental Psychology: Human Perception and Performance, 32, 1243–1265.

Olivers, C.N. (2008). Interactions between visual working memory and visual attention. Frontiers in Bioscience, 13, 1182–1191.

Olson, I. R., & Marshuetz, C. (2005). Remembering "what" brings along "where" in visual working memory. Perception & Psychophysics, 67,185–194.PsychoL 34:33-61.

Robitaille, N., & Jolicœur, P. (2006). Fundamental properties of the N2pc as an index of spatial attention: effect of masking. Canadian Journal of Experimental Psychology, 60, 101–111.

Soto, D., Greene, C.M., Chaudhary, A., & Rotshtein, P. (2012). Competition in Working Memory Reduces Frontal Guidance of Visual Selection. Cereb Cortex. 22(5):1159-69.

Soto, D., Hodsoll, J. P., Rotshtein, P., & Humphreys, G. W. (2008). Automatic guidance of attention from working memory. Trends in Cognitive Science, 12, 342–348.

Soto, D., Humphreys, G.W., & Rotshtein, P. (2007) Dissociating the neural mechanisms of memorybased guidance of visual selection. Proc. Natl. Acad. Sci. U.S.A. 104, 17186–1719.

Soto, D., Humphreys, G. W., & Heinke, D. (2006). Working memory can guide pop-out search. Vision Research, Vision Research 46 (2006) 1010–1018.

Soto, D., Heinke, D., Humphreys, G. W., & Blanco, M. J. (2005). Early, involuntary top–down guidance of attention from working memory. Journal of Experimental Psychology: Human Perception and Performance, 31, 248–261.

Vuilleumier, P.O, & Rafal, R.D. (2000). A systematic study of visual extinction. Between- and within field deficits of attention in hemispatial neglect. Brain; 123:1263-1279.

Wilson, K.D., Woldorff, M.G., & Mangun, G.R. (2005). Control networks and hemispheric asymmetries in parietal cortex during attentional orienting in different spatial reference frames. NeuroImage 25, 668–683.

Woodman, G.F., Jason T. Arita, J.T., & Steven J. Luck. S. (2009). A Cuing Study of the N2pc Component: An Index of Attentional Deployment to Objects Rather Than Spatial Locations. Brain Res. 1297: 101–111.

Woodman, G.F., & Luck, S.J. (2007). Do the Contents of Visual Working Memory Automatically Influence Attentional Selection During Visual Search? Journal of Experimental Psychology: Human Perception and Performance. Vol. 33, No. 2, 363–377.

Woodman, G. F., & Luck, S. J. (1999). Electrophysiological measurement of rapid shifts of attention during visual search. Nature, 400, 867–869.