Visual asymmetries and the effect of gaze direction on memory

Carlei, Christophe

UNIVERSITÉ
DE GENÈVE
FACULTÉ DE PSYCHOLOGIE
ET DES SCIENCES DE L'ÉDUCATION

Section de Psychologie

Sous la direction du Professeur Dirk Kerzel

Visual asymmetries and the effect of gaze direction on memory

THESE

Présentée à la
Faculté de psychologie et des sciences de l'éducation
de l'Université de Genève
pour obtenir le grade de Docteur en Psychologie

par

Christophe Patrice Nazzareno CARLEI

de

France

Thèse No 645
N° d'étudiant: 08-306-004

GENEVE

Septembre 2016

Acknowledgements

Je commencerais par remercier chaleureusement mon superviseur, le professeur Dirk Kerzel avec qui j'ai eu la chance de travailler depuis 2011 lorsque j'étais en 3e année de Bachelor de Psychologie. Il a alors gentiment accepté de m'encadrer pour un projet de recherche libre en dépit du fait que le sujet ne relevait pas directement de ses intérêts de recherche. Ce projet entamé en Bachelor a par la suite donné un mémoire de Master puis la présente thèse de doctorat ! Cinq années se sont écoulées durant lesquelles j'ai énormément appris en travaillant à ses côtés. J'ai particulièrement apprécié la liberté qu'il m'a accordée dans mes recherches scientifiques et dans l'enseignement, sa disponibilité, ses feedbacks toujours constructifs et pertinents ainsi que sa rigueur scientifique. J'aimerais également le remercier tout particulièrement pour avoir su cadrer mes idées afin qu'elles puissent être opérationnalisées en expériences puis être partagé au reste de la communauté scientifique.

J'aimerais également remercier mes collègues de travail ainsi que tous mes amis d'Université qui comme moi ont eu l'opportunité de commencer un doctorat et avec qui j'ai partagé d'innombrables bons moments au cours de ma thèse. Une attention toute particulière à ma compagne et collègue qui m'a soutenu et motivé durant les périodes de crise existentielle auxquelles tout thésard est amené à traverser.

Mes pensées vont également à toutes les monitrices / moniteurs qui se sont succédés au fil des années au sein du laboratoire de cognition visuelle sans lesquelles je n'aurais pas pu réaliser toutes ces études. Un grand merci à eux pour toutes ces heures de passation d'expérience. Je pense également à ces générations d'étudiants en première année de psychologie de l'Université de Genève qui ont participé avec plus ou moins d'enthousiasme à mes nombreuses études.

Je tiens à remercier aussi toutes les personnes qui m'ont aidé au niveau logistique. Que ce soit pour la préparation du matériel, la location des salles ou la programmation de mes expériences. Un grand merci également au McDonald's de Plainpalais qui a financé mes premières expériences et au Fond National Suisse pour avoir soutenu mon projet. Merci également à toutes les personnes qui m'ont donnés du feedback sur mes recherches et qui m'ont aidé à aller de l'avant au niveau de la pensée scientifique.

Pour terminer, je tiens également à remercier mes parents pour m'avoir soutenu et encouragé lors ces années de thèse, ma famille ainsi que tous mes amis de lycée !


Lucie Colpaert
Fabien Venier
Vera Bignoli
Simon Fournier
Ludivine Jargy
Nicolas Burra
Fabien Guilland
Pascale Carlei
Roland Maurer
Françoise Samuel
Jacqueline Gasser
Nazzareno Carlei
Isabelle Descombes
Marion Camelin
Damien Benis
Alexandre Bourquin
Sélim Coll
David Souto
Aurélien Gallice
Patrice Carlei
Dirk Kerzel
Céline Lucken
Jana Pasuljevic
Isabelle Barras
Marion Jovanovic
Emilie Progin
Linda Amrar
Philippe Barras
Alexandre Gaedke
Chantal Vorburger
Sofia Ferreira
Jean-Claude Duvanel
Igor Faulmann
Joseph Roth
Martine Mornacchi
Bérangère Roth
Caroline Barras
Thierry Lecerf
Cyrielle Chappuis
Vincent Widmer
David Framorando
Pierre Batardon
Raphaël Babel
Damien Simond
Ruth Propper
Suzanne Carlei
Emilie Joly
Fanny Lalot
Catherine Thevenot
Donato Cereghetti
Andrés Posada
Lucille Simond
Dieter Javier
Sophie Carlei
Elsa Gogniat
Philippe Iegeais
Alina Miny
Carolyn Trine
Pierre Barrouillet

Scientific Abstract

The goal of the present work was to investigate both horizontal and vertical asymmetries. In Chapter 1: Experiments 1-6 and Experiments 7-9, we used different types of visual search tasks in which geometrical shapes and face stimuli were displayed on peripheral vision. In Chapter 2: Experiments 10-12 and Experiments 13-15, we used gaze direction as a tool to investigate hemispheric asymmetries on visuospatial short-term memory.

In Experiments 1-6, asymmetries between left and right as well as upper and lower visual hemifields were investigated using pop-out search. Participants searched for a shape or a color singleton and reported the orientation of a line segment inside the singleton. The target's line orientation did not pop out, whereas the shape or the color did. We consistently found a lower hemifield advantage for simple detection and identification tasks, which is consistent with previous reports of enhanced visual acuity in the lower visual hemifield. This advantage only disappears when a singleton detection mode is required for identification tasks. Concerning horizontal asymmetry, we found a right hemifield advantage only for identification tasks involving feature search mode. This effect disappears with simple detection tasks and when a singleton detection mode was required. Our results also showed that participants were faster to respond when targets were presented in the right compared to the left visual hemifield, consistent with findings showing that "local" or high-resolution processing is improved in the right visual field. In sum, our findings show that both laterality and elevation affect reaction times when searching for a singleton. Because our task required participants to report a visual detail after parallel search, presenting singletons in the right and lower hemifields, which favor high-resolution processing, results in better performance.

In Experiments 7-9, we again tested visual asymmetries using a visual search task but this time we used faces as stimuli instead of geometric shapes. Holistic processing is better in the left hemifield, reflecting a right hemisphere specialization. Furthermore, object recognition is better in the upper visual field, reflecting stronger projections into the ventral stream. As in the aforementioned set of experiments, we jointly studied horizontal and vertical asymmetries by presenting faces in each quadrant of the visual field. Faces tap into holistic processing and, at the same time, require complex object recognition. In the first experiment, participants had to detect a face with a gaze direction different from the other faces. The participants responded more quickly when targets were presented in the upper left quadrant, which suggests that the

left hemifield advantage for holistic processing and the upper hemifield advantage for object recognition interact, causing improved performance in a single quadrant. In the second experiment, we turned the faces upside down, which eliminates the holistic appearance of faces while leaving their features intact. The left hemifield advantage disappeared, showing that it is related to holistic processing of faces, whereas the upper hemifield advantage persisted. Finally, we made the search task easier by asking observers to search for a face with closed eyes among open eyes or vice versa. The easy search task eliminated the need for complex object recognition since the search could operate on a salient luminance difference. The advantage of the upper visual field disappeared, showing that it reflected an advantage of complex object recognition, whereas the left hemifield advantage persisted because the upright faces continued to trigger holistic processing. In sum, our findings show that both vertical and horizontal asymmetries affect the search for faces and can be selectively suppressed by changing characteristics of the stimuli.

In Experiments 10-12, hemispheric asymmetries were investigated by changing the horizontal position of stimuli that had to be remembered in a visuospatial short-term memory task. Observers looked at matrices containing a variable number of filled squares on the left or right side of the screen center. At stimulus offset, participants reproduced the positions of the filled squares in an empty response matrix. Stimulus and response matrices were presented in the same quadrant. We observed that memory performance was better when the matrices were shown on the left side of the screen. We distinguished between recall strategies that relied on visual or non-visual (verbal) cues and found that the effect of gaze position occurred more reliably in participants using visual recall strategies. Overall, the results show that there is a solid enhancement of visuospatial short-term memory when observers look to the left. In contrast, vertical position had no influence on performance. We suggest that unilateral gaze to the left activates centers in the right hemisphere contributing to visuospatial memory.

In Experiments 13-15, cerebral asymmetries and cortical regions associated with the upper and lower visual fields were investigated using shifts of gaze. Our previous experiments had suggested that gaze shifts to the left or right increase activation of the contralateral hemisphere. We questioned whether looking at one quadrant of the visual field facilitates the recall in various visuospatial tasks. The different components of visuospatial memory were investigated by probing memory for a stimulus matrix in each quadrant of the screen. Firstly, memory of visual images or patterns was probed with a matrix of squares that was

simultaneously presented and had to be reconstructed by mouse click. Better memory performance was found in the upper left quadrant compared to the three other quadrants, indicating that both laterality and elevation are important. Secondly, positional memory was probed by subsequently presenting squares which prevented the formation of a visual image. Again, we found that gaze to the upper left facilitated performance. Thirdly, memory for object-location binding was probed by asking observers to associate objects with specific locations. Higher performance was found with gaze directed to the lower quadrants irrespective of lateralization, confirming that only some components of visual short-term memory have shared neural substrates.

Publications

Experiments 1-6: Carlei, C., & Kerzel, D. (2016). Visual search in the upper vs lower and left vs right visual fields. Manuscript in preparation.

Experiments 7-9: Carlei, C., Framorando, D., Burra, N. & Kerzel, D. (2016). Vertical and horizontal hemi-field asymmetries in face processing. Manuscript in review.

Experiments 10-12: Carlei, C., & Kerzel, D. (2014). Gaze direction affects visuo-spatial short-term memory. *Brain and Cognition*, 90C, 63-68. doi: 10.1016/j.bandc.2014.06.007

Experiments 13-15: Carlei, C., & Kerzel, D. (2015). The effect of gaze direction on the different components of visuo-spatial short-term memory. *Laterality: Asymmetries of Body, Brain and Cognition*, 20(6), 738-754. doi: 10.1080/1357650X.2015.1047380

French Abstract

Lors de ma thèse, le professeur Dirk Kerzel et moi-même, nous sommes intéressés aux asymétries cérébrales. Pour ce faire, nous avons utilisé des paradigmes classiques de présentation visuelle périphérique (voir Chapitre 1) et une nouvelle méthode basée sur la manipulation du regard (voir Chapitre 2). Contrairement à la plupart des chercheurs dans le domaine, nous avons choisi de ne pas uniquement nous focaliser sur la traditionnelle différence entre hémisphère gauche et droit, mais de prendre également en compte les asymétries dites verticales (haut versus bas) qui au niveau cérébral semblent refléter des différences d'activation entre voie dorsale (lobe pariétal) et voie ventrale (lobe temporal). Pour se faire, nous avons utilisé des paradigmes expérimentaux dans lesquels nous n'avons pas uniquement comparé deux (gauche versus droite ou haut versus bas), mais quatre positions, une position dans chaque quadrant visuel.

L'utilisation d'un paradigme classique de présentation périphérique nous a permis d'étudier les asymétries perceptives. Des stimuli visuels sont présentés à un sujet dans son champ visuel périphérique, un stimulus présenté dans l'hémichamp gauche sera représenté directement dans l'hémisphère droit alors qu'un stimulus présenté dans l'hémichamp droit sera directement représenté dans l'hémisphère gauche. De plus, comme mentionné plus haut, on sait qu'il existe également des différences au niveau vertical en termes de voie ventrale et dorsale (hémichamp supérieur versus inférieur). Deux types de stimuli ont été utilisés lors de ces expériences, des formes géométriques et des visages. La littérature existante sur les asymétries horizontales et verticales (Introduction du Chapitre 1) nous a permis de formuler des hypothèses spécifiques sur les résultats attendus qui ont été confirmés. Les conclusions principales de ces expériences étant que la recherche visuelle de formes simples versus de formes complexes naturelles (comme des visages) implique un traitement visuel différent et que ce traitement peut être modulé par la position des stimuli à l'écran. Ainsi, un visage sera plus rapidement traité en haut à gauche alors qu'une simple forme géométrique, dépourvu de sens, sera plus rapidement traité en bas à droite de notre champ visuel. On oppose alors un traitement holistique basé sur la reconnaissance d'objet à un traitement local nécessitant une bonne acuité visuelle. On retrouve alors la différence postulée entre traitements global (hémisphère droit) versus local (hémisphère gauche) et la différence entre reconnaissance d'objets (voie ventrale) et acuité visuelle (voie dorsale). Cependant, il est important de

mentionner que ces différences observées sont fortement dépendantes de la nature de la tâche et de sa difficulté comme nous avons pu l'observer au cours de nos expériences.

Nos yeux bougent des milliers de fois par jour. Le principal objectif des saccades oculaires est de placer l'image d'un stimulus visuel au centre de la fovéa. Ces saccades oculaires sont conscientes, elles sont orientées vers des positions précises pour augmenter l'acuité visuelle en direction de stimuli visuels pertinents. Il existe également des saccades qui sont totalement dépourvues d'un « objectif » visuel, celles-ci peuvent d'ailleurs survenir indépendamment de toute stimulation visuelle. Ces mouvements oculaires ne sont pas intentionnels, on les qualifie de saccades oculaires « aléatoires » ou « spontanées » ou comme des « mouvements oculaires rapides d'éveil ». Ces mouvements oculaires surviennent lorsqu'une personne n'est pas en train de regarder un stimulus visuel spécifique et semble en train de réaliser des processus cognitifs internes (tel que la réflexion ou l'imagination). Bien que ces mouvements oculaires soient visibles à l'œil nu et facilement observable dans la vie quotidienne, ils ont été largement ignorés dans la littérature scientifique qui traite de manière préférentielle les saccades relevant de l'analyse visuelle d'une scène ou de l'attention porté sur des stimuli visuels. Basés sur les différentes théories décrites dans le présent travail portant sur l'observation des saccades non visuelles (programmation neurolinguistique, mouvements des yeux latéraux, fréquence des mouvements oculaires), sur l'impact des mouvements sur la cognition (EMDR, mouvements unilatéraux) et sur les asymétries cérébrales (Introduction Chapitre 1) nous avons postulé l'existence d'un lien fonctionnel entre direction des mouvements oculaires et cognition. Ces saccades oculaires non visuelles pourraient nous permettre inconsciemment de faciliter certains processus cognitifs en activant certaines régions du cerveau. L'observation des saccades spontanées ne semblant pas donner de résultats consistants dans la littérature (voir les parties dédiées aux mouvements oculaires latéraux et à la Programmation neurolinguistique), nous avons choisi de nous intéresser à l'impact de la direction des mouvements oculaires sur la cognition. Si les mouvements non visuels ont bel et bien un rôle fonctionnel, nous postulons alors que le fait de demander à une personne de produire un mouvement oculaire dans une direction spécifique va permettre d'observer ce même effet facilitateur. Nos résultats sont en faveur de cette hypothèse, un mouvement oculaire orienté en haut à gauche améliore la mémoire visuospatiale, possiblement grâce à l'activation du cortex temporal inférieur droit.

Contents

General Introduction

Originally, the main question of my thesis was: "*Why do people move their eyes when they think?*" It is a very interesting question but is perhaps too broad and therefore extremely difficult to answer. In our first experiments (non-reported in the present work), we began by asking people sets of questions involving memory, reasoning and other cognitive functions. They had to perform several tasks such as verbal fluency, and recall of a series of numbers or arithmetic computations. While they were hearing instructions and questions, they were instructed to look straight ahead at a small red LED at the center of their visual field. At the end of each question, the light was turned off and they could give their answer into a microphone, and during that time they were free to move their eyes. While they were thinking of their answer until the moment they responded, their ocular movements were recorded. The goal was to find out if some directional patterns of ocular movements could ease recall of information, possibly according to lateral eye movement literature (see Lateral Eye Movements section) or according to the Neuro-Linguistic Programming model for gaze direction (see Neuro-Linguistic Programming section). Those first experiments were very interesting but also very frustrating. There was definitely something going on between cognition and eye movements, however, because of the myriad of inter-individual differences in free observed eye movements, it was really hard to draw conclusions valid for everybody. For example, and you may notice this yourself when you are speaking with people, one person will tend to have a lot of eye movements in every direction during a conversation whereas another person will have almost no eye movements. Interestingly, another observation that we have made is that some individuals, if forced not to move their eyes, will find it very hard to concentrate and to engage in cognitive tasks while for others this restriction does not seem to affect their behavior at all. This finding is in line with experiments done on frequency of eye movements (see Eye Movement Rate section). How can these huge differences be explained? One of the major problems that we have been facing is that even if you ask exactly the same question to two individuals, you cannot anticipate what will be going on inside their minds, which strategy and what types of internal representation they will retrieve and manipulate. For example, if you ask them to recall a series of words you cannot know if they will associate some words with an internal visual representation or if they will repeat each word mentally. This lack of control and the high variability observed among individuals when dealing with non-visual eye movements

motivates us to stop looking at free (also called spontaneous) eye movements and instead to look at the impact of direction of gaze on cognition.

Looking at literature, we know that unilateral actions (see Unilateral Hand Clenching section) and unilateral visual perception (see Lateralized Presentation and Unilateral Gaze section) are tools to produce contralateral cerebral activity and to ease tasks associated with the activated hemisphere. We also know that bilateral eye movements are a way to increase interhemispheric activity, presumably by repeatedly activating each hemisphere (see EMDR section). Based on literature on spontaneous eyes movements and on how motor activation can alter cognition, we postulated that people naturally move their eyes in specific directions and at a certain rate in order to improve cognition. Based on that assumption, we then proposed that forcing people to direct their gaze in a precise direction could be a way to lead to the same facilitation effect. This technique of requested eye movements heightens experimental control compared to the passive observation of spontaneous eye movements and it is also easier to set up and interpret. This is how the title of my thesis became: "*The impact of direction of gaze on memory*". We worked on unilateral sustained and bilateral eye movements (EMDR). After a long series of experiments, we chose to report in the present work the most pertinent findings that we obtained on the effect of gaze direction on visuospatial short-term memory (Chapter 2). The absence of findings on verbal memory is addressed in the General Discussion. The second chapter (Experiments 10-12 & Experiments 13-15) is composed of two articles already published, they can be found in their original version in annex of the present thesis (Carlei & Kerzel, 2014, 2015).

Subsequently, we wanted to look deeper into perceptual asymmetries which seem to explain the outcomes that we had found. Instead of focusing only on Horizontal Asymmetries or Vertical Asymmetries we choose to take both into account and therefore to look at Quadrant Asymmetries. Again, we conducted numerous experiments, and decided to report only the most important findings in the present work (Chapter 1). In this section, in order to investigate visual asymmetries, direction of gaze was not manipulated. Participants were asked to keep their gaze straight ahead on the center of the screen while different kinds of stimuli were displayed on the four quadrants of their visual field. We compared processing of two types of stimuli, geometrical shapes versus faces. The first chapter is composed of one manuscript in preparation (Experiments 1-6) and one manuscript currently in review (Experiments 7-9).

Chapter 1. Perceptual Asymmetries

Introduction

Hemispheric Lateralization

We know from literature that our two cerebral hemispheres have different processing abilities. Most reported findings show that the left hemisphere is specialized in verbal processing whereas the right hemisphere is more involved in visuospatial processing (Gazzaniga, 2000). Hemispheric specialization (HS) is not unique to the human brain; anatomical and behavioral cerebral asymmetries have also been observed in chimpanzees (Meunier, Vauclair, & Fagard, 2012) and in all vertebrate classes (Ocklenburg & Güntürkün, 2012).

Functional Specialization

Functional lateralization of language was initially related to gray matter (Herve, Zago, Petit, Mazoyer, & Tzourio-Mazoyer, 2013) with the predominance of leftward hemispheric asymmetry in 90% of the population. The network of language is now well known; it includes temporo-parietal (Wernicke's area) and inferior frontal gyrus (Broca's area) connected by the inferior occipito-frontal and longitudinal fasciculi (arcuate, middle & inferior) (Turken & Dronkers, 2011; Vigneau et al., 2006). The right hemisphere specialization is less documented. Recent evidences suggest a functional dominance in attentional reorienting resulting in better visuospatial abilities. At an anatomical level, this is expressed by a rightward asymmetry of the ventral fronto-parietal attentional network composed of the temporo-parietal junction, the inferior part of the middle frontal gyrus, the inferior frontal gyrus and the interior insula (Bartolomeo, Thiebaut de Schotten, & Chica, 2012; Corbetta, Patel, & Shulman, 2008).

More recently, tensor imaging studies using the water diffusion process have given information about the brain anatomical circuitry and allowed researchers to also spot differences in white matter structure between the two hemispheres (Takao, Hayashi, & Ohtomo, 2011; Thiebaut de Schotten et al., 2011). The main finding of this research is that each cerebral hemisphere has its own structural network. The right hemisphere has a more efficient level of interconnection which could explain its involvement in wide processes such as visuospatial integration (Iturria-Medina et al., 2011) and global processing (Vankleeck, 1989).

In turn, the left hemisphere is structured less efficiently but counts more crucial regions which could explain its leading role in a highly demanding process such as language (Herve et al., 2013) or local processing (Lamb, Robertson, & Knight, 1990).

Left Hemisphere and Language

There is currently a debate in literature to determine to what extent HS is indeed inherited from our ancestors (Herve et al., 2013). The issue being the fact that in humans there is a dramatically high occurrence of right-handedness (more than 90%) which is not the case for other species. It has been widely assumed that the co-lateralization of hand preference and language in the left hemisphere has a common basis. As cerebral asymmetry for language can be considered unique to humans, at least with respect to its grammatical structure (Hauser, Chomsky, & Fitch, 2002), certain authors proposed that HS was specific to the human condition. For example, Crow, Close, Dagnall, and Priddle (2009) argued that HS has been possible in humans because of a genetic variation arising from a prior hominid to *Homo sapiens* which relates to the origin of speech and speciation. Other researchers disagree, defending a gestural origin of language and the idea that asymmetries have primate origins and have achieved a distinctive and more exaggerated character during the evolution of humans as their functions became more specialized and complex (M. C. Corballis, Badzakova-Trajkov, & Haberling, 2012; Goldin-Meadow & Alibali, 2013).

Right Hemisphere and Attention

The neural basis of attention is not symmetric between the hemispheres. For instance, it is a well-documented finding that spatial neglect is more frequent after right-hemisphere lesions than after left-hemisphere lesions. The interpretation was that the right hemisphere controls attention in both ipsi- and contralateral visual field, whereas the left hemisphere only controls attention in the contralateral hemifield. Thus, lesions of the left hemisphere do not impair attention in the contralateral, right visual field because the right hemisphere may compensate for the loss (Heilman & Valenstein, 1979; Posner, Walker, Friedrich, & Rafal, 1984). In contrast, lesions of the right hemisphere leave the contralateral, left visual hemifield with reduced attentional capacities because the left hemisphere cannot compensate. Further support for the dominant role of the right hemisphere for attention comes from imaging studies (Shulman & Corbetta, 2012), where the right temporal junction, right ventral cortex and insula form a ventral network which is involved when attention is reoriented to relevant stimuli in a

bottom-up manner. Left visual hemifield stimuli may have more direct access to the right ventral network because their initial representation is in the right hemisphere, whereas stimuli presented to the right visual field have to pass from the left to the right hemisphere. Some recent studies using rapid serial visual presentation (RSVP) and exogenous cueing also provide support for left visual hemifield dominance in attentional tasks with healthy participants. When two RSVP streams were presented simultaneously on the left and right visual field, inconspicuous targets were less frequently missed in the left than in the right visual field, supporting better attentional capacities in the right hemisphere (Asanowicz, Smigasiewicz, & Verleger, 2013). This hypothesis was further supported by a cueing manipulation. When a salient exogenous cue was presented close to the RSVP stream that did not contain the inconspicuous target (invalid cue), the cue was more disruptive when it was presented in the left compared to the right visual field (Smigasiewicz, Weinrich, Reinhardt, & Verleger, 2014). Similarly, invalid cues in the periphery that matched the color of the target in a central RSVP stream caused stronger interference when they appeared in the left compared to the right visual field (Du & Abrams, 2010). Thus, invalid cues in the left visual field capture attention to a larger degree than invalid cues in the right visual field when the experimental task involves strong temporal competition (RSVP).

Frontal Asymmetries

A more recent addition to the list of hemispheric asymmetries emerges from the frontal cortex and focuses mainly on motivation states and episodic memory. The relationship between frontal asymmetries and emotion/motivation-related constructs had been widely investigated in literature (for a review see, Coan & Allen, 2004). Research supports the idea that the left and the right prefrontal cortex are related respectively to positive and negative emotions (R. J. Davidson, 1998; R. J. Davidson, Saron, Senulis, Ekman, & Friesen, 1990; Silberman & Weingartner, 1986). Supporting this theory, some authors using unilateral gaze method (see Investigation Methods section), have found a significant increase of anxiety and depression levels on both clinical and non-clinical population after a sustained unilateral period of left gaze (Schiffer, 1997; Schiffer, Anderson, & Teicher, 1999; Schiffer, Stinchfield, & Pascual-Leone, 2002). Recent findings suggest that, over and above affective valence, motivational direction seems a more pertinent factor to explain frontal asymmetries.

Approach versus Avoidance

Harmon-Jones, Gable, and Peterson (2010) discuss frontal asymmetries of motivation states in a recent review. Approach motivation and emotional valence are often linked, we will tend to approach what we perceived with positive valence and to avoid what is associated with negative valence. However, there are exceptions; the emotion of anger, for instance, where approach motivation is linked to negative valence. Recent findings on anger and even on jealousy suggest that motivational direction is a better predictor than emotional valence for asymmetric frontal activity (Harmon-Jones, Peterson, & Harris, 2009; Harmon-Jones & Sigelman, 2001; Jensen-Campbell, Knack, Waldrip, & Campbell, 2007; Verona, Sadeh, & Curtin, 2009). Greater left over right frontal activity is associated with approach motivation whereas greater right over left frontal activity is associated with avoidance motivation or inhibition (Coan & Allen, 2003; Wacker, Chavanon, Leue, & Stemmler, 2008).

Hemispheric Encoding/Retrieval Asymmetry

Frontal asymmetries of memory were found through early PET studies (Nyberg, Cabeza, & Tulving, 1996; Tulving, Kapur, Craik, Moscovitch, & Houle, 1994). Authors noticed that when participants were learning new materials, their left prefrontal cortex was more activated, however, when participants were engaged in subsequent retrieval tests, their right prefrontal cortex was more activated. The Hemispheric Encoding/Retrieval Asymmetry (HERA) model emerges, proposing that left prefrontal regions are more involved with encoding of new episodic memories and simultaneously in retrieval of information stored in semantic memory. Conversely, right prefrontal regions are more involved with retrieval of episodic memories (Habib, Nyberg, & Tulving, 2003).

However, the relationship between HERA's proposed frontal asymmetries and material-specific asymmetries (i.e. left hemisphere advantage for verbal stimuli versus right hemisphere advantage for visuospatial stimuli) is still not clear and has led to much criticism of HERA. For instance, Kelley et al. (1998) found a greater activity in left over right prefrontal cortex in encoding for words which was postulated by the HERA model. However they found the opposite pattern for faces with a greater involvement of right over left prefrontal cortex. Other authors have come to similar conclusions, with prominent material-specific lateralization activation, left prefrontal cortex for verbal versus right prefrontal cortex for non-verbal stimuli (Kirchhoff, Wagner, Maril, & Stern, 2000; McDermott, Buckner, Petersen, Kelley, & Sanders, 1999; Wagner

et al., 1998). These findings are consistent with the traditional hemispheric specialization that we will discuss below but not with the HERA model. Propper, Brunyé, Christman, and Januszewskia (2012) used the unilateral gaze method to investigate if contralateral activation induced by this method supported the HERA model or the material-specific lateralization hypothesis. In this research, participants were presented with a blank map of the United States and asked to name the states, point to states when the names were read to them, or to name and point simultaneously. Importantly, participants wore glasses (Schiffer et al., 1999) that forced them to look at the map with their gaze directed to the left, center, or right. With gaze directed toward the left or center, performance was best in the naming condition, decreased for the pointing and decreased even further for both tasks simultaneously. In contrast, the difference between naming and pointing was absent with gaze directed to the right. While gaze directed to the right increased activation in the contralateral hemisphere, left hemisphere activation (right gaze) improved recall in the pointing task compared to the other gaze directions. This result is in line with the HERA model, consistent with a specialization of the left prefrontal hemisphere for retrieval of semantic information that spans verbal and spatial information (Habib et al., 2003). In contrast, it does not support the specialization of the right hemisphere for the retrieval of spatial information (Belger et al., 1998; Jonides et al., 1993).

How is it that some studies have found that lateralization in the prefrontal cortex was determined by stages of processing (encoding versus retrieval) while others have found instead that the type of material and processing (verbal versus visuospatial/analytic versus holistic) was a better predictor? Golby et al. (2001) proposed an explanation of the contradictory data by arguing that lateralization of encoding processes is determined by the verbalizability of stimuli. In a preliminary behavioral experiment a dual-task verbal interference paradigm was used to rank the relative verbalizabilities of three classes of non-verbal stimuli (scenes > faces > abstract patterns). Then, in an fMRI study, the research showed that for verbal encoding materials (words), the left inferior prefrontal cortex was more activated, however, for pattern encoding, the least verbalized stimuli, the right inferior prefrontal cortex was more activated. The encoding of stimuli that were intermediate in verbalizability (faces and scenes) resulted in approximately symmetrical activation. Other authors such as Nyberg et al. (2000) think that asymmetries defined by processes and materials can co-exist. They explored their relation experimentally in a PET study, both asymmetries were manipulated and they performed a multivariate partial least squares in order to identify latent variables which represent the largest

sources of experimental variance. This paradigm allowed researchers to find two main latent variables. The first latent variable, a difference between verbal and non-verbal stimuli, gave credit to material-specific asymmetry. The second latent variable, a difference between encoding and retrieval, gave credit to the HERA model. This finding shows that material-specificity can occur independently of process-specificity. Once asymmetries due to material are accounted for, it is possible to observe the prefrontal asymmetries specific to processes formulated by the HERA model.

Horizontal Asymmetries

Investigation Methods

The perceptual asymmetries between the left and right visual hemifields are believed to reflect the functional differences between the left and right hemispheres (Jordan & Patching, 2004; Martinez et al., 1997). Behaviorally, the hemispheric asymmetries can be tested by presenting stimuli to one hemifield (lateralized presentation) or by restricting vision to one hemifield (unilateral gaze). These two methods aim to force processing in the contralateral cortical hemisphere (see Figure 1).

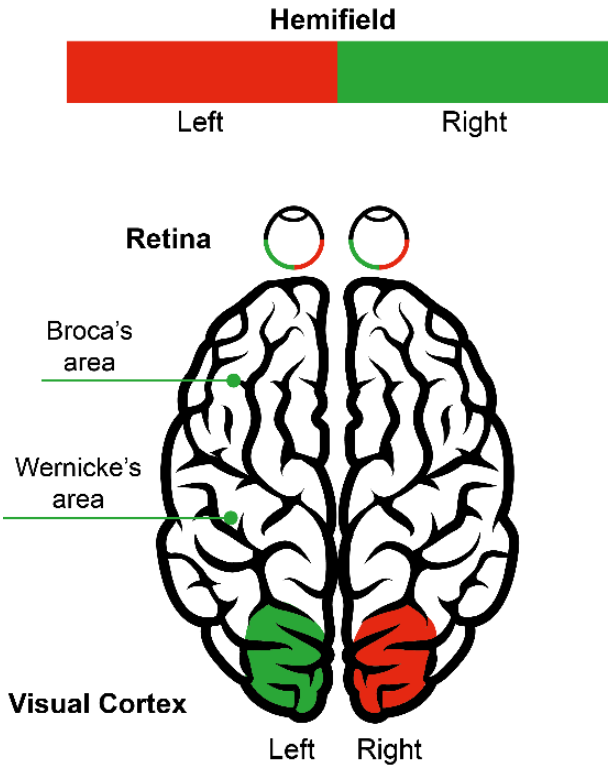

Figure 1. Illustration of horizontal visual asymmetry. The left hemifield is represented in the right part of the occipital cortex whereas the right hemifield is represented in the left part of the occipital cortex.

Lateralized Presentation and Unilateral Gaze

Studies using lateralized presentation rely on the fact that the initial processing of visual stimuli occurs in the opposite hemisphere (Greenberg et al., 1981). Stimuli are displayed either to the right or to the left of the participant's visual field for a really short amount of time (usually less than 150 ms) to ensure that the participant does not move his eyes. This manipulation

allows researchers to investigate if processing of a certain type of stimulus is more efficient when directly processed in the right (left hemifield) or the left hemisphere (right hemifield).

Conversely, the unilateral gaze method obliges participants to receive visual input only from their left or their right hemifield using special equipment such as goggles (Propper et al., 2012; Schiffer, 1997; Schiffer et al., 1999; Schiffer et al., 2002) or lenses (Dimond, Bureš, Farrington, & Brouwers, 1975; Fouty, Otto, Yeo, & Briggs, 1992; Sivak, Sivak, & Mackenzie, 1985). For instance, in order to allow only right visual field vision (left hemisphere), any visual input from the two right hemiretinas of both eyes would be prevented (see Figure 2). This method permits participants to move their head/eyes and stimuli can be presented for an unlimited period of time. Like the motor methods described in the next chapter, this method looks at the long-term effects of unilateral visual stimulation (i.e. unilateral visual deprivation) on cognitive processing. Schiffer et al. (2004) have shown that sustained vision of one hemifield produces strong activation in the contralateral hemisphere despite the connections between the two hemispheres. It is assumed that the visual stimulation, which begins in the contralateral striate cortex, spreads to the occipito-temporal, posterior parietal and dorsolateral prefrontal areas (Schiffer et al., 2004). This general activation of the cortex is thought to facilitate subsequent tasks involving this hemisphere (Propper et al., 2012).

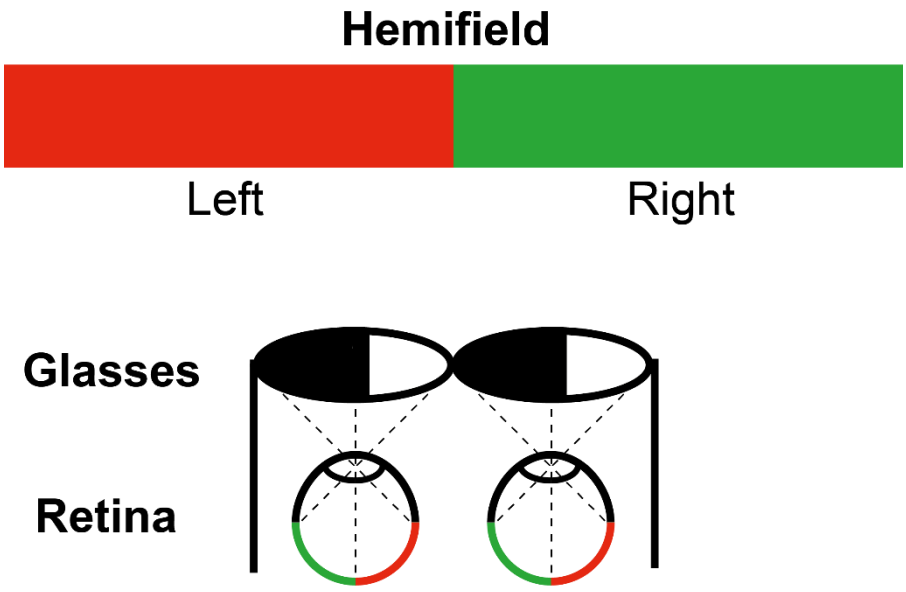

Figure 2. Illustration of the unilateral gaze method. The left hemifield is occulted with goggles allowing input only from the two left hemiretinas of both eyes.

Functional Specialization of Left and Right Hemifield

Verbal versus Visuospatial Processing

As mentioned before, the right hemisphere is specialized in visuospatial processing and the left hemisphere in verbal processing. Therefore, as visual asymmetries reflect functional differences, we can expect that visuospatial stimuli and verbal stimuli will be processed better when displayed in the contralateral hemifield.

For visuospatial processing, we know that pictures are remembered better (Laeng, Overvoll, & Steinsvik, 2007) and visuospatial matrices are recalled faster (Gross, 1972) when displayed in the left hemifield compared to the right. This right hemisphere superiority is also corroborated by studies with a "split-brain" patient (Metcalfe, Funnell, & Gazzaniga, 1995) who showed a right hemisphere superiority for recognizing specific patterns such as visual forms and faces. Also, Fouty et al. (1992) found higher accuracy and shorter reaction times with unilateral left compared to right hemifield presentation when participants were asked to match line orientations to a response set and to make same-different judgments of faces.

For verbal processing, results are mixed, perhaps because of the diversity of experimental methods used. Overall, it seems that visual asymmetries for verbal processing are more pronounced in men versus women. Gross (1972) and Samar (1983) demonstrated that responses in categorization or lexical decision tasks were faster when verbal stimuli were presented in the right visual field. Similarly, performance in naming tasks was better when words (versus nonwords) were presented in the right visual field (Jordan & Patching, 2004; Jordan, Patching, & Thomas, 2003). Using a recognition task of nonsense words, Hannay and Malone (1976) found a better performance in the right visual hemifield but for male participants only. Nonsense words were presented vertically in either the left or right visual field of participants. After a variable delay, a word was presented at the center of the computer screen and participants had to decide if the word was the same as the previously lateralized displayed word. Bradshaw and Gates (1978) also showed that the right visual field advantage was stronger for male than for female participants for verbal processing. For a lexical decision task, males presented the right hemifield advantage (i.e. faster to respond) with manual response and overt naming, while females only exhibited the right hemifield advantage with overt naming. A. W. Young and Ellis (1985) using bilateral tachioscopic presentation of words found the right superiority effect in correct responses for both men and women also using overt

naming. Using the unilateral gaze method, Levick et al. (1993) reported an enhancement in verbal ability when vision was restricted to the right hemifield and improvement in spatial ability when vision was directed to the left. Rather than looking at visuospatial versus verbal processing, more recent research in visual hemifield studies have focused on local versus global processing.

Global versus Local Processing

In a review, Robertson and Lamb (1991) list neuropsychological evidence suggesting separable subsystems in the visual mechanism for processing the organization of parts and wholes. One subsystem is responsible for the global properties of a figure, associated with the right hemisphere, and one emphasizes the local properties of a figure linked with the left hemisphere. To characterize preferential global or local processing, a paradigm with large letters composed of smaller letters was introduced by Navon (1977). Because the identities of the large and small letters are independent, conditions in which the global and the local letters are consistent or inconsistent can be created (Figure 3). Sergent (1982) asked observers to determine whether a small or large target letter was present by pressing a key. Large letters defined the target at a global level, while small letters defined it at a local level. Performance was better in the left than in the right hemifield when global letters had to be detected, whereas the opposite was true for local letters. These behavioral results support the idea that the right hemisphere (i.e. the left hemifield) is specialized in global processing of information, whereas the left hemisphere (i.e. the right hemifield) is specialized in local processing. We think that this dichotomy is consistent with attentional asymmetries mentioned above. On the one hand, we have a right hemisphere with a broad focus (global processing), able to compensate for an eventual deficit of the left hemisphere. On the other hand, we have a left hemisphere with a narrow focus (local processing).

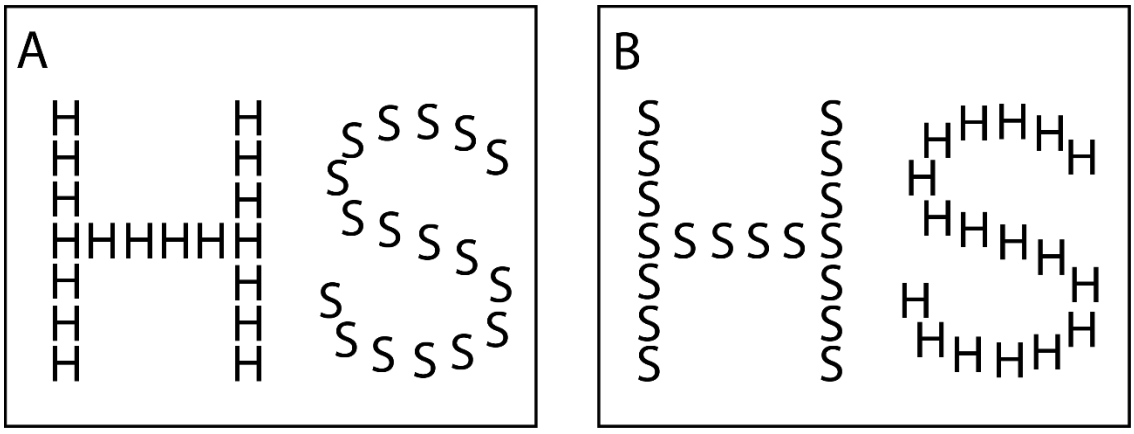

Figure 3. Illustration of stimuli used in the Navon task. Consistent and inconsistent conditions are illustrated respectively in Panel A and B. Global processing relies on large letters (i.e., "H" then "S" in both panels) whereas local processing relies on small letters (i.e., "H" then "S" in Panel A, "S" then "H" in Panel B).

Left Hemifield Advantage for Face Perception

Face perception relies not only on processing of features but on the spatial relations between those features, which is referred to as holistic or global processing (Richler, Cheung, & Gauthier, 2011). Typically, healthy participants tend to show a global processing bias. Darling, Martin, Hellmann, and Memon (2009) have shown that individuals who showed strong global interference were better at identifying the face of a culprit in a lineup after viewing a crime video compared to those showing less global interference. The degree of interference was measured with the Navon paradigm described before. Inversely, individuals unable to recognize faces due to congenital prosopagnosia are more susceptible to interference from conflicting local letters (Avidan, Tanzer, & Behrmann, 2011; Behrmann, Avidan, Marotta, & Kimchi, 2005). Thus, global processing and face perception seem to be correlated and possibly depend on the same underlying neurophysiology. Imaging studies support the idea that holistic processing of faces is enhanced in the left hemifield because face processing is mainly mediated by the right side of the brain. For instance, imaging studies have established that the right fusiform region (Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997), the right occipital face area (Gauthier et al., 2000) and the right posterior superior temporal sulcus (Puce, Allison, Bentin, Gore, & McCarthy, 1998) are involved in face processing. Furthermore, Bentin, Allison, Puce, Perez, and McCarthy (1996) found in an electrophysiological study that human faces evoked a negative event-related potential at about 170 ms (the N170 component), which was larger over the right than the left hemisphere. Finally, damage to the right inferior occipito-

temporal region often leads to prosopagnosia (De Renzi, 1986; De Renzi, Perani, Carlesimo, Silveri, & Fazio, 1994).

Interestingly, this right-hemisphere dominance is not specific to faces, it also appears for body part and gaze processing. Chan, Kravitz, Truong, Arizpe, and Baker (2010) showed that BOLD fMRI responses in the right extrastriate body area were stronger for decoding of body parts in the left than in the right visual field. Neural circuits related to gaze processing are crucial in face perception (review by, Emery, 2000). The right-hemisphere dominance in gaze processing has been established within a network including posterior fusiform gyrus, the parietal lobule, and the inferior and middle temporal gyrus (Wicker, Michel, Henaff, & Decety, 1998). Furthermore, the right superior temporal sulcus was found to code for different gaze directions (Calder et al., 2007). Also, the N170 is larger for eyes presented in isolation than for eyes embedded in a whole face, which was interpreted as possible activation of an eye sensitive region in the right occipito-temporal sulcus (Bentin et al., 1996). At a behavioral level, the right hemisphere dominance leads to better gaze perception when eyes are displayed in the left hemifield. The left hemifield bias has been shown for gaze discrimination (Ricciardelli, Ro, & Driver, 2002) and for gaze cueing (Greene & Zaidel, 2011). Additionally, gaze detection is faster in the left than the right visual hemifield (Conty, Tijus, Hugueville, Coelho, & George, 2006). Altogether, face and gaze processing are mediated by the right hemisphere and a behavioral advantage occurs when stimuli are presented in the left hemifield.

Face processing can also take place in the left hemisphere but in a manner that is regarded as more analytical or part-based (Hillger & Koenig, 1991; Rossion et al., 2000). Bradshaw and Sherlock (1982) have investigated holistic and analytic processing using faces and bugs as stimuli. The participants were instructed to direct their attention to the overall configuration (holistic processing) or to specific feature elements (analytic processing) of outline face and bug stimuli. When holistic processing was required, a left hemifield (i.e. right hemisphere) advantage was observed both for faces and bugs, but the opposite occurred for analytic processing.

Right Hemifield Advantage for Analytic Processing

Polich, DeFrancesco, Garon, and Cohen (1990) used a visual detection search task in which participants had to judge whether all the line displays were vertical (same) or whether a single horizontal line was present (different). Simple line arrays were manipulated by variation

of line density, linear organization and array size in order to obtain two variants of the same task. They found left visual field (right hemisphere) advantage when the display was perceived as a whole but right visual field (left hemisphere) advantage when the display required individual assessment of individual array elements. In another experiment, Polich (1984) investigated analytic processing using a visual tachistoscopic task requiring a fine-grained feature analysis. Stimulus arrays containing a variable number of elements were presented either to the left or to the right hemifield. Participants had to perform a detection task, judging if elements within the array were all the same (all X's) or whether one element (O) was different from the rest. Polich argues that right hemifield (left hemisphere) is superior for visual search when fine-grained feature analysis is required (analytic processing).

Task Demands

Evert, McGlinchey-Berroth, Verfaellie, and Milberg (2003) found that increasing task demands is a way to show the abilities of each hemisphere (global vs. local processing as discussed before). In their study, the researchers compared selective attention on a cued response time task when a target was presented alone (low load condition) or with a competitive distractor (high load condition). In the low load condition, a target letter was displayed in a square situated either to the left or right of a central fixation dot. In the high load condition, the target letter was presented in one square and a distractor letter was simultaneously presented in the other square. The results showed that the costs of invalid cueing were minimal when the right hemisphere processed the target but only in the high load condition. So in this case, the right hemisphere specialization, with its ability to direct attention toward a larger portion of the visual field, was only present when the two hemispheres were in competition, but there was no effect when the task was too easy. This finding is in line with the dominant role of the right hemisphere for selective attention mentioned before (Asanowicz et al., 2013; Du & Abrams, 2010; Smigasiewicz et al., 2014). In another study involving selective attention (Michael & Ojeda, 2005), the difficulty of the task was manipulated by changing the target/distractor similarity. Based on a modified search paradigm, the authors found visual field differences depending on target/distractor physical similarity (low, medium or high). Five symbols made up of vertical and horizontal deep gray lines were briefly presented on the screen, and the subject's task was to identify a predefined target. This set of five stimuli was presented on the left or on the right visual field. The authors found a right hemifield (left

hemisphere) advantage when target/distractor similarity was medium. They interpret this finding as meaning that detecting a target among distractors requires fine grain resolution and, as mentioned before, this ability is thought to rely on left hemisphere processing. When the target/distractor similarity was high, a left hemifield (right hemisphere) advantage was found. The latter result is in line with several neuropsychological studies showing that right hemisphere is also superior to left hemisphere when fine orientation analysis is required (Benton, Hannay, & Varney, 1975; P. M. Corballis, Funnell, & Gazzaniga, 2002). Again, no differences were found when the task was too easy, i.e. when the target/distractor similarity was low. Kitterle, Christman, and Hellige (1990), when investigating hemispheric asymmetries in the processing of low vs. high spatial frequencies, did not find any differences for detection tasks but found differences for identification tasks. It is therefore possible that some simple detection tasks are not difficult enough to elicit hemisphere asymmetries. Poynter and Roberts (2012) conducted two visual search tasks, one requiring feature search and one requiring feature-conjunction search. Authors adjusted attentional distribution to suit task difficulty. For feature search, better target detection and faster reaction time were observed in the left hemifield presentation (right hemisphere). For feature-conjunction search the opposite was true, with an advantage in the right hemifield presentation (left hemisphere). The conclusion was that each hemisphere is specialized in one type of search processing (feature vs. features conjunction). For simple feature detection (i.e. parallel search), a global view of the visual gives a right hemisphere advantage. In contrast, in the feature-conjunction search condition, global processing is not enough, localized attentional processing is needed, leading to a left hemisphere advantage.

Vertical Asymmetries

A number of studies have proposed that visual processing also differs between the upper and lower visual hemifields. In a review, Christman and Niebauer (1997) concluded that vertical asymmetries are at least as strong and prevalent as horizontal asymmetries.

Anatomical Differences

At a cortical level, the upper and lower visual hemifields are respectively represented on the lower and upper cortical sheets of the occipital lobe (see Figure 4). The division in area V1 separates the two vertical hemifields within each hemisphere. Previc (1990) suggested that anatomical segregation promoted functional specialization for the different types of visual processing and argued that perceptual capacities of the visual field have been shaped by environmental constraints. Based on an evolutionary perspective, he proposed that the lower visual field became specialized for near vision because of its involvement in reaching and other manipulations performed in peripersonal space, whereas the upper visual field became specialized in visual search and object recognition toward extrapersonal space. When fixing a target object (e.g. while picking fruit), reaching and grasping occurs in the lower visual field, while visual search for and recognition of objects occurs in the upper visual field. Each hemifield adapted its type of visual processing based on the task that it usually performed. In the lower visual field, the principal task is the perception and manipulation of closer objects which require visuomotor coordination and spatial perceptual abilities. As objects are manipulated in this hemifield they could appear blurred and in motion, so Previc also proposed that the lower hemifield specialized in sensory processing of low spatial and high temporal frequencies (global processing). In contrast, in the upper hemifield, the principal task is to search for and recognize distant objects. Since object recognition requires the discrimination of fine details, the upper visual field specialized in high-level perceptual processing of high spatial frequencies (local processing).

Furthermore, Previc proposed that vertical asymmetries can be related to the two functionally and anatomically separate processing streams for visual processing, the ventral and the dorsal stream. Indeed, at an anatomical level, the lower cortical sheets (upper visual field) project more into the ventral stream of the temporal lobe, whereas the upper cortical sheets (lower visual field) project more into the dorsal stream in the parietal cortex (Fecteau, Enns, &

Kingstone, 2000). The ventral stream (also known as the "what" pathway) is involved in object identification and recognition, whereas the dorsal stream (also known as the "where" pathway) mainly processes visuospatial information, such as motion, distance and location (Goodale & Milner, 1992) (see Figure 4), which is consistent with the specialization of hemifield mentioned above. This dichotomy between upper and lower visual fields seems to begin before visual processing.

At the retina level, there is a higher concentration of receptors and ganglion cells in the superior than in the inferior hemiretina at eccentricities exceeding 6° (Croner & Kaplan, 1995; Curcio & Allen, 1990). Recent findings concerning monkeys have shown that representation of the visual space in the superior colliculus was not symmetrical (Hafed & Chen, 2016) as it was commonly assumed (Ottes, Vangisbergen, & Eggermont, 1986). The superior colliculus is involved in visual-motor processing, target selection and attention. This layered midbrain structure contains retinotopic maps of the visual field in superficial layers and spatially registered eye movement maps in deeper layers (Sparks & Nelson, 1987). Hafed and Chen (2016) have found that receptive fields in the upper superior colliculus were smaller with a higher spatial resolution compared to lower superior colliculi. In a similar vein, Mayo, DiTomasso, Sommer, and Smith (2015) reported that ~70% of response fields in the frontal eye field were upper visual field neurons. The frontal eye field is involved in eye movement exploration; the over representation of upper visual field neurons both in the frontal eye field and superior colliculus support the assumption of upper visual field specialization in visual exploration and object recognition. On the contrary, the higher concentration of receptors and ganglion cells far from the fovea in the superior retina and the large receptive fields in the superior colliculus support the assumption that the lower hemifield is specialized in motion/sensory processing.

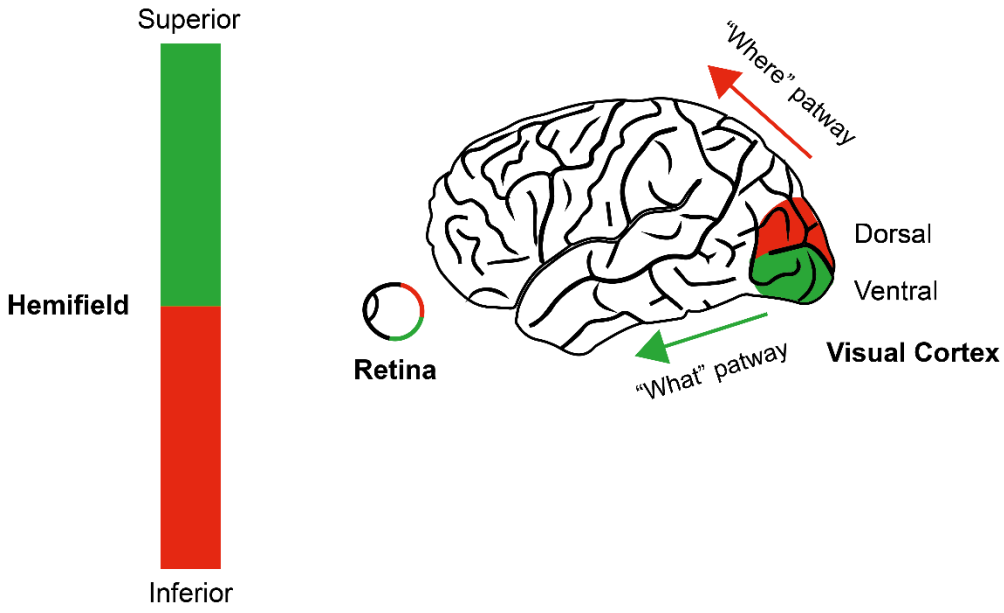

Figure 4. Illustration of vertical visual asymmetries and processing streams. The superior hemifield is represented in the ventral part of the occipital cortex whereas the inferior hemifield is represented in the dorsal part of the occipital cortex. The dorsal stream ("where" pathway) project into the parietal lobe whereas the ventral stream ("what" pathway) project into the temporal lobe.

Attentional Asymmetries

However, the evaluation of Previc's hypothesis is mixed, particularly with respect to attentional asymmetries. For instance, He, Cavanagh, and Intriligator (1996) claimed that attentional resolution was better in the lower visual field by showing lower visual field advantages in difficult search tasks, but no differences in basic search tasks. In contrast, Carrasco, Talgar, and Cameron (2001) showed that attention, as measured by the effects of exogenous cueing, was similar in the upper and lower visual fields, whereas perceptual performance was better in the lower visual field. Meanwhile, Rezec and Dobkins (2004) showed that discrimination of basic visual features was better in the lower visual field when search involved the complete visual field, suggesting an attentional bias to the lower visual field, whereas discrimination at cued locations in the upper or lower visual field were equal, suggesting that perceptual performance was about equal. Overall, vertical asymmetries, just like horizontal asymmetries (as mentioned above), seem to rely on task demands and selective attention. Competitive mechanisms between the two streams have been revealed by varying task demands (Jokisch & Jensen, 2007). Additionally, Milner and Goodale (1995) introduced the distinction between the dorsal and ventral streams in terms of the behavioral goal. They

proposed that, depending on the purpose, the same attribute (e.g. orientation) can be processed in the ventral stream when judgments have to be made and reported, or in the dorsal stream if orientation is used to guide an action.

Despite the mixed results for attentional asymmetries, more recent research supports Previc's hypothesis that sensory processing is improved in the lower visual field, whereas the upper visual field is specialized in conscious perception and object recognition.

Functional Specialization of Upper and Lower Hemifield

Upper Hemifield Advantage for Object Recognition

As mentioned before, object processing was found to be better in the upper hemifield, associated with the ventral stream, than in the lower visual hemifield. For instance, research has shown that localizing a target among distractors (Feng & Spence, 2014), discrimination between words and nonwords (Goldstein & Babkoff, 2001) and naming letters in a categorical judgment of spatial relationships (i.e. above vs. below, Niebauer & Christman, 1998) are better in the upper visual field.

Processing of faces also seems to be facilitated in this particular hemifield, it has been observed that encoding of faces in the upper hemifield resulted in better recall or showed stronger effects of inhibition. Felisberti and McDermott (2013) observed that recognition of faces associated with cooperating behaviors was better when these faces were encoded in the upper hemifield. In another study, Kessler and Tipper (2004) showed that long-term inhibition induced by a no-go cue was stronger when the face was presented in the upper hemifield, or more precisely in the upper-left quadrant. While these studies combine perceptual and memory processes, there are also studies focusing on short-term priming. Quek and Finkbeiner (2014a) asked participants to make left or right reaching movements to classify the gender of a target face above or below the central fixation. Each target face was preceded by a masked prime face that was either congruent (i.e. the same gender as the target) or incongruent (i.e. the opposite gender to the target). The effect of congruency on reaching trajectories occurred earlier for faces presented in the upper hemifield and the proportion of correct responses was also higher. The advantage for sex categorization of faces in the upper visual field was not an attentional bias because performance to stimuli in the upper visual field was unaffected when endogenous attention was directed to the lower visual field (Quek & Finkbeiner, 2015). Vertical

asymmetries can also be observed using other complex natural objects, for instance, Quek and Finkbeiner (2014b) observed an upper-field advantage for hands.

Lower Hemifield Advantage for Sensory Processing

In contrast, the lower hemifield, which is more involved in near vision, seems to be specialized in sensory processing. Over and above the fact already discussed that this hemifield is more associated with the dorsal stream, we also know that there are some basic anatomical asymmetries that can also explain its functional specialization (Croner & Kaplan, 1995; Curcio & Allen, 1990; Hafed & Chen, 2016).

Behavioral studies have found vertical asymmetries favoring the lower visual field in different types of motion processing such as motion in depth (Edwards & Badcock, 1993; Levine & McAnany, 2005), anisotropy of motion (Raymond, 1994), chromatic motion (Bilodeau & Faubert, 1997), threshold for motion (Rezec & Dobkins, 2004) and motion segmentation (Lakha & Humphreys, 2005). Moreover, two electroencephalogram (EEG) studies, recording an electrophysiological response to changes in motion direction, suggest the existence of an automatic detection mechanism for motion stimulation which is enhanced in the lower part of the visual field, even under unattended stimulation conditions (Amenedo, Pazo-Alvarez, & Cadaveira, 2007; Kremlacek, Kuba, Chlubnova, & Kubova, 2004). Other studies have found an advantage in the lower visual field for contrast sensitivity (Cameron, Tai, & Carrasco, 2002; Carrasco et al., 2001; Carrasco, Williams, & Yeshurun, 2002). Again, neurophysiological studies have supported these behavioral findings. A magnetoencephalography (MEG) study using contrast patterns (Portin, Vanni, Virsu, & Hari, 1999), have shown that visual suprathreshold information arriving from the lower visual field is enhanced in the human visual cortex close to the calcarine fissure, suggesting an over-representation of the lower visual field at a cortical level. This interpretation is supported by the greater number of receptors and ganglion cells in the superior retina mentioned above. Fioretto et al. (1995) in an EEG study, found higher visual-evoked potentials (VEPs) and event-related potential (ERP) amplitudes in the lower hemifield compared to the upper hemifield when stimulating with high-contrast checkerboards. Other findings report superior abilities of the lower hemifield for spatial resolution (Cameron, Tai, Eckstein, & Carrasco, 2004; Carrasco, Mclean, Katz, & Frieder, 1998; Rezec & Dobkins, 2004), orientation (Raymond, 1994), hue (Gordon, Shapley, Patel, Pastagia, & Truong, 1997; Levine & McAnany, 2005) or perception of illusory contours (Rubin, Nakayama, & Shapley, 1996). In a

clinical study on children showing a binocular lower visual field impairment due to brain damage, Dutton et al. (2004) also provides evidence of the crucial role of this hemifield in motion processing and in simultaneous perception (global processing).

Quadrant Asymmetries

Most of the time, horizontal and vertical asymmetries have been investigated separately and only a few studies have looked at both at the same time (e.g. Hagenbeek & Van Strien, 2002). As both horizontal and vertical effects matter when processing visual information, comparing visual quadrants gives us a unique opportunity to investigate not only main effects of visual fields, but also possible interactions (e.g. Kessler & Tipper, 2004). Therefore, in our experiments reported hereafter, we decided to use search displays that would allow us to probe processing in each quadrant (Figure 5).

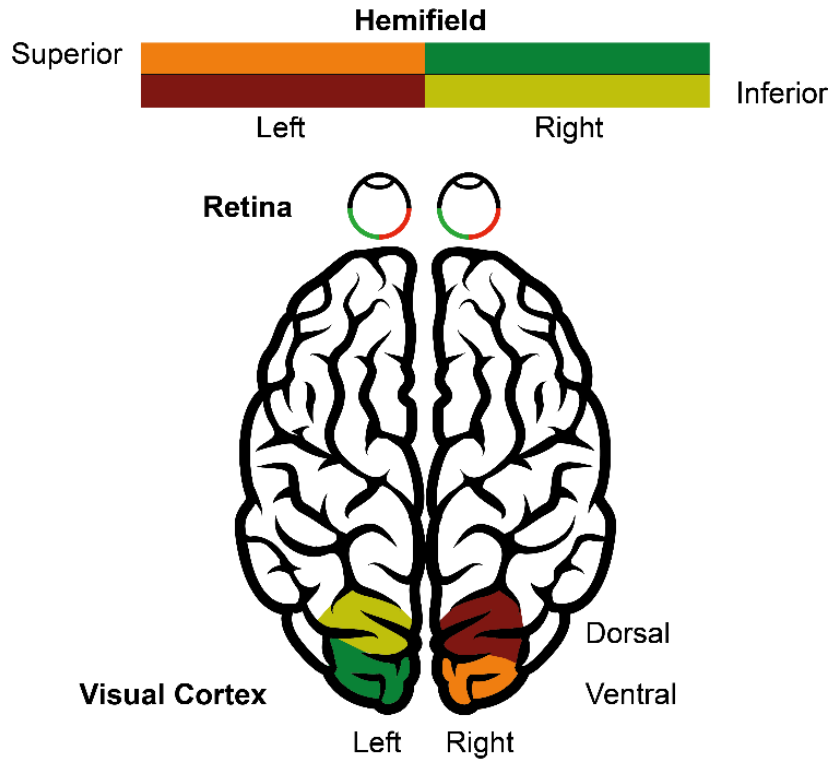

Figure 5. Illustration of visual quadrant asymmetries. Each quadrant of our visual field is represented in a specific part of the occipital cortex.

The asymmetries existing in our visual field were investigated using simple geometric shapes (Experiments 1-6) versus complex natural shapes/faces (Experiments 7-9).

Based on the literature mentioned above, we expected those two types of stimuli to lead to differences in horizontal and vertical asymmetries and possible interactions between quadrants.

Visual asymmetries in visual search tasks for simple geometric shapes

Experiments 1-6

Overview of experiments

We conducted six experiments in which we used different versions of a visual search task (Figure 6). The report of these experiments in literature is currently in preparation.

In Experiments 1-2, we decided to use a compound search task (detection and identification tasks), an additional singleton paradigm without distractors (Theeuwes, 2010). Participants searched for one aspect (i.e. the shape singleton in Experiment 1, Figure 6A or the color singleton in Experiment 2, Figure 6B) but responded to another aspect (the line orientation inside the target). They had to perform a parallel search and then to determine the orientation of a line inside the singleton. Participants had to hold in mind the rules (which key to press depending on the line orientation). Our stimuli cannot be processed holistically (like face stimuli used in Experiments 7-9) but rather required an individual assessment of features: A shape or a color plus a line orientation. As analytical or part-based processing is associated with the left hemisphere (Bradshaw & Sherlock, 1982; Hillger & Koenig, 1991; Rossion et al., 2000; Sergent, 1984), we therefore expect to find a right visual field/left hemisphere advantage similar to Polich (1984) in his visual search task. Concerning vertical asymmetry, we expect a lower hemifield advantage, based on the fact that as mentioned before, lower visual field is better for sensory processing of simple stimuli on orientation (Raymond, 1994), contrast (Cameron et al., 2002; Carrasco et al., 2001; Carrasco et al., 2002; Portin et al., 1999) and hue (Gordon et al., 1997; Levine & McAnany, 2005).

In Experiment 3, we changed the search mode by randomizing the target shape. So even though observers knew they had to search for a singleton shape they did not know which shape it was. Some authors have manipulated the difficulty of their tasks and argued that hemispheric asymmetries disappeared when the task was too easy (Evert et al., 2003; Kitterle et al., 1990; Michael & Ojeda, 2005). However, in our knowledge, nobody had investigated the effect of the predictability of the task on hemispheric asymmetries. As observers cannot anticipate the identity of the target in the display, the task should be harder, we therefore expect longer RTs for this experiment.

There is currently a debate in the literature to determine to what extent attentional capture can modulate top-down processes. Bacon and Egeth (1994) proposed that attentional capture depends on the search mode induced by the experimental situation. When the target is predictable, as in Experiments 1-2, a feature search mode is favored, participants performed a goal-directed selection; the target shape remained the same within a block of trials. However, when the target is unpredictable, as in the present experiment, participants have to search an odd element and a singleton detection mode is required; the target shape varied randomly from trial to trial. On the other hand, Theeuwes (2010) proposed that selection of the target occurs exclusively in a stimulus-driven fashion in the early stages of perceptual processing and goal-driven control only occurs after the initial saliency-based capture. We still expect a right visual field advantage, however, for vertical asymmetries several outcomes are possible. As mentioned before, vertical attentional asymmetry findings are mixed (Carrasco et al., 2001; He et al., 1996; Rezec & Dobkins, 2004). If a lower advantage is still present in this experiment, we could argue that attentional resolution is better in the lower visual field independently of goal driven control, if not we could think that goal driven control play an important role in vertical asymmetries in addition to the task difficulty.

In Experiments 4 and 5, we used a simple target detection task in order to better understand our previous effects. This task required a parallel mode of visual search because the target only differs from other stimuli on one feature (shape or color). We used the same stimulus displays as in Experiments 1 and 2, participants only had to respond if a singleton is present based on shape (Experiment 4, Figure 6A) or on color (Experiment 5, Figure 6B). As in the first two experiments, we still anticipate a lower visual field advantage. However, for horizontal asymmetries several interpretations are possible. Poynter and Roberts (2012) suggested that the left hemifield/right hemisphere is more efficient for classic feature search involving parallel search. They reported a left hemifield/right hemisphere advantage in a simple detection task in the whole visual field when participants were asked to find an orange vertical line target among orange and green horizontal lines. In contrast, other authors using a unilateral presentation did not find any horizontal asymmetries for detection tasks and they suggested that detection tasks are not difficult enough to elicit hemisphere asymmetries. Michael and Ojeda (2005), for instance, using lines segment presentation when the target/distractor similarity was low, or Kitterle et al. (1990) in spatial frequencies task. On the opposite, Polich (1984) using a simple unilateral detection task has found a right hemifield/left hemisphere

advantage when participants had to detect if elements within the array were all the same (all X's) or whether one element (O) was different from the rest. Based on literature, three different outcomes are therefore possible for horizontal asymmetries.

Experiment 6 had the same design as Experiment 4 but the task is unpredictable as Experiment 3. As mentioned above outcomes for detection tasks are mixed in particular for horizontal asymmetries. By keeping the same task while manipulating the predictability we could be able to determine if predictability and indirectly task difficulty could play a role. By randomizing the shape singleton our task became more difficult, this change in search mode and increase of difficulty may be sufficient to lead to horizontal visual asymmetries that are not present when the task is too easy. Concerning vertical asymmetries, we still expect a lower visual field advantage.

Experiment 1

Method

Participants

Twelve individuals participated in this experiment (18-22 years, 2 males). All participants were right-handed undergraduate psychology students at the University of Geneva and reported normal or corrected-to-normal visual acuity, they participated in this experiment for class credit.

Stimuli and Apparatus

The experiment was conducted in a dimly lit room, participants were seated at a distance of 45 cm from a CRT screen. Participants' head position was stabilized with a chin rest in front of the center of the screen. The experiment was controlled by Matlab (The MathWorks, Inc., Natick, MA) using the Psychophysics Toolbox extensions. Participants' eye movements were monitored by the experimenter from outside the experimental booth with the help of the image of the eye provided by an EyeLink 1000 eye-tracker (SR-Research, Ontario, Canada). Eye movements were not recorded or analyzed, but the experimenter assured that participants followed the instructions and intervened if necessary. Displays were composed of eight stimuli made up of geometrical forms (circle or diamond; 2 cm x 2 cm or 2.5° x 2.5° of visual angle, height x width). At the center of each stimulus, a bar of 1 cm x 0.2 cm or 1.3° x 0.25° of visual angle, height x width) was drawn in gray. Each display was composed by seven identical geometrical forms and one different (i.e. a shape singleton). The shape singleton was either a

circle or a diamond (counterbalanced across participants), see Figure 6A for an example of display.

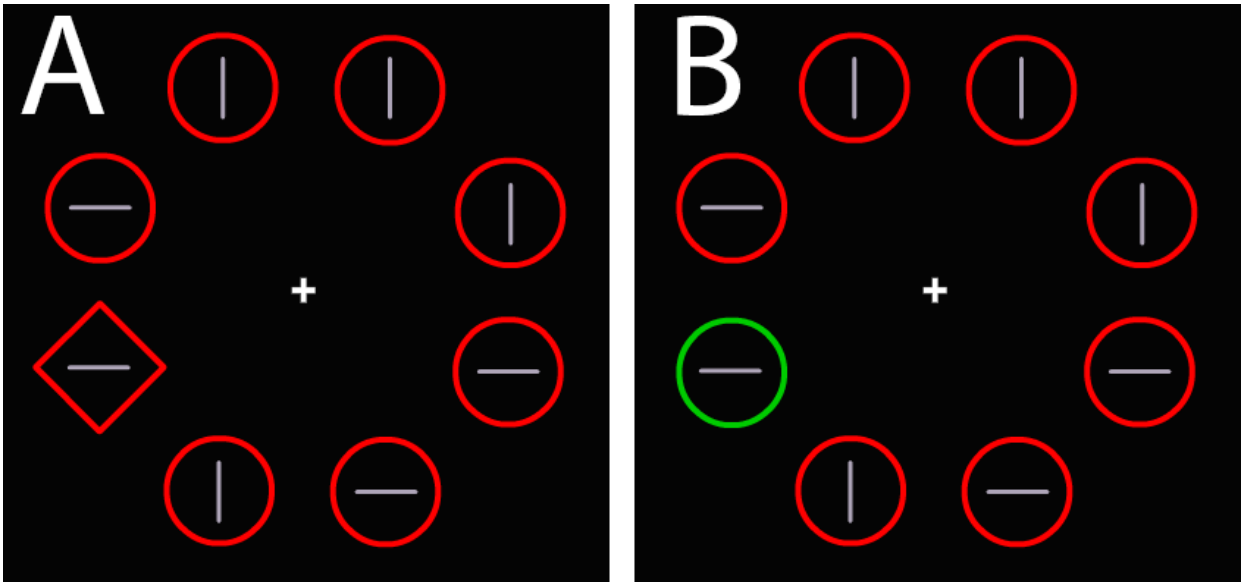

Figure 6. Examples of displays used in Experiments 1 to 6. In panel A, one display used in Experiments 1-3-6, the shape singleton is a diamond. In panel B, one display used in Experiments 2 and 5, the color singleton is green.

Experimental Task

Participants went through two counterbalanced sessions. In one session, the stimuli were green in the other they were red. The shape singleton was the same for each subject across the two sessions. Each session was composed of eight blocks of 48 trials (384 trials for one session). At the end of each block, participant could take a break. Thus, in total, each participant completed 768 trials (384 trials*2 sessions).

The task of the participant was to report the line orientation inside the shape singleton. Participants were asked to respond as fast as possible when pressing one of two keys on a standard keyboard (counterbalanced across participants) with their right hand. If the participant made a mistake or anticipated his response (RT < 200 ms), a message was immediately displayed at the center of the screen (e.g., “incorrect response”; “anticipation”). Before the experimental task, participants completed 48 trials in which they were trained to perform the task while maintaining eye fixation at the center of the screen.

Results and Discussion

The mean average of correct responses was 96%. Mean average of late trials, outliers and choice errors are reported in Table 2. Preliminary analyses showed that stimulus color (red versus green) did not affect performance.

A repeated-measures ANOVA (Elevation: upper, lower by Laterality: left, right) on RTs in correct trials, showed an effect of elevation, $F(1,11) = 6.44$, $p = .028$, $\eta^2P = .369$, with shorter RTs to targets in the lower than in the upper visual hemifield (659 vs. 671 ms) and an effect of laterality, $F(1,11) = 10.92$, $p = .007$, $\eta^2P = .498$, with shorter RTs to targets in the right than in the left visual hemifield (657 vs. 673 ms). Means RTs for each visual quadrant are reported in Figure 7A and the differences between hemifields are shown in Table 1. No interaction effect between elevation and laterality was found, $F(1,11) = .964$, $p = .347$. As we postulated that participants will be faster in the lower right quadrant compared to the three others, we performed paired simple t-tests to test this hypothesis. All t-tests were significant ($p < .01$) suggesting an advantage to the lower right quadrant compared to the three others. No effect of position was found on the percentage of correct responses.

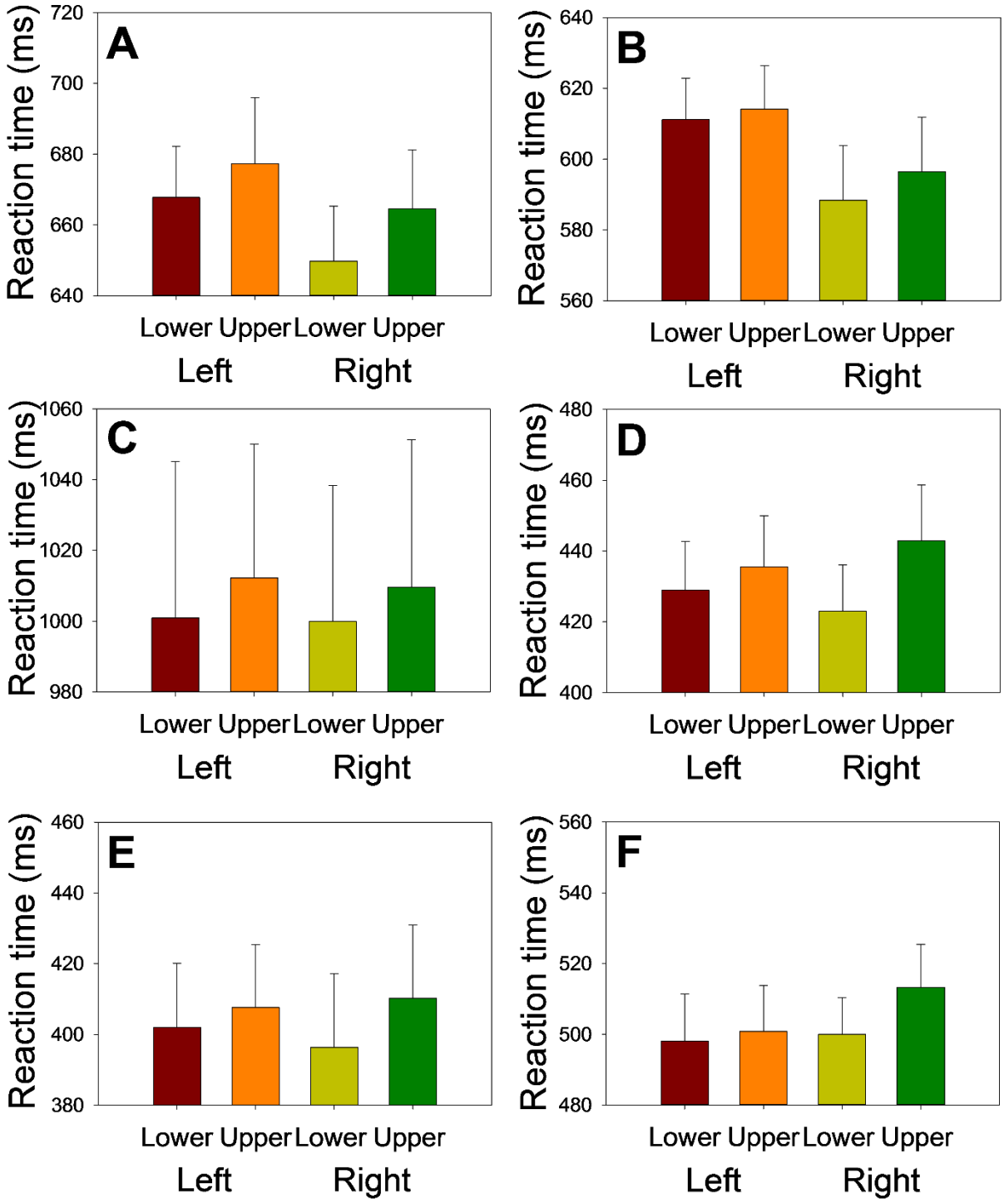

Figure 7. Results from Experiments 1 to 6 are shown in panels A to F, respectively. Mean reaction time and standard error on correct trials are shown as a function of visual quadrants (lower left, upper left, lower right, upper right).

The results are in line with our hypotheses, we were able to find a double effect of laterality and elevation. Our participants were faster to identify a shape singleton when displayed in the right versus left visual field and in the lower versus upper visual field. Despite

the fact that the interaction effect between laterality and elevation was not significant, complementary analyses based on our hypothesis suggested the superiority of the lower right quadrant among the three others.

Table 1. Differences between lower and upper hemifields and between right and left. Positive numbers indicate that there was an advantage for the lower or right hemifield.

Experiment	Lower hemifield advantage		Right hemifield advantage	
	RT	SD	RT	SD
1: Identification (shape)	12 ms *	16.66	15 ms *	16.18
2: Identification (color)	5 ms *	5.35	21 ms *	19.46
3: Identification (random shape)	10 ms	48.45	2 ms	35.99
4: Detection (shape)	13 ms *	9.32	- 1 ms	17.80
5: Detection (color)	10 ms *	7.58	1 ms	9.51
6: Detection (random shape)	8 ms *	10.03	- 7 ms	17.24

Note. RT = reaction time, SD = standard deviation, asterisk = significant at 5%.

Experiment 2

The goal of this experiment was to replicate our previous effects (lower and right hemifield advantage) using another target feature (color instead of shape).

Method

All participants were right-handed undergraduate psychology female students at the University of Geneva. There were nine female individuals (18-21 years), all participants reported normal or corrected-to-normal visual acuity and participated in this experiment for class credit. All displays were composed by eight identical geometrical forms, one of them has a different color from the others (i.e. a color singleton). The color singleton was red or green (counterbalanced across participants), see Figure 6B.

Participants went through two counterbalanced blocks. In one session, the stimuli were green in the other they were red. The color singleton was the same for each subject across the two sessions. As in Experiment 1, each session was composed of eight blocks of 48 trials (384 trials for one session) and at the end of each block, participant could take a break. The task of the participant was to report the orientation of a line inside the color singleton (versus the shape singleton in the first experiment). Again, participants were asked to respond as fast as

possible when pressing one of two keys on a standard keyboard (counterbalanced across participants) with their right hand. Other methodological details were identical to Experiment 1.

Results and Discussion

The mean average of correct responses was 97%. Again, preliminary analyses showed that stimulus color did not affect performance.

A repeated-measures ANOVA (Elevation: upper, lower by Laterality: left, right) on RTs in correct trials, showed an effect of elevation, $F(1,8) = 9.88$, $p = .014$, $\eta^2P = .533$, with shorter RTs to targets in the lower than in the upper visual hemifield (600 vs. 605 ms) and an effect of laterality, $F(1,8) = 9.71$, $p = .014$, $\eta^2P = .548$, with shorter RTs to targets in the right than in the left visual hemifield (592 vs. 612 ms). Again, no interaction effect, $F(1,8) = .55$, $p = .478$. As in Experiment 1, we wanted to test the superiority of the lower right quadrant in accordance with our hypothesis. The three t-tests were significant ($p < .05$) suggesting an advantage to the lower right quadrant compared to the three others. Again, no effect of position was found on the percentage of correct responses.

We compared Experiment 2 with Experiment 1, a repeated-measures ANOVA with two intra-subject factors (Elevation: upper, lower by Laterality: left, right) and one inter subject factor (Experiment: 1, 2) showed three main effects but no interaction effects. We were able to replicate the effect of elevation, $F(1,19) = 9.44$, $p = .006$, $\eta^2P = .332$, with shorter RTs to targets in the lower than in the upper visual hemifield (629 vs. 638 ms) and the effect of laterality, $F(1,19) = 21.01$, $p < .001$, $\eta^2P = .525$, with shorter RTs to targets in the right than in the left visual hemifield (625 vs. 643 ms). We also found an experiment effect, $F(1,19) = 8.18$, $p = .010$, $\eta^2P = .301$. Task demands in the present task were lower than in the previous experiment. On average, participants were faster to respond in Experiment 2 (603 ms) compared to Experiment 1 (665 ms), suggesting that searching for a color target was easier than searching for a shape target.

Concerning horizontal and vertical asymmetries, results are in line with our hypotheses. As in Experiment 1, we were able to replicate the double effect of laterality and elevation changing the feature of the target. Furthermore, we were also able to suggest that the lower right quadrant is superior for this type of visual search.

Experiment 3

Randomizing the target shape changes the search mode. When the target remains fixed, observers search for a particular feature (feature search mode) and can make a goal-directed selection (Bacon & Egeth, 1994). In contrast, when the target and distractor identities are randomly swapped, observers have to search for the odd element (singleton detection mode). In this experiment, we were particularly interested to investigate how predictability will affect visual asymmetries.

Method

The method was identical as previously. The following changes have been made in order to investigate singleton detection mode (versus feature search mode in previous experiments). The color of the stimuli and the target shape were randomized. The target (singleton shape) varied randomly between a diamond and a circle. That is, the target of one trial could be the distractor on the following trial. The search display was either red or green. Participants worked through 384 trials (spread in 4 blocks).

Twelve right-handed students participated. One participant was excluded because of his very low percentage of correct response (only 23%). The final sample was composed of eleven participants (19-37 years, 3 males).

Results and Discussion

The mean average of correct responses was 81%. Preliminary analyses showed that stimulus color did not affect performance. A repeated-measures ANOVA (Elevation: upper, lower by Laterality: left, right) on RTs in correct trials, showed no effect of elevation, $F(1,10) = .517$, $p = .489$, and no effect of laterality, $F(1,10) = .028$, $p = .870$. We did not find any effect of position on the percentage of correct responses.

We compared Experiment 3 with Experiment 1, a repeated-measures ANOVA with two intra-subject factors (Elevation: upper, lower by Laterality: left, right) and one inter subject factor (Experiment: 1, 3) showed an experiment effect. Task demands in the present task were higher than in Experiment 1 (fixed target shape and color), which is evident in the longest overall RTs in the present experiment compared to Experiment 1 (1004 ms vs. 665 ms); effect of experiment, $F(1,21) = 68.70$, $p < .001$, $\eta^2P = .766$.

When participants cannot anticipate the target, laterality and elevation effects disappear. This result is surprising, we postulated to replicate the right visual field advantage found in the two previous experiments because of part-based processing being more associated with left hemisphere (Bradshaw & Sherlock, 1982; Hillger & Koenig, 1991; Rossion et al., 2000; Sergent, 1984). Concerning vertical asymmetries, we were also expecting to replicate the lower advantage, especially because we were increasing the difficulty of the task. Based on our results, predictability of the task seems to be a crucial factor when looking at visual asymmetries, goal-driven control seems to play an import role for right/lower hemifield advantages to occur. However, we should be careful to interpret our results; as we can see in Table 1, the variance among participants is huge in this experiment. Overall, standard deviation in the present experiment (42.22 SD) is almost three times bigger than in Experiments 1-2 (14.84 SD). Also, as mentioned in Table 1, choice errors are twice bigger in Experiment 3 (9.7%) compared to Experiments 1-2 (4.2%) and more participants are also too slow to respond (> 2s); 0.2% of late trials in Experiments 1-2 versus 3.6% in Experiment 3.

Experiment 4

We set up the present experiment in order to better understand our previous effects. We were interested to know if visual asymmetries that we previously observed will remained using the same visual search paradigm but decreasing task demands.

Method

Stimulus displays used in the present experiment were the same used in Experiment 1, the only difference was that some homogeneous displays were presented as well (with no shape singleton). In 20% of the trials, the shape singleton was absent and observers had to refrain from responding. The shape singleton was a circle or a diamond and the color of the search display was green or red. Both shape singleton and display color were counterbalanced across participants. If the singleton was present, participants were asked to respond as fast as possible by pressing one key on the keyboard with their right hand. Lines inside shapes were still displayed as previously but their orientation was not pertinent to the task anymore. Participants worked through 480 trials (spread across 4 blocks).

Twelve right-handed students participated. Results of one participant were not analyzed due to computer failure for one block. The final sample was composed of eleven participants (19-22 years, 5 males).

Results and Discussion

The average of correct responses was 99%. Preliminary analyses showed that stimulus color did not affect performance.

A repeated-measures ANOVA on the RTs in correct trials show an effect of elevation, RTs were shorter in the lower than in the upper visual hemifield (426 vs. 439 ms), $F(1,10) = 22.30$, $p = .001$, $\eta^2P = .690$ but not no effect of laterality, $F(1,10) = .02$, $p = .893$. We did not find any effect of position on the percentage of correct responses.

We compared Experiment 1 (identification) with Experiment 4 (detection). A repeated-measures ANOVA with two within-subject factors (Elevation: upper, lower by Laterality: left, right) and one between subject factor (Experiment: 1, 4) showed an interaction effect between laterality and experiment, $F(1,21) = 5.22$, $p = .033$, $\eta^2P = .199$ but no interaction effect between elevation and experiment, $F(1,21) = .035$, $p = .853$. Comparing performance between the discrimination task in Experiment 1 and the current detection task showed that task demands were lower with detection. Overall RTs in Experiment 1 were 665 ms versus 433 ms in the present experiment; effect of experiment, $F(1,21) = 118.31$, $p < .001$, $\eta^2P = .849$.

We successfully replicated the lower hemifield advantage found in Experiments 1 and 2. Concerning horizontal asymmetries, based on literature and as mentioned before, many outcomes were possible for simple detection tasks. Some authors reported a left hemifield advantage (Poynter & Roberts, 2012), others reported a right hemifield advantage (Polich, 1984) while others did not find any horizontal asymmetries (Evert et al., 2003; Kitterle et al., 1990; Michael & Ojeda, 2005). Our results support the latter authors, as the stimuli used were identical to Experiment 1, we can postulate that this lack of result is due to the cognitive load which was not sufficient to lead to hemispheric asymmetries.

Experiment 5

We set up this experiment in order to investigate if we could replicate results obtained in Experiment 4 using a different singleton feature in our detection task.

Method

Again, stimulus displays used in the present experiment were the same used in Experiment 2, the only difference is that some homogeneous displays were also presented (with no color singleton). As in Experiment 4, participants had to perform a simple target detection task, indicating the presence of the target. In 20% of the trials, the color singleton was absent and observers had to refrain from responding. The color singleton was red or green and the shape of the search display was a circle or a diamond. Both color singleton and display shape were counterbalanced across participants. If the singleton was present, participants were asked to respond as fast as possible by pressing one key on the keyboard.

Participants worked through 480 trials (spread across 4 blocks). Eight right-handed students participated in this study (19-34 years, 3 males).

Results and Discussion

The mean average of correct responses was 99%. A repeated-measures ANOVA on the RTs in correct trials show an effect of elevation, RTs were shorter in the lower than in the upper visual hemifield (399 vs. 409 ms), $F(1,7) = 13.33$, p = .008, $\eta^2P = .656$ but not for laterality, $F(1,7) = .19$, $p = .676$.

A repeated-measures ANOVA with two intra-subject factors (Elevation: upper, lower by Laterality: left, right) and one inter subject factor (Experiment: 4, 5) show an effect of elevation. RTs were shorter in the lower than in the upper visual hemifield (413 vs. 424 ms), $F(1,17) = 32.93$, $p < .001$, $\eta^2P = .659$ but there were no effects of laterality, $F(1,17) = .011$, $p = .918$ or for Experiment, $F(1,17) = 1.52$, $p = .234$.

We compared Experiment 1 (identification) with Experiment 5 (detection). A repeated-measures ANOVA with two intra-subject factors (Elevation: upper, lower by Laterality: left, right) and one inter subject factor (Experiment: 1, 5) showed an interaction effect between laterality and experiment, $F(1,14) = 5.33$, $p = .037$, $\eta^2P = .276$, but no interaction effect between elevation and experiment, $F(1,14) = 1.47$, $p = .245$. Comparing performance between the discrimination task in Experiment 1 and the current detection task showed that task demands were lower with detection. Overall RTs in Experiment 1 were 665 ms and 404 ms in the present experiment, which is statistically different, $F(1,14) = 65.77$, $p < .001$, $\eta^2P = .824$.

We replicated in this experiment our previous findings using a color instead of a shape detection task. The elevation effect was still present which is consistent with the fact that the

lower visual field is better for sensory processing of color (Gordon et al., 1997; Levine & McAnany, 2005).

Experiment 6

This experiment was designed in order to investigate if predictability would affect visual asymmetries observed in detection tasks as in identification task (Experiment 3).

Method

The experimental design was the same used in Experiment 4 with the following changes. As in Experiment 3, both shape singleton and display color were randomized. Participants worked through 480 trials (spread across 4 blocks). Twelve right-handed students participated (19-22 years, 1 male).

Results and Discussion

The average of correct responses was 99%. A repeated-measures ANOVA on the RTs in correct trials show an effect of elevation, RTs were shorter in the lower than in the upper visual hemifield (499 vs. 507 ms), $F(1,11) = 7{,}65$, $p = .018$, $\eta^2P = .410$ but no effect of laterality. As in previous experiments, the analysis of the percentage of correct responses did not show any effects.

We compared Experiment 1 (identification) with Experiment 6 (detection), a repeated-measures ANOVA with two intra-subject factors (Elevation: upper, lower by Laterality: left, right) and one inter subject factor (Experiment: 1, 6) showed an interaction effect between laterality and experiment, $F(1,22) = 10.97$, $p = .003$, $\eta^2P = .333$, but no interaction effect between elevation and experiment, $F(1,22) = .56$, $p = .463$. Comparing performance between the discrimination tasks in Experiment 1 and the current detection task showed again that task demands were lower with detection. Overall RTs in Experiment 1 were 665 ms and 503 ms in the present experiment, which is statistically different, $F(1,22) = 66.62$, $p < .001$.

Again we successfully replicate Experiments 4-5 even with randomizing shape singleton and display color. Using a singleton detection mode instead of feature search mode does not seem to impact the lower hemifield advantage for detection tasks as it does for identification tasks (Experiment 3).

Table 2. Additional information about Experiments 1 to 6.

Experiment	Late trials	Outliers	Choice errors	False alarms
1: Identification (shape)	0.4%	2.9%	4.9%	X
2: Identification (color)	0%	2.54%	3.6%	X
3: Identification (random shape)	3.6%	2%	9.7%	X
4: Detection (shape)	0%	1.9%	X	1.5%
5: Detection (color)	0%	1.7%	X	1.2%
6: Detection(random shape)	0%	2.1%	X	2.4%

Visual asymmetries in visual search tasks for complex natural shapes/faces

Experiments 7-9

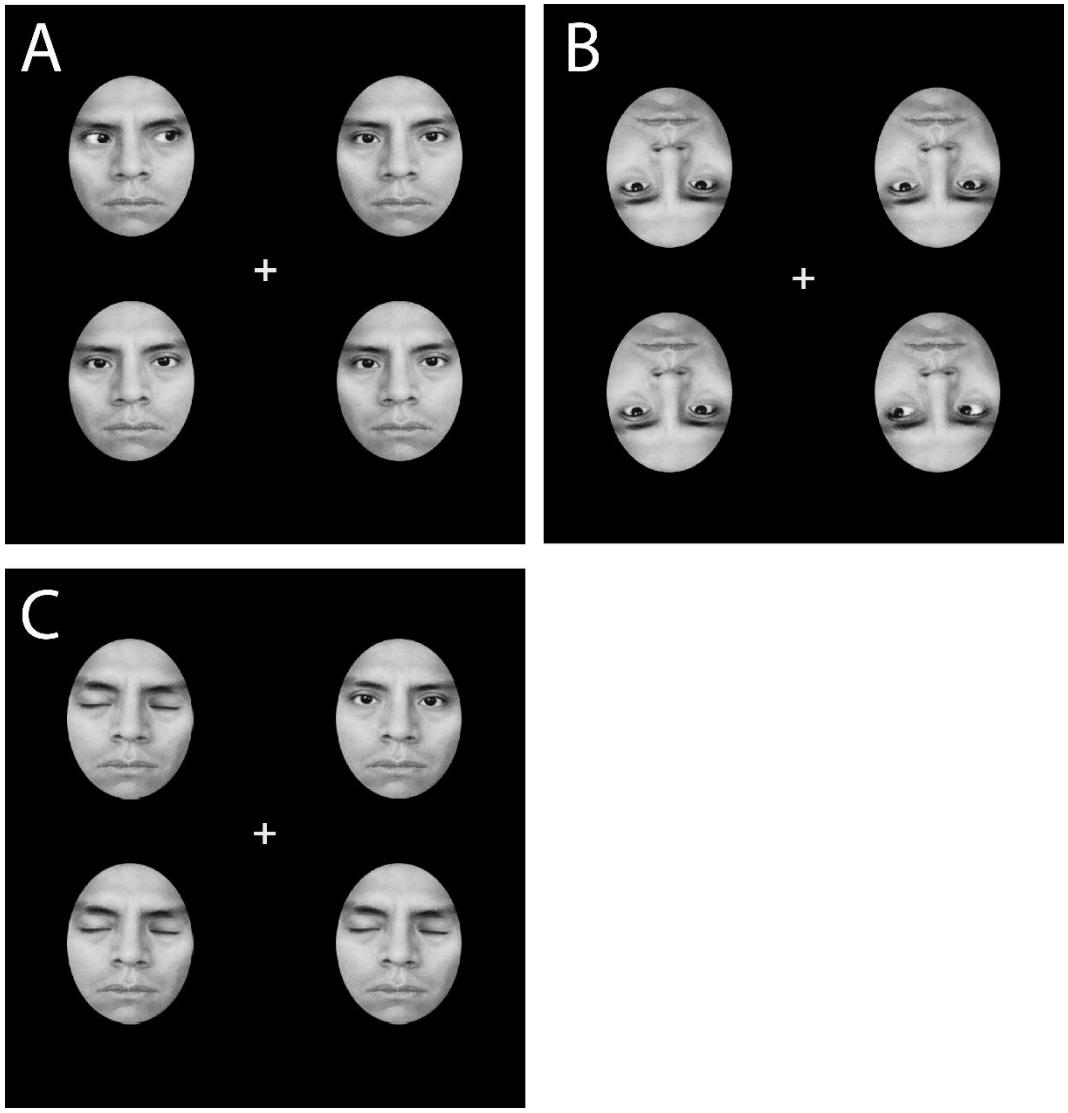

Figure 8. The displays used in Experiments 7, 8 and 9 are shown in panels A, B and C, respectively.

Overview of Experiments

In the current study, we employed a visual search task to investigate whether the left and upper hemifield advantages in the processing of faces or complex objects can also be established in a basic perceptual task. While the left hemifield bias for faces is well established for perceptual processes (e.g. Bentin et al., 1996), there is only scarce evidence for the upper hemifield advantage. Previous research has investigated face recognition after retention intervals of minutes (Felisberti & McDermott, 2013; Kessler & Tipper, 2004) or short-term priming (Quek & Finkbeiner, 2014a, 2014b, 2015). While both processes are related to basic perceptual processes, none measures the efficiency of perceptual processes directly. Therefore, a study investigating the efficiency of visual search for faces as a function of the visual quadrant is warranted. The manuscript of Experiments 7-9 is currently in review in "Visual Cognition".

In Experiment 7, participants searched for a face with a gaze that was different from the remaining faces (see Figure 8A) and signaled its presence or absence (50% probability each). In one block of trials, the target singleton was a straight among averted gazes and in another block, it was an averted among straight gazes. Based on literature mentioned in the Introduction, faces in an upright orientation are expected to automatically trigger holistic processing, we therefore anticipate a left hemifield (i.e. a right hemisphere) advantage (Bentin et al., 1996; Bradshaw & Sherlock, 1982; Darling, Martin, et al., 2009). Further, as faces represent complex objects, we are also expecting an upper hemifield advantage (Felisberti & McDermott, 2013; Quek & Finkbeiner, 2014a, 2015).

In Experiment 8, we changed the orientation of the faces (see Figure 8B). By inverting the faces, we prevented the use of a holistic strategy (Freire, Lee, & Symons, 2000) while keeping the same stimuli and instructions given to participants. With inverted faces, analytic processing is forced because featural information (i.e. the size or shape of the eyes, nose and mouth) is conveyed in relative isolation (Carey & Diamond, 1977). That is, face-inversion results in a disruption to configural information that depends on face orientation, but the processing of featural information is not affected (Farah, Tanaka, & Drain, 1995). We expect to cancel the left hemifield advantage with this stimuli manipulation. However, as the upper visual field advantage is not specific to face processing but extends to object recognition in general (e.g. Christman & Niebauer, 1997), we expect the vertical asymmetry to persist.

In Experiment 9, we manipulated the saliency of the gaze singleton (see Figure 8C) by decreasing the similarity between target and non-targets. Faces were presented in a canonical

view and the target was a face with closed among open eyes in one block of trials and the opposite in another block of trials. As in Experiment 7, we expect participants to use holistic processing for upright face stimuli that should result in a left hemifield advantage. However, we expect the advantage of the upper hemifield to disappear because the decision about the presence or absence of the target can be based on basic visual features. Notably, the difference in luminance caused by the white of the eye is sufficient to perform the task. Object recognition is not required and the superiority of the upper hemifield does not play out.

Experiment 7

Method

Participants

All participants were right-handed undergraduate psychology students at the University of Geneva. Sixteen individuals took part in this experiment, but one subject was excluded from the analyses because his percentage of correct answers was too low (63%). The final sample was composed of fifteen individuals (18-37 years, 2 males). All participants reported normal or corrected-to-normal visual acuity and participated in this experiment for class credit. All procedures were approved by the ethics committee of the "Faculté de Psychologie et des Sciences de l'Education" at the University of Geneva and were in accordance with the 1964 Declaration of Helsinki. Before the experiment, participants gave their written informed consent.

Stimuli and Apparatus

The experiment was conducted in a dimly lit room, participants were seated at a distance of 45 cm from the screen. Participants' head position was stabilized with a chin rest in front of the center of the screen. The experiment was controlled by Matlab (The MathWorks, Inc., Natick, MA) using the Psychophysics Toolbox extensions. Participants' eye movements were monitored by the experimenter from outside the experimental booth with the help of the image of the eye provided by an EyeLink 1000 eye-tracker (SR-Research, Ontario, Canada). Eye movements were not recorded or analyzed, but the experimenter assured that participants followed the instructions and intervened if necessary. A gray fixation cross of 1.3° was shown in the center of the display. Four ovals showing human faces (4.8° x 5°, width x height) were shown in the lower left, upper left, lower right, and upper right of a virtual square at an eccentricity of 2.5° (from the center of the screen). The face database is from George, Driver,

and Dolan (2001).The face items were cropped to exclude the facial contour and hairline. The pictures showed a set of six different faces (3 females and 3 males). Only one face was shown on a single trial. In 50% of the trials, the gaze of one of the four faces was different (gaze singleton). That is, an averted gaze appeared among otherwise straight gazes or a straight gaze appeared among otherwise averted gazes. The averted gaze was directed to the right with respect to the participants' point of view.

Experimental Task

The task was to indicate the presence or absence of a gaze singleton by pressing with his right hand, one of two designated keys (left or right arrow). Visual error feedback was provided after choice errors, anticipations (RTs < 200 ms) and late trials (RTs > 3 s). Data was collected in two sessions of 512 trials each. In one session, observers detected a straight gaze among averted gazes and in the other session, observers detected an averted gaze among straight gazes. Session order was counterbalanced across participants. In half of the trials, the gaze singleton was present. On target absent trials, all gazes were the same. On average, the duration of the experiment was 45 min. Before the experiment, participants completed 48 trials in which they were trained to perform the task while maintaining eye fixation at the center of the screen.

Results and Discussion

RTs were trimmed by removing trials with RTs longer than 2.5 times the standard deviation of the respective condition mean, resulting in the exclusion of 1.1% of the trials in addition to the 0.1% excluded by the online criterion of 3 s for late trials. The percentage of correct responses was 89%. We analyzed only target-present trials. Means RTs as a function of visual quadrants are shown in Figure 9A and the differences between hemifields are shown in Table 3.

A repeated-measures 2 (target gaze: straight, averted) x 2 (elevation: lower, upper) x 2 (laterality: left, right) ANOVA on RTs in correct trials showed an effect of gaze, $F(1,14) = 11.65$, $p = .004$, $\eta_P^2 = .454$, with shorter RTs to averted than straight gaze targets (911 vs. 998 ms), an effect of elevation, $F(1,14) = 10.31$, $p = .006$, $\eta_P^2 = .424$, with shorter RTs to faces in the upper than in the lower visual hemifield (916 vs. 993 ms) and an effect of laterality, $F(1,14) = 8.01$, $p = .013$, $\eta_P^2 = .364$, with shorter RTs to targets in the left than in the right visual hemifield (918 vs. 990 ms). We also observed an interaction effect between elevation and laterality, $F(1,14) =$

10.38, p = .006, η_P^2 = .426. Inspection of Figure 9A shows that RTs were shorter in the left than in the right hemifield and also in the upper than in the lower hemifield. However, it is also clear that the difference between upper and lower quadrant was more pronounced in the left hemisphere than in the right hemisphere, which is reflected in the significant interaction.

The same ANOVA as above on correct responses did not show an effect of gaze, F(1,14) = .06, p = .808, but an effect of elevation, F(1,14) = 9.71, p = .008, η_P^2= .410, with higher percentage correct to targets in the upper than in the lower visual hemifield (88% vs. 82%) and an effect of laterality, F(1,14) = 7.14, p = .018, η_P^2 = .338, with higher percentage correct to targets in the left than in the right visual hemifield (88% vs. 81%).

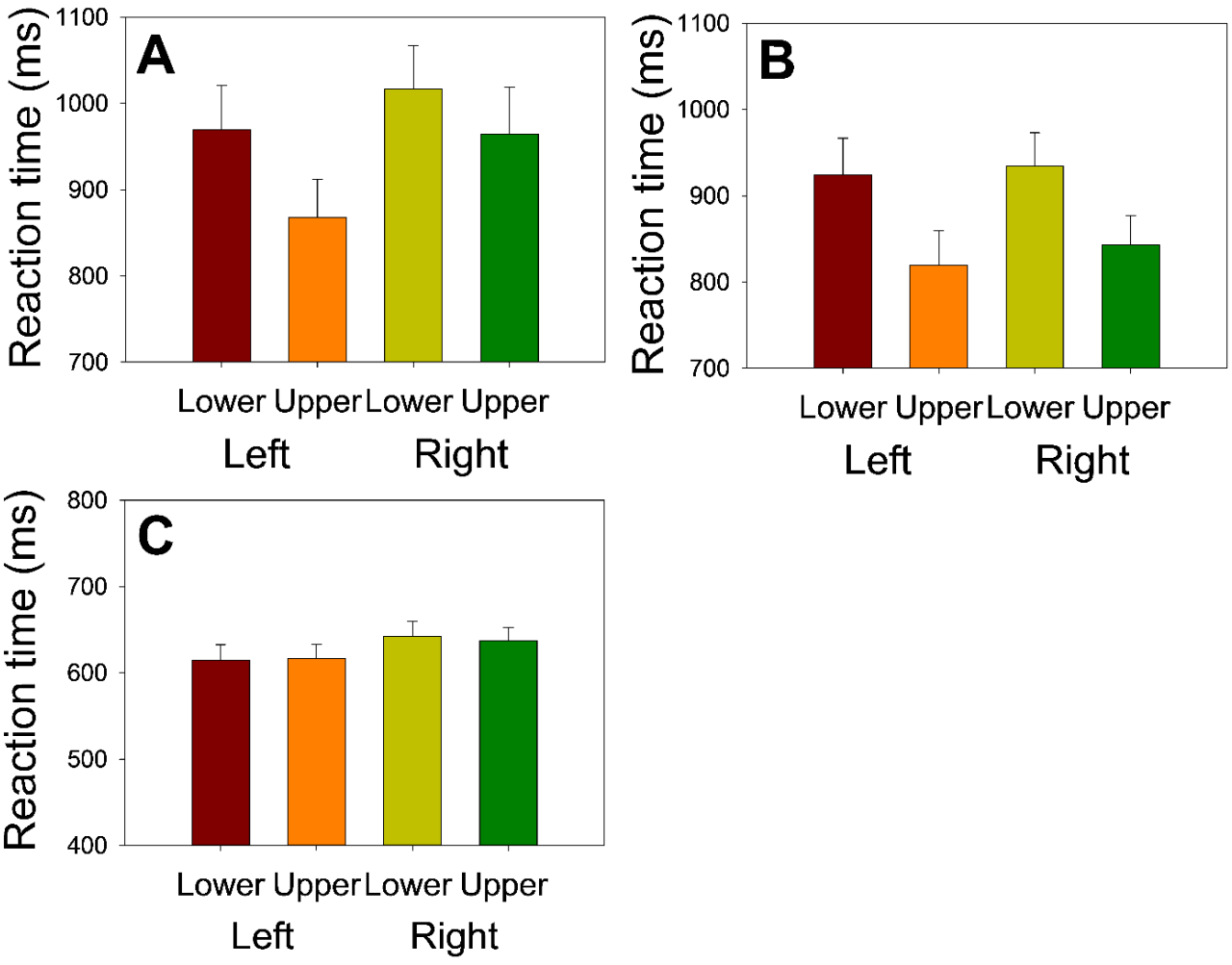

Figure 9. Results from Experiments 7 to 9 are shown in panels A to C, respectively. Mean reaction time is shown as a function of the visual quadrant (lower left, upper left, lower right, upper right). Note that the y-axis in Experiments 7 and 8 starts at 700 ms, whereas it starts at 400 ms in Experiment 9.

In accordance with our hypothesis, we found that RTs were faster in the left and upper hemifields. The interaction between elevation and laterality showed that RTs were particularly short in the upper left quadrant of the visual field. We also found an effect of gaze direction, showing that participants were faster to detect an averted among straight gazes than the opposite.

Table 3. Differences between right and left, and between lower and upper hemifield. Positive numbers indicate that there was an advantage to the left or upper hemifield.

Experiment	Left hemifield advantage		Upper hemifield advantage	
	RT	PE	RT	PE
7: Face singleton	72 ms *	7% *	77 ms *	6% *
8: Faces upside down	17 ms	4%	98 ms *	15% *
9: Very salient singleton	27 ms *	4% *	1 ms	0.4%

Note. RT = reaction time, PE = percentage errors, asterisk = significant at 5%.

Experiment 8

In this experiment, we presented the faces upside down. Reversing faces is a well-known technique to prevent holistic processing (Freire et al., 2000), which we expect to cancel the advantage of the left hemifield. In contrast, the advantage of the upper hemifield that we observed in Experiment 7 is not expected to change, because this advantage is not specific to faces but to object recognition in general (Christman & Niebauer, 1997).

Method

Thirteen right-handed female students from the same pool as above participated in this experiment. Their ages ranged between 19 and 25 years. The methods were as in Experiment 7 except that the face stimuli were turned upside down (see Figure 8B).

Results and Discussion

Applying the same criteria as in Experiment 7 resulted in the exclusion of 1.2% outliers and 0.1% late trials. The overall percentage of correct responses was 85%. Mean RTs as a function of visual quadrants are shown in Figure 9B and the differences between hemifields are shown in Table 3.

A repeated-measures 2 (Target Gaze: straight, averted) x 2 (Elevation: lower, upper) x 2 (Laterality: left, right) ANOVA on RTs in correct trials showed an effect of gaze, $F(1,12) = 6.17$, $p = .029$, $\eta_P^2 = .340$, with shorter RTs when the target gaze was averted than straight (849 vs. 912 ms), an effect of elevation, $F(1,12) = 53.11$, $p < .001$, $\eta_P^2 = .816$, with shorter RTs to faces in the upper than in the lower visual hemifield (831 vs. 929 ms), but no effect of laterality, $F(1,12) = 1.15$, $p = .304$.

The same ANOVA on the percentage of correct responses did not show an effect of gaze, $F(1,12) = 0.48$, $p = .831$, or laterality, $F(1,12) = 3.08$, $p = .105$, but showed an effect of elevation, $F(1,12) = 62.05$, $p < .001$, $\eta_P^2 = .838$, with more correct responses to faces in the upper than in the lower visual hemifield (89% vs. 74%).

To evaluate differences between Experiments 7 and 8, we conducted a 2 (Elevation: upper, lower) x 2 (Laterality: left, right) x 2 (Experiment: 7, 8) mixed-factors ANOVA. The interaction of laterality and experiment, $F(1,28) = 4.46$, $p = .044$, $\eta_P^2 = .138$, confirmed that the advantage of the left hemifield disappeared in Experiment 8 when the faces were shown upside down. The interaction of elevation and experiment was not significant, $F(1,28) = 0.65$, $p = .428$, confirming that the upper hemifield advantage was not affected by the change in orientation. Also, the difficulty of the task was unaffected by orientation, as the main effect of experiment was not significant, $F(1,28) = 0.99$, $p = .329$. Mean RTs in Experiments 7 and 8 were 954 and 896 ms, respectively.

The results of Experiment 8 are in line with our hypotheses. By reversing faces we were able to prevent participants from using holistic processing, which canceled the left hemifield (right hemisphere) advantage.

Experiment 9

In this experiment we manipulated the saliency of the gaze singleton by decreasing the similarity between target and non-targets. The goal of this experiment was to test if vertical asymmetries persist with a much easier task. Blockwise, participants searched for closed eyes among open eyes or the opposite, which can be accomplished by looking for a luminance difference caused by the white of the eyes. Therefore, complex processes of object recognition are not required. Because the advantage of the upper visual hemifield concerned object recognition, we expect the vertical asymmetry to disappear (for a similar argument, see Quek & Finkbeiner, 2014a). In contrast, the faces were shown in an upright position, which

automatically resulted in holistic processing. Therefore, the enhanced processing of faces in the left hemifield should prevail.

Method

Twelve students ranging in age from 18 to 23 years participated. Methods were as in Experiment 7 with the exception that the eyes were open or closed (see Figure 8C). When the eyes were open, the gaze was directed straight ahead. Participants were asked to detect the presence of a face with open eyes among faces with closed eyes in one session, and the presence of a face with closed eyes among faces with open eyes in another session.

Results and Discussion

Applying the same criteria as in the previous experiments, 1.4% outliers and 0.06% late trials were excluded. The percentage of correct responses was 96%. Means RTs as a function of visual quadrants are shown in Figure 9C and the differences between hemifields are shown in Table 3.

A 2 (Target Eye Closure: open, closed) x 2 (Elevation: lower, upper) x 2 (Laterality: left, right) repeated-measures ANOVA on RTs in correct trials showed an effect of eye closure, $F(1,13) = 13.78$, $p = .003$, $\eta_P^2 = .515$, with shorter RTs to detect open among closed eyes than the opposite (593 vs. 658 ms), an effect of laterality, $F(1,13) = 14.45$, $p = .002$, $\eta_P^2 = .526$, with shorter RTs to targets in the left than in the right visual hemifield (612 vs. 639 ms) but no effect of elevation, $F(1,13) = 0.02$, $p = .902$.

The same ANOVA on the percentage of correct responses showed an effect of eye closure, $F(1,13) = 14.76$, $p = .002$, $\eta_P^2 = .532$ with better performance when the target was a face with open eyes than with closed eyes (95% vs. 93%), an effect of laterality, $F(1,13) = 12.52$, $p = .004$, $\eta_P^2 = .491$ with better performance to respond to faces in the left than in the right visual hemifield (96% vs. 92%) and no effect of elevation, $F(1,13) = 0.302$, $p = .592$.

To evaluate differences between Experiments 7 and 9, we conducted a 2 (Elevation: upper, lower) x 2 (Laterality: left, right) x 2 (Experiment: 7, 9) mixed-factors ANOVA. The significant interaction of elevation and experiment, $F(1,28) = 9.50$, $p = .005$, $\eta_P^2 = .253$, showed that the advantage of the upper hemifield disappeared in Experiment 9. In contrast, the interaction of laterality and experiment did not reach significance, $F(1,28) = 3.28$, $p = .081$, showing that the advantage of the left hemifield persisted, although it tended to be smaller (27

vs. 72 ms). Also, RTs were overall shorter in Experiment 9 than in Experiment 7 (628 vs 954 ms), $F(1,28) = 42.9$, $p < .001$, showing that the task was easier.

Reducing task demands canceled the upper visual field advantage. However, task difficulty did not influence the horizontal asymmetry, because the faces were presented in upright orientation and holistic processing was triggered automatically.

Discussion

In this chapter we investigated vertical and horizontal asymmetries in visual search with either simple geometric shapes (Experiments 1-6) or face stimuli (Experiments 7-9). In these two sets of experiments, we tried to keep the same stimulus displays while changing the mode of processing and the task difficulty. Given that the literature was sometimes inconsistent, our goal was to get a better understanding of what factors really matter in visual search tasks when dealing with horizontal and vertical asymmetries. Our main finding is that identification of simple geometric shapes is faster when a known target is located in the lower right part of the screen, whereas detection of a gaze singleton face is faster when a similar target is located in the upper left part of the screen. Details of this dichotomy are discussed below. To sum up, it is important to take into account both laterality and elevation in visual search tasks. Moreover, the nature of the task has a huge impact on these effects.

Vertical Asymmetries: Sensory Processing versus Object Recognition

In searches for simple geometric shapes, we consistently found a lower hemifield advantage for simple detection and identification tasks. This advantage only disappears when a singleton detection mode is required for identification tasks. However, we cannot conclude that this effect is specific to feature search mode because we also found it in a singleton detection task (Experiment 6). As mentioned previously, this lack of result could be biased in part by the extreme difficulty of the task and by the huge variability that we noted between participants. More research is needed to clarify this finding. A possible complementary experiment would be to randomly vary the target shape but to maintain the same display's color through blocks. Having the target changing on only one feature may decrease the difficulty while preserving the non-predictability of the task. As mentioned above, the lower hemifield advantage was expected and it is consistent with literature showing that sensory processing is better in the lower hemifield. Perception of orientation (Carrasco et al., 2001; Previc, 1990; Rezec & Dobkins, 2004), direction of motion (Rezec & Dobkins, 2004) and color (Gordon et al., 1997; Levine & McAnany, 2005) were found to be better in the lower visual field (see also Previc, 1990). Our results showed that this advantage does not seem to be influenced by the type of task (detection versus identification) or by the nature of the target feature to identify (shape versus color). The lower visual hemifield advantage was present for both detection of shape

(Experiment 1), color (Experiment 2) targets and for identification of line orientation in shape (Experiment 4, 6), and color (Experiment 5).

In searches for faces, we found the opposite effect with an upper hemifield advantage for detection of a gaze singleton (Experiment 7). Furthermore, we observed that the upper hemifield advantage remained with upside down faces (Experiment 8), suggesting that the advantage of object recognition in the upper hemifield is not dependent on the mode of processing (holistic versus analytic) but is instead specific to the processing of complex objects. As mentioned previously, faster RTs when face targets were presented in the upper compared to the lower hemifield were expected because object recognition is better in the upper visual field (Chambers, McBeath, Schiano, & Metz, 1999; Christman & Niebauer, 1997; Felisberti & McDermott, 2013; Kessler & Tipper, 2004; Quek & Finkbeiner, 2014a, 2014b). Decreasing the task difficulty by enhancing the saliency of the target canceled the upper hemifield advantage in Experiment 9, showing that complex object recognition contributed to the vertical asymmetry. In the latter experiment, we manipulated the saliency of the gaze target. By decreasing task demands, we specifically suppressed the advantage of the upper hemifield. This finding is in line with previous studies investigating vertical asymmetries in the processing of letters or spatial relations (reviewed in Christman & Niebauer, 1997). For instance, performance in the upper visual field was found to be superior for word-nonword discrimination (Goldstein & Babkoff, 2001), letter naming in a trigram (Hagenbeek & Van Strien, 2002), or categorical judgments of spatial relationships (i.e. above vs. below, Niebauer & Christman, 1998). Therefore, we conclude that the upper hemifield advantage is not specific to face stimuli as is the case for the left hemifield advantage. Instead, the upper hemifield advantage is dependent on task complexity. When the detection task could be based on basic visual features (i.e. a luminance difference between open and closed eyes), requirements on object recognition were low and the superiority of the upper hemifield did not play out.

At the cerebral level, our results are in line with Previc's interpretation that vertical asymmetries can be related to the two streams for visual processing: The ventral and the dorsal streams. As mentioned before, the lower cortical sheets (upper visual field) project more into the ventral stream of the temporal lobe, whereas the upper cortical sheets (lower visual field) project more into the dorsal stream in the parietal cortex (Fecteau et al., 2000). While high-level processing such as object recognition takes place in the ventral stream, the dorsal stream is specialized in low-level processing such as sensory processing. Interestingly, Milner and

Goodale (1995) introduced the distinction between the dorsal and ventral streams in terms of the behavioral goal. Our results in Experiment 9 suggest that the strategy of the participant also seems to be important. Indeed, despite the fact that face stimuli were still displayed to the participant, it seems that those stimuli were no longer processed by the ventral pathway because participants could now perform the task based on separate basic visual features without having to process the entire face. Moreover, our lower visual field advantage for geometrical shapes is also in line with other findings detailed in the Introduction, such as the higher concentration of receptors and ganglion cells in the superior hemiretina than in the inferior hemiretina (Croner & Kaplan, 1995; Curcio & Allen, 1990) and the over-representation of the lower visual field at a cortical level (Portin et al., 1999).

Horizontal Asymmetries: Analytic versus Holistic Processing

In searches for simple geometric shapes, we only found a right hemifield advantage for identification tasks involving feature search mode. This effect disappears with simple detection tasks and when a singleton detection mode was required. For the latter, as mentioned before, we think that this finding must be interpreted with caution. We will only be able to clarify what it really going on through further experimentation. The right hemifield advantage for identification tasks was expected since our stimuli required an individual assessment of features and could not be processed holistically. As mentioned before, analytical or part-based processing is associated with the left hemisphere (Bradshaw & Sherlock, 1982; Hillger & Koenig, 1991; Rossion et al., 2000; Sergent, 1984). For low level detection tasks the results were mixed; some authors did not find any horizontal asymmetries (Evert et al., 2003; Kitterle et al., 1990; Michael & Ojeda, 2005) while some reported either left (Poynter & Roberts, 2012) or right hemifield advantage (Polich, 1984). In the detection tasks that we used (Experiments 4-6) we did not find any effect. Over and above the type of task used (identification versus detection), the crucial factor seems to be task demands and selective attention. If we were to consider the work of Polich (1984), who found a right hemifield advantage for detection tasks, the error rates and response times in his study increased depending on the amount of display items (4, 9, 16). Therefore, it seems that serial attention was needed, the target did not pop out. Additionally, in Polich's experiments, as in most experiments on visual asymmetries, no hemispheric competition is occurring; stimuli were displayed either to the left or to the right visual hemifield. When selective attention is important to perform a task, like in our series of experiments,

several studies claim that visual hemifield differences may occur only if the task is sufficiently difficult (Evert et al., 2003; Kitterle et al., 1990; Michael & Ojeda, 2005). We therefore believe that with a really easy identification task, the right hemifield advantage will disappear as in simple detections tasks. Finally, the non-result in Experiment 6 on horizontal asymmetries could be interpreted in several ways. Based also on Experiment 3, we could argue that the right hemifield advantage disappears when singleton mode is required. However, we have to be careful with Experiment 3. Maybe this lack of horizontal asymmetries may not be due to the processing mode but simply to the task demands. Indeed, in Experiment 6, even if participants had to perform a singleton search, this task was still significantly easier than our identification tasks.

In searches for faces, once again we found the opposite effect with a left hemifield advantage for detection of a gaze singleton (Experiment 7). Faster RTs when face targets were presented in the left compared to the right hemifield were expected given that holistic processing is better in the left hemifield (Bentin et al., 1996; Bradshaw & Sherlock, 1982; Hillger & Koenig, 1991; Rossion et al., 2000; Sergent, 1984). In Experiment 8, we were able to suppress the left hemifield advantage by presenting faces upside down, a well-known method to prevent holistic processing of faces (Freire et al., 2000). Meanwhile, featural information is not affected by orientation, which allows the processing of upside down faces to proceed analytically (Farah et al., 1995). Conty et al. (2006) found that the left hemifield advantage was also present when only the eye region was displayed, which may initially seem to contradict the role of holistic processing. Similarly to our task, their participants had to detect if a gaze singleton was present or not. However, the laterality effect disappeared when the nose and eyebrows were concealed from the eye region, reinforcing the idea that the left hemifield advantage is specific to holistic processing.

Quadrant Asymmetries

The contribution of our experiments was to investigate the efficiency of a basic perceptual process (i.e. visual search) in all quadrants of the visual field and to not only compare hemifields. In the two series of experiments we were able to discover that one quadrant was superior to the other three. With geometrical shapes, in Experiments 1-2, we did not find any interaction between horizontal versus vertical asymmetries. The absence of interaction suggests that the lower hemifield advantage for RTs was as pronounced in the right hemifield

as it was in the left hemifield. However, further analyses based on our hypotheses had suggested that participants were faster to respond in the lower right quadrant compared to the other three quadrants.

For face processing, similar to the inhibition of face recognition performance in Kessler and Tipper (2004), the search was particularly efficient when targets were presented in the upper left quadrant of the visual field. In Experiment 7, the interaction effect was due to a more pronounced difference between the upper and lower quadrant in the left hemifield than in the right hemifield. The advantage of the upper left quadrant over the others is consistent with a recent MEG study. B. Lee, Kaneoke, Kakigi, and Sakai (2009) compared extrastriate brain activity of participants engaged in a contrast-based visual search task. Square areas were randomly displayed in quadrants of the visual field. They found different response properties in the upper compared to the lower hemifield in the left hemifield. However, we note that this study focused on low-level contrast perception and more research is needed to better understand the neural basis of the upper-left bias in visual search with complex stimuli.

Attentional Asymmetries

While we have not directly addressed the issue of eventual asymmetries in the distribution of attention, our results argue against the involvement of attention. For geometric shapes, the right hemifield advantage found in Experiments 1-2 and the absence of horizontal asymmetries for Experiments 3-6 does not support the right hemisphere advantage for attentional capacities when hemispheric competition is occurring (Asanowicz et al., 2013; Du & Abrams, 2010; Smigasiewicz et al., 2014). We think that this absence of left visual field advantage in our results is due to the fact that we used tasks that are very different from attentional tasks like RSVP or exogenous cueing. We believe that the visual search task that we used, the additional singleton paradigm without distractor, mainly relies on perceptual asymmetries. Moreover, additional experiments (non-reported in the present manuscript) suggest that even a traditional additional singleton paradigm does not show a stronger interference with distractors displayed in the left hemifield.

For face processing (Experiments 8-9), if attention had been preferentially directed to the left or upper hemifield, we would have expected a horizontal or vertical asymmetry, even with inverted faces or in an easy, saliency-based search task. However, the asymmetries disappeared, suggesting that the nature of the stimuli determines the left and upper hemifield

advantage and not an attentional preference. A similar conclusion was reached by Quek and Finkbeiner (2014a), who demonstrated that the greater susceptibility for priming in the upper hemifield persisted even when participants directed their attention to the lower hemifield because the target was more likely to appear below than above fixation.

Search Asymmetries

A second finding concerns face processing. We found that detection was faster for averted among straight gazes than for straight among averted gazes. This finding contradicts the stare-in-the-crowd effect which reflects faster detection of a straight gaze surrounded by averted gazes than the opposite (Conty et al., 2006; Doi & Ueda, 2007; Doi, Ueda, & Shinohara, 2009; Palanica & Itier, 2011; von Grunau & Anston, 1995). We assume that this difference is explained by the different head orientation in our study. More precisely, faces were turned sideways in the "stare-in-the-crowd" paradigm in order to prevent symmetry effects (Conty et al., 2006; Doi & Ueda, 2007; Doi et al., 2009; Palanica & Itier, 2011), while faces were directed straight at the observer in the present study. As a result, the distribution of white around the pupil with straight gaze was symmetrical. In contrast, it was asymmetric in averted gaze, which explains the faster RTs for averted than for straight gaze targets. In classical studies, it has been demonstrated that the search for an asymmetrical stimulus among symmetrical stimuli is faster than the opposite. For example, Treisman and Gormican (1988) found that the detection of a tilted line among vertical lines was faster than the opposite. The authors supposed that the tilted line is coded as a vertical line with an added feature (the tilt of the line) which pops out in visual search. Hence, we suggest that the averted gaze is coded as a straight gaze but with an added feature, which makes it easier to detect. The results of Experiment 8 support this conclusion. Inverting faces normally cancels the stare-in-the-crowd effect (Senju, Hasegawa, & Tojo, 2005), but in Experiment 8, an averted gaze was still detected faster than a straight gaze, even though the faces were upside down and holistic processing was not possible.

Chapter 2. Movement and Cognition

Introduction

In Chapter 1 we discussed hemispheric specialization and how lateralized presentation and unilateral gaze, forcing initial processing in the contralateral cortical hemisphere, could reflect the functional differences of the two hemispheres. Another method to induce contralateral hemisphere activation is unilateral actions (e.g. contracting the right hand or looking to the right). Unilateral clenching and sustained unilateral gaze are thought to facilitate cognitive processes present in the activated hemisphere (Harmon-Jones, 2006; Propper et al., 2012; Propper, McGraw, Brunye, & Weiss, 2013).

Manual Movements

Unilateral Hand Clenching

A commonly used paradigm to induce contralateral cortical activation is to perform unilateral motor contraction of one hand (Benaron et al., 2000; Goldstein, Revivo, Kreitler, & Metuki, 2010; Greenberg et al., 1981; Harmon-Jones, 2006; Propper et al., 2013). Contraction of the right hand for 90 seconds causes alpha suppression (i.e. an index of activation) in the contralateral (left) hemisphere at the mid-frontal and central scalp site (Harmon-Jones, 2006). The exact neural pathway is not yet known; we assume that activation of mid-frontal regions by hand contractions is possible via cortico-cortical connections between the motor cortex and the dorsolateral prefrontal cortex. Interestingly, clenching could be used as a means to investigate functional asymmetry. The contralateral activation of the motor cortex resulting from unilateral hand contraction spreads to more frontal areas and this contralateral activation may facilitate behaviors associated with that hemisphere. The assumption of a spread of activation from sensory regions to the entire hemisphere is the same as that postulated by the unilateral gaze method described in Chapter 1.

As mentioned before, approach motivated states have been related to the activity of the left frontal cortex (Harmon-Jones, Sigelman, Bohlig, & Harmon-Jones, 2003; Jones & Fox, 1992). As a result, it has been shown that contraction of the right hand increased approach motivation (Harmon-Jones, 2006), aggression (Peterson, Shackman, & Harmon-Jones, 2008)

and persistence in attempting to solve insoluble problems (Schiff, Kenwood, Guirguis, & Herman, 1998). Also related to prefrontal asymmetries, Propper et al. (2013) tested the HERA model mentioned above using unilateral hand clenching. Consistent with the presumed mode of processing of each hemisphere postulated by the HERA model, memory performance improved when participants clenched the right hand before encoding and the left hand before recall. Non-related to prefrontal asymmetries but to Hemisphere Specialization in general, contraction of the left hand enhanced creative thinking and processing of global visual stimuli which are associated with the right hemisphere functioning (Gable, Poole, & Cook, 2013; Goldstein et al., 2010) whereas contraction of the right hand increased processing of local stimuli (Gable et al., 2013).

It was assumed in these studies that the contralateral hemispheric activation induced by clenching persists even after their termination, facilitating subsequent behaviors relying on the functions of the involved hemisphere (Harmon-Jones, 2006), a "persistent activity model". Recently, Cross-Villasana, Gropel, Doppelmayr, and Beckmann (2015) proposed an alternative model, the "reduced activity model". Based on Transcranial Magnetic Stimulation (TMS) studies (Baumer, Munchau, Weiller, & Liepert, 2002; Brasilneto et al., 1993; Zanette et al., 1995), the researchers proposed that motor contraction did not lead to persistent activity in a given hemisphere but instead to a state of reduced cortical activity. In an EEG experiment, they tested the state of cortical activity during and after unilateral hand contractions. During hand contractions, their findings were different from previous studies mentioned above (Gable et al., 2013; Harmon-Jones, 2006; Peterson et al., 2008); they reported bilateral cortical activation instead of the expected contralateral activation. They explain that this may be due to the fact that they used within-subject instead of between-subject factors. After hand contractions, they showed a state of globally reduced cortical activity, especially when the left hand was used. They proposed that this state was due to inhibitory mechanisms activated during repetitive contractions. Furthermore, this reduction of cortical activity prior to tasks could facilitate performance by facilitating task-specific cortical activation and preventing interference from other non-pertinent cortical regions.

To sum up, how hand clenching affects cognitive activity is still unclear. This method is relatively new and more neurophysiological research is needed to understand the neural substrate behind it and its mode of functioning.

Ocular movements

Observation of Spontaneous non-visual Saccades

It is interesting to note that research on eye movements has mostly focused on visually triggered saccades (Land & Tatler, 2009). The main purpose of saccadic eye movements is to place the projection of a visual stimulus on the part of the retina with the highest spatial resolution (Godijn & Theeuwes, 2002; L. R. Young & Sheena, 1975). Far less research has been conducted on non-visual saccades that occur when a person is not looking at a specific visual stimulus, but is engaged in some internal cognitive processing such as thought or imagination. Unlike visual saccades, this particular type of eye movement is devoid of visual purpose, occurs independently of visual stimulation and is not consciously controlled. Non-visual saccades have been described as "random", "spontaneous" (Lynch, 1980; Weitzenhoffer & Brockmeier, 1970) or as "waking ocular rapid movements" (Amadeo & Shagass, 1963; Tebecis & Provins, 1975). They are often not even noticed by the person performing them, suggesting that non-visual eye movements are rather automatic and do not require conscious attention.

Sociocultural Explanation

One explanation of these non-visual ocular saccades could be sociocultural. In social interactions, we automatically disengage from mutual eye contact by making non-visual saccades. There seems to be a "good amount" of eye contact in everyday life situations; 3-4 seconds on average (Binetti, Harrison, Coutrot, Johnston, & Mareschal, 2016), either overlong or overly short periods of mutual eye contact will make us feel uncomfortable (Cook, 1977; Kendon & Cook, 1969). For instance, looking somebody continuously in the eyes can be disturbing and according to circumstances interpreted as a sign of seduction or on the contrary of hostility. Reversely, in no eye contact situations, people also experience a lot of discomfort. This lack of mutual gaze is also a diagnostic tool for clinical symptoms such as autism and schizophrenia (Sasson et al., 2007). Research in social psychology has shown that maintaining or breaking visual contact has an important social role, signaling in particular intimacy, dominance and social competence (Argyle & Dean, 1965; Argyle, Lalljee, & Cook, 1968; Exline & Messick, 1967). If we are to explicitly ask people to speak without any ocular movement, most individuals report that staring at their interlocutor distracts them and that it is more difficult for

them to concentrate on their thoughts (Doherty-Sneddon, Bruce, Bonner, Longbotham, & Doyle, 2002).

The sociocultural explanation hypothesis can indeed explain some non-visual eye movements but is insufficient to get the whole picture. Why is it that gaze shifts are not random and occur more often when we asked people questions?

Release of Cognitive Resources

Studies have pointed out that disengagement of mutual gaze during a conversation is not random but happens with a kind of regularity. It occurs above all when people reflect during the planning of a speech (Beattie, 1978; Kendon, 1967), or between sentences (Goldman-Eisler, 1967). We also know that we produce more ocular movements when we speak than when we listen (Argyle & Ingham, 1972; Bavelas, Coates, & Johnson, 2002) and when topics of conversation are complex (Exline & Messick, 1967). Cognitive studies have demonstrated that these gaze shifts liberate cognitive resources, particularly when people have to go deeply into what they are talking about (Beattie, 1981; Doherty-Sneddon & Phelps, 2005). Avoiding somebody's gaze should allow us to free ourselves from visual information and so to have more available cognitive resources for internal processes which would facilitate thinking and memorization.

However, the hypothesis that we produce non-visual ocular saccades with the sole intention of releasing visual information is again not enough to explain the whole phenomenon. This hypothesis cannot explain why people carry on doing ocular saccades once they have broken visual contact (Weiner & Ehrlichman, 1976) or why they move their eyes in non-social situations. Why is it that people continue to produce non-visual saccades in a sterile environment (Hiscock & Bergstrom, 1981; Micic, Ehrlichman, & Chen, 2010), in total darkness (Ehrlichman & Barrett, 1983) or even with their eyes closed (Ehrlichman, Micic, Sousa, & Zhu, 2007)?

Lateral Eye Movements

In a clinical study, Day (1964) noticed that some patients, when asked to answer a question, tended to consistently shift their gaze to the left or to the right. He proposed that the direction of these eye patterns might be related to personality and subjective experience differences between individuals. Again with a clinical population, Duke (1968) supported Day's finding by observing directional patterns which showed that, on average, participants made 86

percent of their lateral eye movements in the same direction. Moreover, lateral eye movements occur more often in response to reflective questions (e.g., “How long do you think our involvement in Vietnam will continue?”; “What three qualities do you think most women seek in prospective husbands?”) than to factual questions (e.g., “How much is two plus two?”; “Are you married?”). Subsequently, Bakan (1969) was the first author to propose a link between lateral eye movements and hemispheric asymmetries in a paper on lateral eye movements and hypnotic susceptibility. In line with Day (1964), who proposed that lateral eye movements were linked to personality characteristics, Paul Bakan proposed that a predominance of left eye movements was an indicator of a greater hypnotizability and clearer imagery.

Moreover, some researchers investigating this hypothesis proposed that the lateralization of these ocular movements was the result of secondary motor responses triggered by asymmetries in the activation of the cerebral hemispheres (Kinsbourne, 1972; Kocel, Galin, Ornstein, & Merrin, 1972). From then on, researchers working on lateral eye movements stopped looking at individual differences (right versus left “movers”) and began to focus on the type of questions eliciting either left or right functioning. For instance, Kinsbourne (1972) found that right-handed people usually turn their head and eyes to the right when solving verbal problems whereas they look up and left for numerical and spatial problems. The assumption made was that, during ongoing activity, shifts either to the left or to the right reflect right-hemisphere versus left-hemisphere predominance. Other findings also suggested that the direction in which people look while thinking reflects the lateralization of the underlying cerebral activity (Gur, 1975; Schwartz, Davidson, & Maer, 1975).

Ehrlichman and Weinberger (1978) wrote a critical review against this model of lateral eye movement. They reported that out of 19 experiments (reported in 15 articles), only 9 had found the predicted pattern of more right lateral eye movement for “left hemisphere” questions. For “right hemisphere” questions, findings tended to report more upward movements and stares, however, the lateral eye movement hypothesis did not make any prediction for vertical eye movements and stares. Moreover, Ehrlichman & Weinberger mentioned that studies on this topic are extremely heterogeneous which makes them difficult to compare. Concerning their methodology, they notably differ in terms of questions, scoring and social situation. The validity of questions is one of the principal issues; each researcher tends to define his own sets of questions which are supposed to selectively engage either the left or the right hemisphere without any control. Only into one EEG study; Morgan, Mcdonald,

and Macdonal (1971) did actually make sure that different sets of questions were leading to hemispheric differences in terms of cerebral activation. Another issue is that, especially for visuospatial questions, researchers were sometimes not able to check that participants were actually thinking about questions or whether they just made up an answer (e.g. asking a participant; "How many doorknobs are there in your apartment?"; "What does your living room look like?"). Due to these mixed results between verbal and visuospatial questions (see also, Macdonald & Hiscock, 1992; Raine, 1991) research on lateral eye movements ceased.

Once again, the model proposed, even if it seems to work partially, was not sufficient to embrace the whole phenomenon of non-visual eye movements. In particular lateral eye movement literature was unable to explain vertical eye movements and stares.

Eye Movement Rate

Following on from lateral eye movements, a new area of research continues to use verbal and visuospatial questions but has completely abandoned directional patterns; instead it has observed that the frequency of eye movements was dependent on the task. Weiner and Ehrlichman (1976) reported that eye movement rate was higher for verbal tasks than for spatial tasks. On average, people make about 1.5-2 times as many eye movements per unit time when answering verbal questions rather than visuospatial questions. Eye movement rate was computed for each question by dividing the number of observed eye movements by the number of seconds from the end of the question to the end of the participant's answer. This difference was independent of visual stimulation because it occurred when individuals had to look either at a face or an oval in a visually complex environment, or in complete darkness (Ehrlichman & Barrett, 1983). However, the underlying cause for the difference in behavior may not be the different nature of cognitive processes for verbal and spatial questions, but rather the extensiveness of the implied memory search. Tasks requiring extensive searches result in more saccades than tasks requiring less extensive searches (Bergstrom & Hiscock, 1988; Ehrlichman & Barrett, 1983). In more recent studies on eye movement rate, it was concluded that looking for information in long-term memory increases the number of saccades, whereas maintenance of and attention to information in working memory decreases the number of saccades (Ehrlichman & Weinberger, 1978; Micic et al., 2010). In support of this assumption, a recent finding by Vrij, Oliveira, Hammond, and Ehrlichman (2015) showed that people displayed more saccadic eye movements when telling a lie compared to people telling the truth. This is

consistent with earlier research arguing that lying is associated with a more long-term memory search compared to truth telling (Ganis, Kosslyn, Stose, Thompson, & Yurgelun-Todd, 2003).

Ehrlichman et al. (2007) have proposed a model that underlines the links between memory and non-visual ocular movements at a neuroanatomical level. To sum up, they postulated that memory systems can affect saccadic generation via the saccadic portion of the oculomotor system. We know that the superior colliculus contains neurons involved in saccadic eye movements and stares (Munoz & Everling, 2004) and relates information about saccades planning (Munoz, 2002) to the brain gaze circuitry (Sparks, 2002). Execution of saccadic eye movements induced bilateral frontal eye field activation in the prefrontal cortex (Petit, Clark, Ingeholm, & Haxby, 1997) as well as other extrastriate areas of the contralateral hemisphere like parietal regions (Macaluso, Driver, & Frith, 2003). Frontal, parietal and temporal memory-related cortices are linked to the superior colliculus via both direct and indirect neural connections (Distel & Fries, 1982). More specifically, the medial temporal lobe which is involved in retrieval form long-term memory (Schacter & Wagner, 1999; Squire, Stark, & Clark, 2004) may affect saccadic frequency through the dorsolateral prefrontal cortex which is involved in oculomotor control (Cabeza, Dolcos, Graham, & Nyberg, 2002; Pierrot-Deseilligny, Muri, Nyffeler, & Milea, 2005).

This strong functional linkage between specific parts of the medial temporal lobe, such as the hippocampus and oculomotor control areas, is corroborated by a recent finding on macaques (Shen, Bezgin, Selvam, McIntosh, & Ryan, 2016) suggesting that the anatomical architecture of the primate brain is organized in such a way that memory and visuo-oculomotor system can potentially exchange information. Furthermore, Howard Ehrlichman has proposed that activation of the collicular saccadic zone and the resultant high saccadic frequency could be related to information search though long-term memory, whereas the activation of the collicular fixation zone could be related to maintenance of information in working memory. Ehrlichman and Micic (2012) also proposed that eye movement rate might be related to the increased hemispheric interaction found by Christman, Garvey, Propper, and Phaneuf (2003), mentioned below in EMDR research. However, this relation is unclear; the small spontaneous eye movements which rarely cross the visual midline are very different from the large bilateral saccades in EMDR.

While numerous studies have confirmed a correlation between certain types of cognitive processing and eye movement rate, a clear functional role of saccade rate could not

be established. If spontaneous eye movements facilitate search in long-term memory, their suppression should impair performance which seems not to be the case. Micic et al. (2010) asked half of the participants to recall a list of words with free gaze, while the other half was instructed not to move their eyes during recall and to look steadily at a dot in front of them. While individuals report that the task was subjectively more difficult without moving the eyes, performance did not differ between free gaze and fixation.

Neuro-Linguistic Programming

Further claims of a causal link between gaze direction and behavior come from Neuro-Linguistic Programming (NLP). As in the other areas of research mentioned above, NLP looks at spontaneous eye movements and postulates that somehow directional eye movements can facilitate cognitive processing. NLP is a set of models and techniques aimed at improving communication skills (Bandler & Grinder, 1982). This discipline is currently considered as a pseudo-science by most researchers (Witkowski, 2010). Nevertheless, it is interesting to note that the NLP model argues that non-visual eye movements ("ocular access") reflect our way of thinking and that gaze direction may unconsciously help us to retrieve existing mental representations or to create new ones (Buckner, Meara, Reese, & Reese, 1987). Like the lateral eye movement model, the NLP model makes precise assumptions depending on the direction of saccadic movements. In addition to horizontal, the model also includes vertical eye movements, proposing functional differences among six positions of the visual field. For instance, the NLP model on eye movements claims that looking to the upper left is a way to increase the retrieval of images from memory (Figure 10). This model is notably used by NLP practitioners through therapy or personal improvement for "calibration" and "synchronization" (Bandler & Grinder, 1979). It should give information about internal processes by giving us an idea of how our interlocutor imagines an event, and the sensorial memory that he needs. Despite the fact that this model has never been supported by scientific literature, some books presenting new forms of learning methods aimed at teachers are entirely based on it (Thiry, 2006; Thiry & Lellouche, 2007).

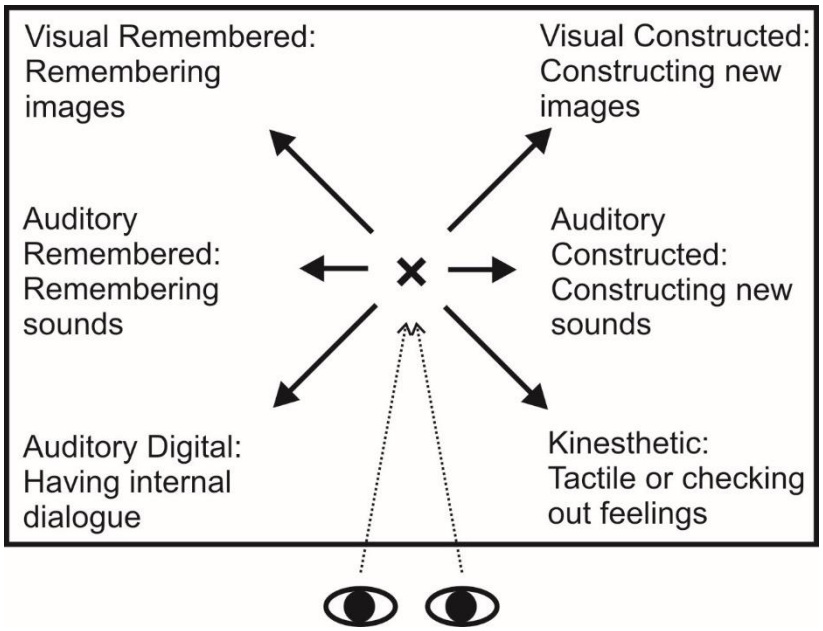

Figure 10. Diagram of the associations between gaze direction and cognitive processes according to Neuro-linguistic Programming. The associations are thought to hold for 80% of the right-handed and 50% of the left-handed population. Gaze direction is given with respect to the participants' point of view.

Very few experimental studies have tried to test the NLP model on eye movements. According to the tenets of NLP, gaze direction is associated with certain cognitive processes, looking to the upper right facilitates the construction of new images, while looking to the upper left facilitates remembering images. Based on this model and material from the internet, Wiseman et al. (2012) derived the hypothesis that lying was accompanied by eye movements to the upper right while telling the truth was accompanied by eye movements to the upper left. In a series of three experiments, they were unable to confirm this proposition. A similar finding obtained by Mann et al. (2012) did not observe any effect either. However, the principal issue is that this research did not test the NLP model directly but instead tested assumptions that oversimplified it, the model per se being hard to test. To our knowledge, only Ahmad (2013) have tried to test the whole model in a proper way. The authors developed six questions in order to tap into each presumed cognitive process, e.g., "Do you have a favorite song/music? Can you play that in your head?". Given that this question involves verbal recall the eye pattern should be toward the lateral left. Then, for each question, they calculated the percentage of participants showing the expected eye movement. With the exception of visual recall (64%), less than half of the respondents do indeed show the gaze direction pattern postulated by NLP for the remaining pattern (i.e. visual constructed, auditory remembered, auditory constructed,

kinesthetic and auditory digital). As mentioned in the Introduction, we were also faced with a lack of results in our own experiments trying to experimentally test this model. The first limitation of the NLP model is similar to the one already discussed for lateral eye movements. In order to properly test assumptions of this model, the validity of the questions used should be checked beforehand. Additionally, participants might elect different strategies and thus might show different gaze patterns when confronted with the same problem. Even with really specific questions it is almost impossible to oblige a participant to access only one sensory representation.

Based on these findings and those reported on frequency, we can postulate that eye movements may be able to improve the recall of certain type of information, however, there is clear evidence showing that they are not mandatory. Even if the phenomenon of spontaneous eye movements is still not understood, there is some evidence that the execution of eye movements changes cognitive functioning. Instead of passively observing spontaneous eye movement patterns, some authors have chosen to manipulate saccadic activity in order to investigate these changes.

Request of specific directional eye movements

EMDR

EMDR stand for “Eye Movement Desensitization and Reprocessing” and refer to a brief therapy, described as a “neuro-emotional integration by ocular movements” that is used, in particular, to treat people suffering from post-traumatic stress disorder (PTSD) (P. R. Davidson & Parker, 2001; Shapiro, 1996). This therapy is an integrative eight-phase treatment approach guided by the adaptive information processing (AIP) model developed by Francine Shapiro (Shapiro, 2012). According to this model, a trauma is an event not fully processed by the brain and therefore not integrated with other memories. The experience remains stored with emotions, physical sensations and beliefs associated with the original events. Future similar experiences will automatically trigger the unprocessed memory and will alter the present event (Shapiro & Laliotis, 2011). The technique of EMDR aims to address the current, everyday problems of patients suffering from PTSD by accessing the dysfunctional stored memory. A unique component of EMDR is the use of bilateral eye movements as part of the treatment process (periods of 30 seconds), which is thought to engage the natural processes by which the problematic memory will be transmuted into appropriately stored memory (Shapiro, 2001).

While patients are moving their eyes back and forth between left and right, they are simultaneously instructed to think about a traumatic memory. Repetition of the procedure aims to change the nature of the memory from sensory (problematic) to declarative (appropriately stored).

The efficacy of EMDR had long been a matter of debate and has received much criticism (McNally, 1999; Perkins & Rouanzoin, 2002). However, recent meta-analyses have found sustained and lasting treatment effect, particularly for the treatment of PTSD (Bisson et al., 2007; Bradley, Greene, Russ, Dutra, & Westen, 2005; Seidler & Wagner, 2006). Many organizations, such as the American Psychiatric Association, Inserm or the National Institute for Clinical Excellence, have acknowledged this method. Also, the U.S. Department of Veterans Affairs & Department of Defense and the International Society for Traumatic Stress Studies designated EMDR as an "A" level treatment which stands for "A strong recommendation that clinicians provide the intervention to eligible patients" (Shapiro, 2012). Despite the fact that today EMDR is a first-line therapy to treat PTSD, the action mechanism of this therapy remains controversial (Rogers & Silver, 2002; Shapiro, 2012). For some authors, EMDR is no different from traditional exposure treatments and eye movements do not add anything to this therapy (P. R. Davidson & Parker, 2001; Pitman et al., 1996).

Few theoretical explanations have been proposed to explain the functional role of eye movements in EMDR. Shapiro initially proposed that saccades performed in EMDR are similar to the saccades of rapid eye movement sleep (REM) but gave no clear explanation of how such mimicry might lead to clinical improvements. Stickgold (2002) corroborated this assumption by pointing out that bilateral eye movements induce a neurobiological state similar to REM sleep by redirecting the attention from left to right in a repetitive way. In his model of trauma processing, he proposed that EMDR's eye movements can activate sleep-dependent memory processing, which has broken down in the face of overwhelming trauma. He proposed that this constant shift of attention by inducing a REM-like state facilitates cortical integration of traumatic memories into associative cortical networks without interference from hippocampal mediated episodic recall. Thus, bilateral stimulation may compensate for the lack of REM sleep in PTSD patients (Ross et al., 1994), allowing them to reprocess events. His claim is consistent with the finding that the majority of eye movements during REM sleep are horizontal (Hansotia et al., 1990) and with the growing amount of evidence showing the importance of REM sleep on episodic memory (Stickgold, 2005; Stickgold & Walker, 2013). However, although eye

movements play a crucial role, other bilateral stimulation such as auditory or tactile could also shift the brain into this REM-like state (Stickgold, 2008).

Both treatments and laboratory studies have tried to investigate the effectiveness of the eye movement component in EMDR, with mixed results. For instance, Wilson, Silver, Covi, and Foster (1996) found a specific effect of eye movements in a broad clinical population, whereas Renfrey and Spates (1994) did not find any effect of eye movements on PTSD patients. Many laboratories were able to find decreases in vividness and/or emotionality on autobiographical memories (Barrowcliff, Gray, Freeman, & Macculloch, 2004; Gunter & Bodner, 2008; van den Hout, Muris, Salemink, & Kindt, 2001).

In addition, we can ask ourselves if bilateral eye movements completely outside the EMDR protocol can improve cognitive processing even without any emotional component. In laboratory studies, other authors report a variety of memory effects such as increased episodic retrieval (Christman et al., 2003), attentional flexibility (Kuiken, Chudleigh, & Racher, 2010) or recognition of true memory (Parker, Buckley, & Dagnall, 2009). For instance, Christman et al. (2003) asked participants to make large ocular movements from left to right for 30 seconds before recalling a list of words or autobiographical events. The authors found that horizontal saccades improved recall, while vertical saccades did not have any effect. The authors' interpretation was that lateral saccades resulted in sequential activation of the left and right hemispheres, which reduces preexisting hemispheric asymmetries while improving hemispheric interaction (Christman & Garvey, 2001) and subsequently improved episodic memory. This interpretation is compatible with the idea mentioned before that bilateral saccades induce a REM-like state. Interhemispheric coherence measured by EEG increases significantly during REM sleep (Barcaro et al., 1989; Dumermuth & Lehmann, 1981). However, in the recent literature, some authors using EEG measurements did not find evidence to support this interhemispheric interaction hypothesis. Samara, Elzinga, Slagter, and Nieuwenhuis (2011) did not find the expected interhemispheric interaction and Propper, Pierce, Geisler, Christman, and Bellorado (2007) found a decreased interhemispheric EEG coherence in the anterior prefrontal cortex.

Even if most EMDR research has used eye movements, it is important to mention that, over the past decade, many therapists have started to replace eye movements with other forms of bilateral stimulation such as auditory or tactile stimuli (Shapiro, 2012; van den Hout et al., 2011). Very few studies have investigated the effect of other sensory input, and again the

results are mixed. Effectiveness of eye movements compared to motor actions was more consistently found in non-clinical studies, however, other procedural elements of EMDR were not involved, for more on this topic see, C. W. Lee and Cuijpers (2013). For instance, Servan-Schreiber, Schooler, Dew, Carter, and Bartone (2006) on a clinical population found that bilateral auditory stimulation reduced subjective distress. In contrast, Nieuwenhuis et al. (2013) comparing bilateral eye movements, tactile and auditory stimulations have found improved memory retrieval for eye movements and tactile stimulation but not for auditory stimulation. When comparing the effect of eye movements versus auditory stimulation on the reduction of vividness of negative memories, van den Hout et al. (2011) suggests that both are effective but that eye movements are superior.

Gaze Direction

The literature on non-visual eye movements is still incomplete; no model can actually explain the whole phenomenon. At present, there is no clear evidence showing that looking to one side activates the contralateral hemisphere and leads to an advantage for cognitive processes within this hemisphere. However, there is some reason to believe that this is the case based on the literature mentioned above. So far, no research has investigated the impact of vertical saccades on cognitive processing (used as a control condition in EMDR research). Similar to horizontal asymmetry, we can ask if either looking upward or downward activates brain areas that are also involved in treating stimuli from the respective vertical hemifields. According to this hypothesis and based on vertical asymmetry mentioned above, looking up will activate ventral parts of the brain such as temporal lobes, whereas looking down will activate dorsal parts of the brain such as the parietal lobe (Figure 5). If so, gaze direction oriented toward different quadrants of the visual field could lead to the activation of the ventral versus dorsal stream of the contralateral hemisphere and ease some cognitive tasks associated with those areas in everyday life situations. As mentioned before, investigating spontaneous eye movements is quite difficult. Instead of asking questions and looking at directional patterns, we proposed in our experiments to impose gaze direction to the participant in order to see if one gaze direction can improve performance of participants on a specific task.

Different Components of Visual Short-Term Memory

Visuospatial working memory can be subdivided into at least two separable storage systems (Logie, 2003); one for maintaining visual information (such as appearance), and the other for maintaining spatial information (such as the location of objects). Darling, Della Sala, and Logie (2009) provided evidence for these two distinct subsystems in visuospatial working memory by selectively disrupting memory in the retention interval. While dynamic noise selectively disrupted visual memory for the appearance of letters, a manual tapping task selectively disrupted location memory for the position of squares. Another technique to selectively investigate visual and positional memory is to change the presentation mode. Pickering, Gathercole, Hall, and Lloyd (2001) asked participants to remember the position of black squares that were either shown simultaneously as a black-and-white pattern or one after the other in an empty matrix. The assumption was that the simultaneously presented squares were stored in the visual subsystem whereas the sequentially presented squares were stored in the positional subsystem.

Finally, Kessels, Kappelle, de Haan, and Postma (2002) argued for a third subsystem of spatial memory with separate brain structures, which the researchers referred to as object-location binding. Based on a study with patients after an ischemic stroke, they concluded that the left hemisphere was more involved in binding object identities to known positions, whereas the right hemisphere was critical for positional memory.

The effect of gaze direction on visuospatial short-term memory

Experiments 10-12

Overview of experiments

We set out to explore the effect of gaze direction in a task that involved visuospatial information. In contrast to Propper et al. (2012), we do not focus on semantic long-term memory, but on visuospatial short-term memory (VSTM). Intuitively, VSTM tasks are closer to the perceptual tasks reviewed above that consistently showed better performance for visuospatial information directed at the left hemisphere by right hemifield presentation. Our basic assumption is that gaze directed to the left or right will increase contralateral cortical activity. As the right hemisphere is more strongly associated with visuospatial processing, we expect better performance on VSTM tasks when gaze is directed to the left. For elevation, we do not have precise expectations. While categorical judgments of position (i.e. below vs. above) were better in the upper visual field, judgments of distance (i.e. close vs. far) were better in the lower visual field (Niebauer & Christman, 1998). Encoding the matrix positions involves judgments of both categorical spatial relations and distances. Therefore, it is not clear what to expect when gaze is directed upward or downward.

Our experimental task required observers to memorize the positions of filled squares in a five-by-five matrix (see Figure 11). Immediately after stimulus presentation, they had to reproduce the positions by mouse click in a response matrix that was shown at the same position as the stimulus matrix. To avoid ceiling or floor effects, the session started by a pre-test of the visual span and the number of filled squares in the experiment was adjusted according to individual performance in the span test. We compared memory performance with gaze directed to the left to memory performance with gaze directed to the right. In addition, we varied the vertical position of the stimuli by presenting the stimuli in opposite quadrants. We opposed the upper left and lower right quadrant in Experiment 10 and in Experiment 11, and the lower left and the upper right quadrant in Experiment 12. The original paper of the present experiments can be found in annex (Carlei & Kerzel, 2014).

Experiment 10

Method

Participants

Participants were twenty-one right-handed students (9 females, aged from 18 to 35) at the University of Geneva. Handedness was measured by a self-report. It has been reported that memory for verbal material of consistent right-/left-handers improve when they make saccadic eye movements for 30 s before the memory test (Lyle, Hanaver-Torrez, Hacklander, & Edlin, 2012; Lyle, Logan, & Roediger, 2008). Presumably, consistent right-handed individuals benefit from the saccade task because their relatively weaker hemispheric interaction increases when saccades are made. Because we tested visuospatial memory and our hypotheses do not relate to the strength of hemispheric interactions, we had no a priori reason to exclude inconsistent right-handers in the current task. If anything, this decision made our study more conservative because the less homogeneous sample increased the random error. The data of one participant was lost due to computer failure. At their arrival, participants participated in a lottery to win 50 Swiss Francs.

Stimuli and Apparatus

Observers' head movements were restrained by a chin/forehead rest at 118 cm from the ground. The experiment was controlled by E-Prime (v1.2) and the stimuli were generated by a video-projector. The visual stimulus was a five-by-five matrix of 50 x 50 cm (or 17.4°x 17.4° of visual angle, width x height) shown on a projection screen (170 x 130 cm, or 46.7° x 39.1°) at a distance of 160 cm. When the matrix was shown in a quadrant, there was a margin of 2 cm (0.7°) to the edge of the screen. The eyes were approximately at the horizontal and vertical center of the screen.

A variable number of cells in the matrix were filled. The presentation time was 1 s per filled square (e.g. for a matrix with three filled squares, the presentation time was 3 s). The filled squares marked positions that had to be remembered. Figure 11 shows three sample stimuli. For each number of squares, there were 10 different matrices that were randomly assigned to the experimental conditions. The matrices had been created to avoid patterns that were easy to remember, such as clusters, lines, or geometric figures. Because of the small number of trials, it was important to make sure that all matrices had the same difficulty. This was confirmed by

one-way ANOVAs on the percent correct responses of matrices containing the same number of squares, which did not produce any significant results.

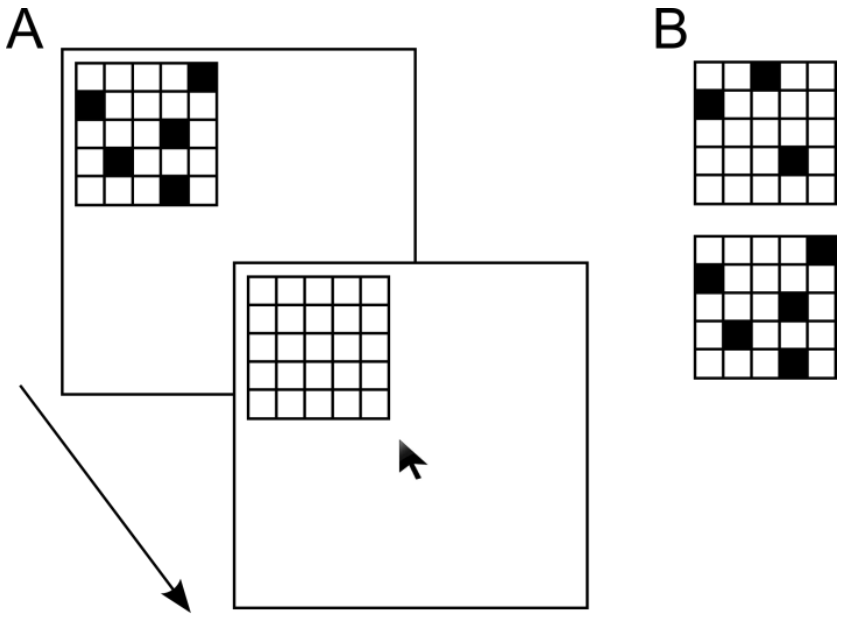

Figure 11. Illustration of stimuli and procedures. (A) Sample trial with the stimulus matrix in the upper left quadrant of the screen (not drawn to scale). The presentation time was 1 s for each filled square. Then, the response matrix appeared at the same position as the stimulus matrix, together with a mouse cursor in the center. Participants clicked on the remembered cells in the response matrix. Participants using a counting strategy may encode the number of cells from the left edge for each row, resulting in the code 5, 1, 4, 2, 4 from top to bottom. When more than one square was presented per row or rows were empty, this had to be remembered in addition to the square positions. (B) Two sample matrices with three and five filled squares, respectively.

Procedure and Span Evaluation

In the first part of the experimental session, we determined the visuospatial span for each subject (see Lecerf & de Ribaupierre, 2005). The matrix was presented in the center of the screen. Immediately after the presentation of the stimulus matrix, the screen went blank for 150 ms. Then, an empty response matrix appeared at the same position as the stimulus matrix. We hoped that the brief flicker introduced by the blank period would erase an iconic image of the stimulus matrix. At the same time as the response matrix, the mouse cursor appeared in the center of the screen. Then, participants indicated the remembered positions by clicking on the cells of the matrix. Response time was unlimited and it was possible to reset the response matrix after response errors. A response was considered correct if all square positions were correctly reproduced.

After seven practice trials, the span evaluation started with two filled squares. There were three consecutive repetitions for each number of squares. When at least one trial of the three repetitions was correct, the number of squares was subsequently increased by one. When the participant failed all three repetitions, the procedure stopped and the previous number of squares with at least two correct responses was considered the participant's memory span. The maximal span was limited to seven because otherwise, it was more likely that participants encoded the empty spaces rather than the filled squares.

Experimental Task

The procedure was as in the span evaluation with the following exceptions. Participants worked through ten trials with a number of squares corresponding to the memory span, followed by ten trials with an additional square (span + 1). In both blocks, stimulus matrices were presented randomly either in the upper left or in the lower right quadrant. On each trial, the response matrix was presented at the same position as the stimulus matrix. Presentation times and response acquisition were as in the span test. Overall, there were 20 experimental trials resulting from the combination of the two numbers of squares (span, span + 1), two stimulus positions (upper left, lower right), and five repetitions. A new pattern of filled squares was presented on each trial. It took about 20 minutes to complete the experiment (including practice trials and span procedure).

Results and Discussion

The mean memory span, the range of the span, and memory performance as a function of gaze direction (Experiments 10 to 12) and strategy (Experiments 11 and 12) are shown in Table 4. A response was counted as correct if the positions of all filled squares in the matrix were reproduced correctly. As presentation of the squares was simultaneous, the order of mouse clicks in the matrix was not taken into account. We calculated the mean percentage of correct responses for each location and number of squares. A repeated-measures ANOVA (2 matrix positions: upper left, lower right; 2 number of squares: span and span + 1) showed that the percentage of correct responses was higher when the number of squares corresponded to the memory span than when one square was added (64% vs. 53%), $F(1,19) = 8.88$, $p = .008$, $\eta^2_p = .32$. We were surprised by the very good performance in trials with span + 1 squares (53% correct responses). Apparently, our procedure underestimated the span in the experimental trials. While the term "span" seems inappropriate with such a high-level of performance, we

nonetheless keep it for lack of a better term. When the matrix was shown in the upper left corner, performance was better than when it was shown in the lower right corner (63% vs. 54%), $F(1,19) = 5.52$, $p = .029$, $\eta^2_P = .23$. The effect of stimulus position is consistent with our hypothesis that looking to the left activates the right hemisphere, which is experienced as facilitation of the respective lateralized cognitive function (i.e. visuospatial memory). The interaction of matrix position and number of squares was not significant, $p = .150$.

Table 4. Results from Experiments 10 to 12. The span refers to the number of square participants were able to memorize (see text). In Experiment 10, individual strategies were not measured. In Experiment 12, the interaction between strategy and gaze direction was not significant, but we nonetheless report the means as a function of gaze direction and strategy.

Experiment	Span		Memory Performance Gaze Left vs. Right		
	Mean	Range	Overall	Visual Strategy	Verbal Strategy
10	5.55	4-7	64% vs. 53%	-	-
11	5.29	3-7	63% vs. 58%	82% vs. 50%	45% vs. 62%
12	5.57	3-7	59% vs. 49%	66% vs. 61%	60% vs. 38%

Experiment 11

In order to explain the inter-individual variability in the effect of gaze direction, we examined the modulating effect of strategies used to solve the task. After informal questioning of the participants, we discerned two main strategies. The visual strategy involved remembering the complete image or the shape created by the squares. The counting strategy involved remembering the position of individual squares by counting the number of empty cells relative to some reference point. For instance, participants may recall the number of empty cells from the left edge for each row containing a filled square (see Figure 11). We expected that participants relying on the counting strategy would be differently influenced by gaze direction. Looking to the left is expected to facilitate performance when a visual strategy is used because of the right hemisphere's greater involvement in visuospatial memory. In contrast, the counting strategy involves mental repetition of words or numbers, which depends on verbal rather than visuospatial memory. Therefore, looking to the right may facilitate performance

when a counting strategy is used because of the left hemisphere's specialization for verbal stimuli.

Method

Thirty-five students at the University of Geneva (25 female, 4 left-handed, aged from 20 to 35 years) participated in this experiment. The experimental procedure was the same as in Experiment 10 with the following exceptions. Trials with a number of squares corresponding to the span and trials with span + 1 squares were presented in random order. Further, the position of the subject relative to the screen was slightly changed. The screen was closer to the participant (144 cm instead of 160 cm). Therefore, the visual angle subtended by the matrix increased from 17.4° to 20.9°. The height of the chin rest was raised by 4 cm (now at 122 cm from the ground), which brought the eyes closer to the center of the screen.

In order to determine the strategy, we asked participants at the end of the experiment to describe their strategy. Participants were classified according to their reports during debriefing. Individuals who reported having counted the black squares on every trial in order to remember the position of squares were classified into the counting strategy. Individuals who reported having tried to remember matrices as a whole were classified into the visual strategy. Participants who reported having used both strategies depending on the pattern of filled squares were classified into the mixed strategy.

Results

The results are presented in Figure 12. There were 10 participants using the visual strategy, 13 participants using counting, and 12 participants alternating between the two. Because the number of squares had not interacted with the effect of gaze direction in Experiment 10, we collapsed across this factor. A mixed-factors ANOVA (2 Gaze Directions: upper left, lower right; 3 Strategies: visual, counting, mixed) confirmed better performance when participants looked at the upper left compared to the lower right (63% vs. 58%), $F(1,32) = 7.95$, $p = .008$, $\eta^2_P = .20$. There was no main effect of strategy, $F(2,32) = 1.07$, $p = .353$, but an interaction between gaze direction and strategy, $F(2,32) = 37.79$, $p < .001$, $\eta^2_P = .70$. To follow up on this interaction, we compared the upper left and the lower right for the three groups. A t-test showed that there were more correct answers for matrices in the upper left than in the lower right quadrant for participants with a visual strategy (82% vs. 50%), $t(9) = 7.69$ $p < .001$, confirming the results of Experiment 10. On the other hand, there was an opposite effect with

the counting strategy (45% vs. 62%), $t(12) = 16.01$, $p = .002$, and no effect with a mixed strategy (65% vs. 61%), $t(11) = 1.45$, $p = .175$.

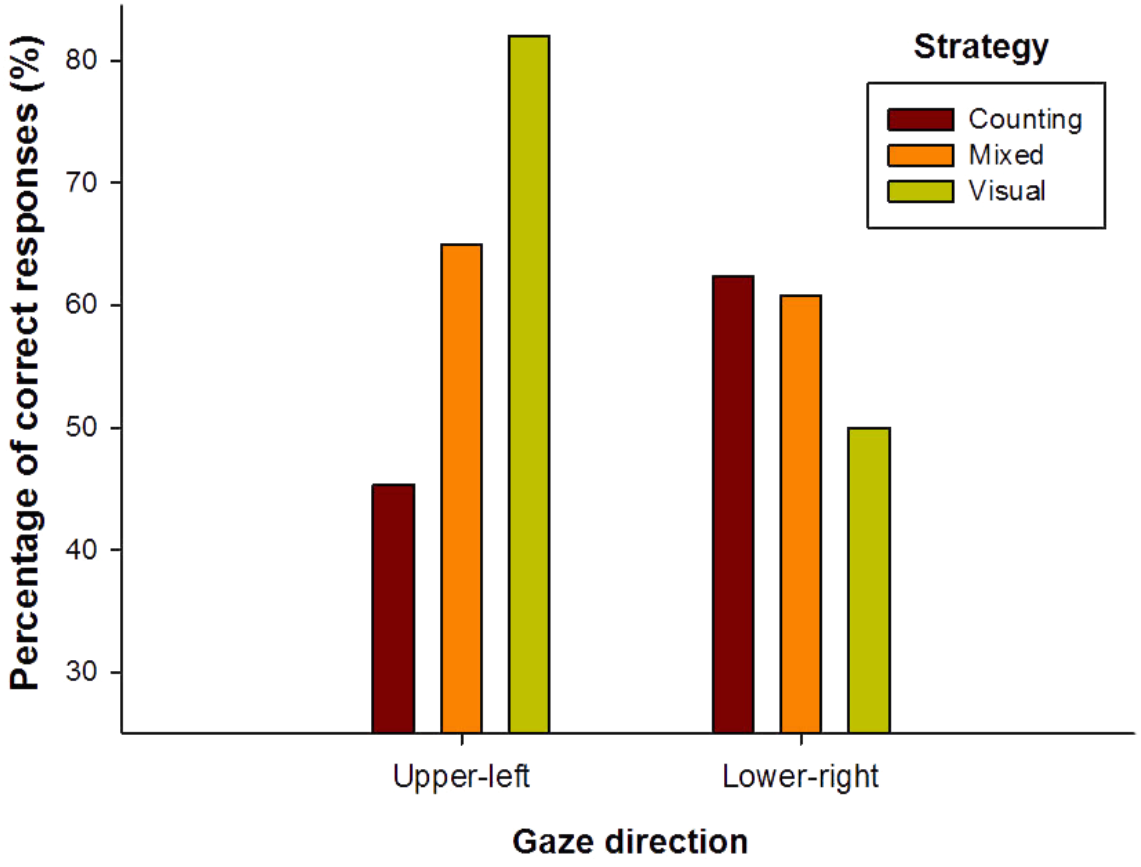

Figure 12. Results from Experiment Percentage of correct responses is shown as a function of gaze direction and strategy.

Discussion

We replicated the effect of gaze direction with a larger sample and found a strong modulation by strategy. Participants using a visual strategy showed better performance with gaze directed at the upper left quadrant. We suggest that the visual strategy relies on visuospatial memory, which improves when the right hemisphere is activated by directing gaze to the left. The results from the group using the counting strategy are also interesting. Under the assumption that these participants transformed the visual stimulus into a verbal code, activation of the left hemisphere would have been beneficial. Consistent with this idea, better performance was observed when gaze was directed to the right. Participants using a mixed

strategy showed no effect of gaze direction, which makes sense when considering that a given gaze direction either facilitates or degrades performance depending on the strategy.

Experiment 12

In Experiments 10 and 11, a difference was observed between gaze directed at the upper left quadrant and gaze directed at the lower right quadrant, which we attributed to activation of the contralateral hemisphere. However, the two gaze directions examined so far confound laterality (left, right) and elevation (up, down). Beyond the dichotomy between left and right, as mention in the Introduction, there are also studies focusing on differences between the upper and lower visual field. For example, attentional resolution was found to be enhanced in the lower visual field (He et al., 1996), which may be explained by enhanced visual discrimination (Carrasco et al., 2001). Similarly, the segmentation of an image into figures and background (Rubin et al., 1996) and goal-directed actions (Danckert & Goodale, 2001; Khan & Lawrence, 2005; Krigolson & Heath, 2006) are performed better in the lower than the upper visual field. While most studies point to an advantage of processing in the lower visual field (overview in Danckert & Goodale, 2003), visual search (Previc & Naegele, 2001), letter naming (Hagenbeek & Van Strien, 2002), and distance judgments (Niebauer & Christman, 1998) were found to be better in the upper visual field. Given the complexity of the literature on this topic, it is difficult to predict whether there would be an advantage of the upper or lower visual field for the VSTM task of Experiments 10 and 11. Therefore, we do not have any predictions about whether looking upward or downward would facilitate performance.

To examine whether laterality or elevation caused the asymmetry observed in Experiments 10 and 11, we examined the lower left and the upper right quadrant (instead of the upper left and lower right). If presentation above and not presentation to the left explained the facilitation in Experiments 10–11, we should find better performance for the upper right than for the lower left quadrant in the current experiment. In addition, we developed questions to allow for a more objective classification of participants. As in the previous experiment, the visual and counting strategies should lead to opposite effects, because they rely on different hemispheres.

Method

Thirty students at the University of Geneva (25 female, 2 left-handed, aged from 19 to 27), participated. All individuals received a voucher for a lunch at MacDonald's worth 11.30 Swiss Francs.

The same procedure was used as in the second experiment with the following exceptions. The matrices were shown in the upper right quadrant of the screen or in the lower left quadrant (i.e. vertical positions were inverted relative to Experiment 10). Further, participants filled in a questionnaire at the end of the session in order to determine the strategy. Participants rated how often they used each strategy on a scale from zero to three: 0 = never, 1 = sometimes, 2 = often, 3 = every time. Four questions were administered in French. Here, we report the English translation. For the visual strategy, we asked: ''I imagined a global shape to better remember the position of squares'' and ''I imagined isolated shapes to better remember the position of certain squares''. For the counting strategy, we asked: ''I counted the total number of squares displayed in the grid'' and ''I mentally repeated numbers corresponding to positions of squares (lines and/or columns)''. If a participant had a score equal or superior to four on two questions of the same strategy, the participant was categorized into the respective strategy, except if his score on the other strategy was equal or superior to three. In this case, the participant was categorized into the ''mixed'' strategy. A participant having scores inferior to four on both sets of questions was also categorized into ''mixed''. The criterion of four was selected a priori because it indicated that the participant had indicated at least ''often'' (score of 2) on both questions or ''every time'' (score of 3) on one question. Therefore, a total score of 4 indicated that the participant had used the respective strategy frequently. Unless the participant obtained a similar score on the other strategy, we think it was justified to classify the participant into the respective strategy. Some additional questions unrelated to strategies were administered but these are not reported.

Results

A mixed-factors ANOVA (2 Gaze Directions: lower left, upper right; Strategy: visual n = 14, counting n = 4, mixed n = 12) confirmed a significant effect of gaze direction with better performance when gaze was directed at the lower left than at the upper right quadrant (59% vs. 49%), $F(1,27) = 6.74$, $p = .015$, $\eta^2_P = .20$. Performance also depended on strategy and was

better with the visual (63%) than with the counting or mixed strategies (49% and 45%, respectively), $F(2,27) = 3.65$, $p = .039$, $\eta^2_P = .21$. The interaction was not significant, $p = .420$.

Discussion

Performance was better when gaze was directed at the lower left vs. upper right quadrant. This result confirms our hypothesis that looking to the left increases activation of the right hemisphere, which facilitates performance on VSTM tasks. Comparison of Experiment 12 with Experiments 10–11 suggests that the elevation of the stimuli does not play a role. Further, there was no interaction with strategy. Rather, the advantage of the lower left position was independent of strategy, which may be due to the small number of participants using a counting strategy (only 4 participants).

Experiments 13-15

Overview of experiments

The main difficulty we encountered in Experiments 10-12 is based on the fact that visuospatial matrix task does not exclusively depend on visuospatial memory but can also be done with the help of verbal memory. In retrospect the form that we drew up to ''categorize'' participants according to strategies used was widely insufficient and very subjective. In order to confirm our previous results and to investigate other components of short-term memory, we were looking for "pure" tasks requiring visuospatial memory. Our present goal is to investigate the effects of gaze direction on three distinct types of short-term memory: Visual memory, positional memory and object-location binding. Our main prediction is that gaze directed to the left activates centers in the right hemisphere, which improves performance on tasks involving visual and positional memory. In contrast, directing gaze to the right activates centers in the left hemisphere, which improves performance on tasks involving object-location binding (see Kessels et al., 2002). As in Experiments 10 to 12, we compared opposing quadrants in separate groups of participants to disentangle the effects of laterality and elevation. We presented the matrices in the upper left or the lower right in one group, and in the lower left or the upper right in the other group.

In Experiment 13, we focused on visual memory and attempted to replicate previous results with improved methods. As in Experiments 10-12, we asked participants to memorize the position of black squares in a matrix that was presented simultaneously and to reproduce the square positions after the stimulus offset (see Figure 13A). The main manipulation concerned about the position of the matrix on the computer screen and the corresponding gaze direction. The matrix was presented in one of the four quadrants. To prevent verbal coding of the square positions, the phonological loop was blocked (Pelizzon, Brandimonte, & Favretto, 1999). We hope to replicate better performance when participants look to the left, which we attributed to right hemisphere activation (Experiments 10-12). For elevation, we still do not have precise expectations.

In Experiment 14, we investigated the positional subcomponent of spatial memory. The squares were presented sequentially instead of simultaneously to prevent participants from encoding the global shape of the pattern (see Figure 13B). We expect to replicate findings observed for visual memory with better performance when gaze is directed to the left.

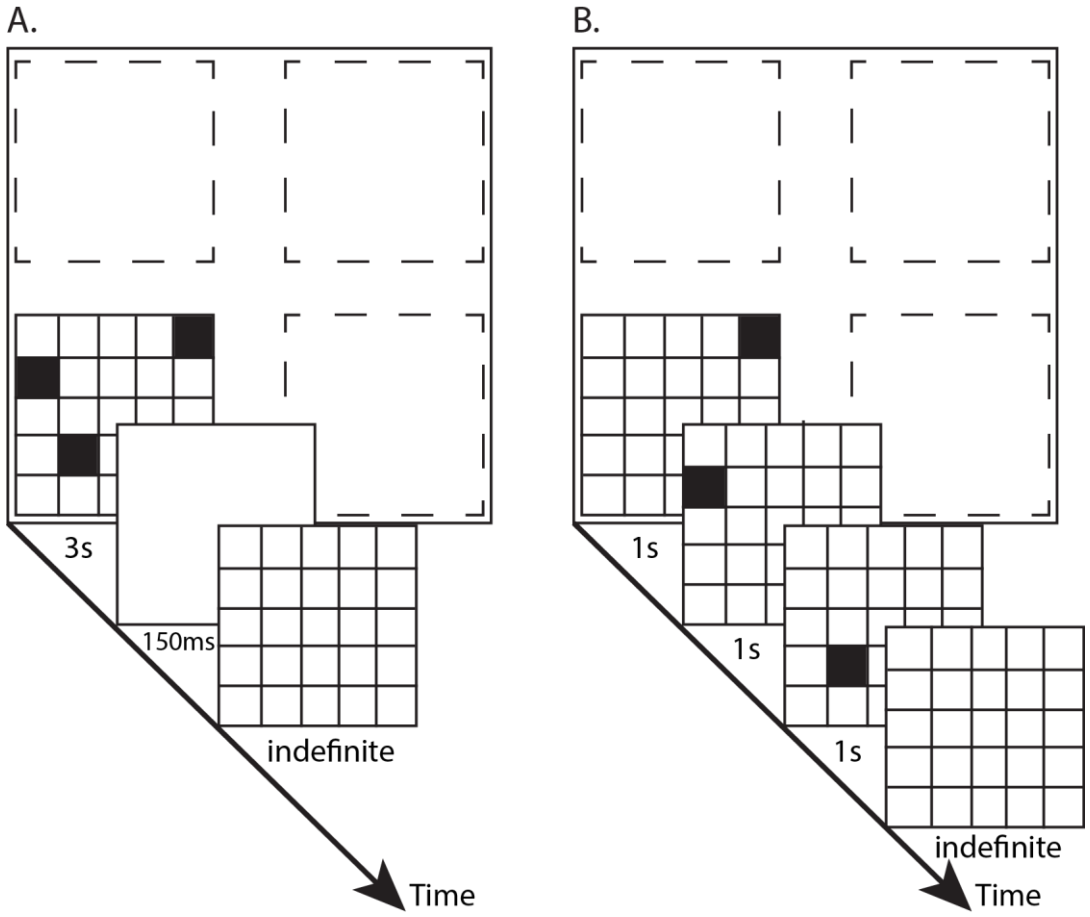

Figure 13. Simultaneous and sequential presentation modes in Experiments 13 and 14 are illustrated in panels A and B, respectively. With simultaneous presentation, presentation time was increased by one second for each square. With sequential presentation, each square was shown for one second. At the end of stimulus presentation, a response matrix appeared in the same location. Participants clicked on the cells to respond. There was no time constraint.

In Experiment 15, we investigated object-location binding in a variant of our matrix task that was similar to Kessels et al. (2002). Participants were asked to memorize Japanese symbols at their respective locations. Subsequently, blue dots replaced the Japanese symbols and participants had to recall the Japanese symbol at each dot location (see Figure 15). Given that the selected Japanese symbols are visually complex, the capacity to discriminate may play a significant role. As there is some evidence that visual discrimination, as well as attentional and spatial resolution, are better in the lower visual field, we expect better performance when gaze is directed to the lower quadrants. The original paper of the present experiments can be found in annex (Carlei & Kerzel, 2015).

Experiment 13

Methods

Participants

Participants were 35 right-handed female students (aged from 17 to 35) at the University of Geneva. All participated for a course credit. Handedness of all students was assessed by the Edinburgh Handedness Inventory (Oldfield, 1971), but only strongly right-handed participants with a score equal or above 80 on a scale of 100 participated in the present experiment (see Christman, Propper, & Dion, 2004). We chose to restrict our sample to right-handed women because gender and laterality influence cerebral specialization (Grabowska, Herman, Nowicka, Szatkowska, & Szelag, 1994; Tzourio-Mazoyer et al., 2010). Furthermore, we also chose strongly right-handed participants because we know that their memory performance is more affected by eye movements (Lyle et al., 2008). By doing so, we hope to create a more uniform sample and increase our chances of finding reliable differences. Following consent, participants were randomly assigned to one of the two groups. We had 17 participants for the first and 18 participants in the second group.

Stimuli and Apparatus

Participants' head position was stabilized with a chin rest at 40 cm from the screen center in a dimly lit room. The experiment was controlled by E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA). Eye movements were monitored by the experimenter from outside the experimental booth with the help of the image of the eye provided by an EyeLink 1000 eye-tracker (SR-Research, Ontario, Canada). Eye movements were not recorded or analyzed, but the experimenter assured that participants followed the instructions to look at the stimulus matrix. No deviations from the instructions were noted, probably because it was very difficult to perform the task in peripheral vision.

The visual stimulus was a five-by-five matrix of 8 × 8 cm (or 11.3° × 11.3° of visual angle, width × height) shown on a computer screen (30 × 39 cm, or 36.9° × 44.3°). When the matrix was shown in a quadrant, there was a margin of 0.4 cm (0.6°) to the edge of the screen. A variable number of cells in the matrix were filled depending on the visual span of each participant.

The filled squares marked positions that had to be remembered. In order to avoid patterns that were easy to remember such as clusters, lines or geometric figures, matrices had

been created and selected previously. The same 20 matrices were used for all participants, but their assignment to the experimental conditions was random.

Procedure and Span Evaluation

The procedure was almost the same as the one we used in Experiments 10-12, but this time the phonological loop was blocked in order to force visual encoding. Participants had to repeat two nonsense syllables throughout the experiment (i.e., "badabada"), which prevented participants from recoding the matrices as a series of numbers (e.g. one number for each column containing a square). The syllables were presented via headphones and participants had to repeat the syllables at the same tempo (1 syllable/second) and approximate volume. Compliance in the articulatory suppression task was monitored by the experimenter. A failure to comply was to miss a syllable, to not respect the tempo or to be inaudible to the experimenter. All our participants managed to follow this instruction.

In the first part of the experimental session, we determined the visual span for each participant (see Lecerf & de Ribaupierre, 2005). For the span evaluation, matrices were always displayed at the center of the screen. The presentation time was one second per filled square (e.g. for a matrix with three filled squares, the presentation time was three seconds). Subsequently, the screen went blank for 150 ms and finally, an empty response matrix was displayed. The blank period between the stimulus and the response matrix created a flicker that erased the iconic image of the stimulus matrix. When the response matrix was shown, the mouse cursor was available, so that the participant could indicate the remembered positions by clicking on the respective squares. There was no time limit during the response period. Once the participant was satisfied with the response, she confirmed it by clicking on a separate button. A trial was considered correct if all square positions were correctly reproduced. At the beginning of the experiment, participants went through seven practice trials followed by immediate performance feedback. Then, the span evaluation started with two filled squares. For each number of squares, three consecutive repetitions were performed. When at least one trial of the three repetitions was correct, the number of squares on the next trial was increased by one. When the participant failed all three repetitions, the procedure stopped and the previous number of squares with at least two correct responses was considered the participant's memory span.

Experimental Task

The procedure was as in the span evaluation with the following exceptions. Stimulus and response matrix were not shown in the center, but in one of the quadrants. Before presentation of the stimulus matrix, the fixation cross was replaced for 250 ms by an arrow guiding participants to the quadrant of the upcoming matrix. No feedback was given. The duration of the experiment was about 20 minutes (including practice trials and span procedure).

Participants worked through 20 trials following from a 2 (number of squares: Span, span + 1) × 2 (diagonally opposed quadrants) × 5 (repetitions) design. Participants in the first group saw matrices in the upper left and in the lower right quadrants, whereas participants in the second group saw matrices in the lower left and the upper right quadrants of the screen.

Results and Discussion

The mean memory span and the range of the span are shown in Table 5. The mean percentage of correct responses for each condition collapsed across span and span + 1 is shown in Figure 14A. For the first group, the percentage of correct responses was higher in the upper left corner than in the lower right corner (68% vs. 53%), $F(1, 16) = 24.27$, $p < .001$, $\eta^2_P = .60$. This result confirms that activation of the right hemisphere by looking toward the left improves visuospatial short-term memory (Experiments 10-12).

For the second group, there was no difference between the lower left and the upper right corner (50% vs. 50%), F(1, 17) = 0, p = 1. Further, we performed a mixed-design analysis of variance (ANOVA) with one within-subjects (2 matrix positions: left, right) and one between-subjects factor (2 vertical positions: upper left/lower right, lower left/upper right). We found a main effect of matrix position, $F(1, 33) = 5.99$, $p = .020$, $\eta^2_P = .154$, and an interaction effect, $F(1, 33) = 5.99$, $p = .020$, $\eta^2_P = .154$, showing that only the upper left was better than the remaining conditions.

Thus, the advantage of stimuli on the left, which we had observed previously (Experiments 10-12), only occurred when the stimuli were presented in the upper left corner. This discrepancy may be explained by differences in the procedure and sample. In our previous research, we separated participants according to the strategy they used to perform the task. We suspected that participants who transformed the visual stimulus into a visual code (i.e. a mental image) relied on visual memory, whereas participants who transformed the visual stimulus into a verbal code (i.e. numbers representing positions) relied on verbal memory.

However, the classification of participants was post hoc and possibly unreliable because there was no way of knowing whether a certain coding strategy had been consistently applied. Blocking the phonological loop is a more reliable way to disengage verbal memory. Also, the sample size for either strategy was small in our previous study, which may have prevented a significant interaction to emerge. Further, the current sample was selected with respect to gender (only women) and laterality (only strongly right-handed), whereas the previous sample was completely random. Thus, our present methods reduced the measurement error, which may explain why the effect of gaze direction was confined to a smaller area of space (upper left quadrant vs. entire left side).

Table 5. Results from Experiments 13–15. The span refers to the number of square participants were able to memorize.

Experiment	Span	
	Mean	Range
13	5.4	3-7
14	4.6	3-7
15	4.6	3-7

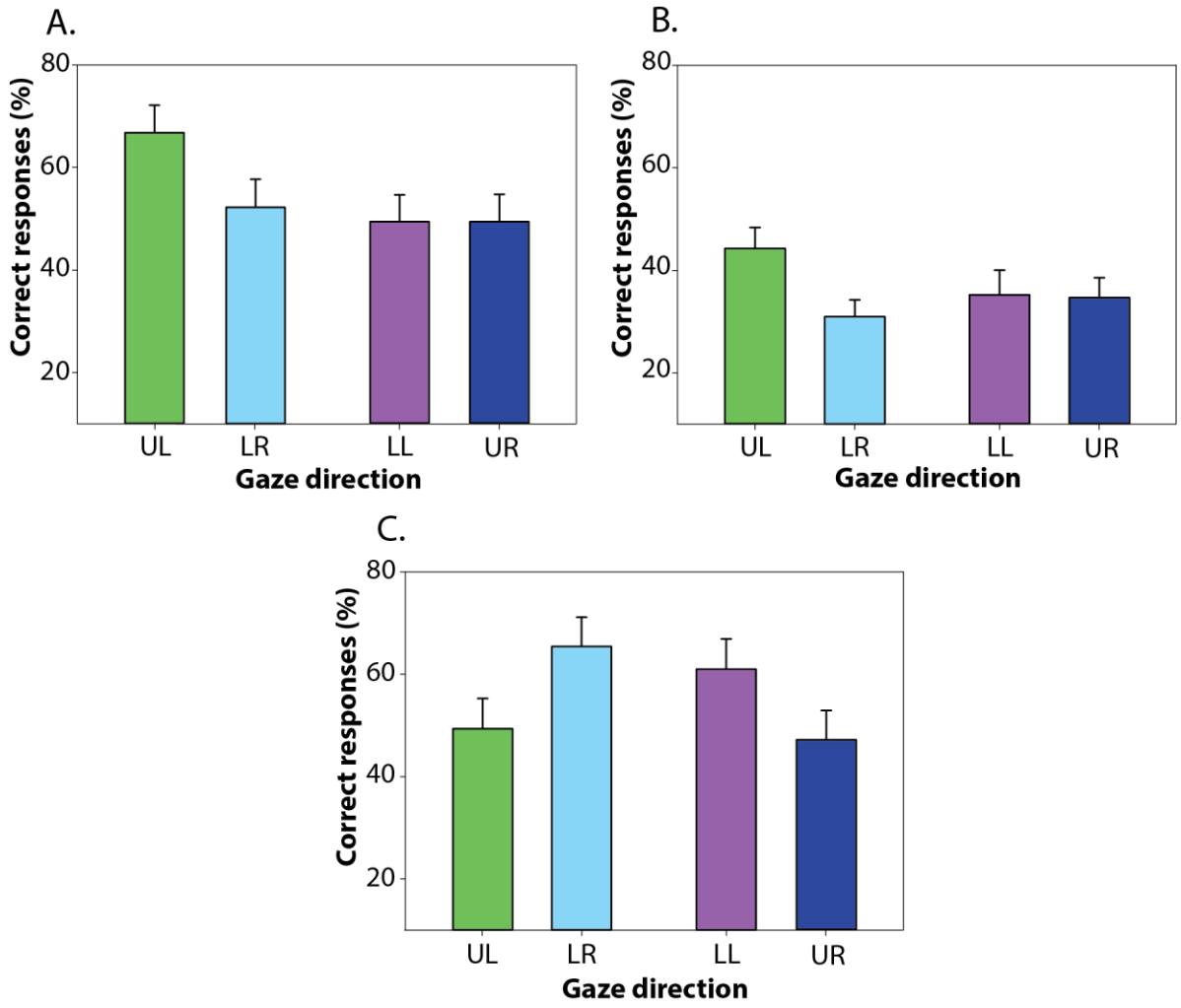

Figure 14. Results from Experiments 13, 14 and 15 are shown in panels A, B and C, respectively. Percentage of correct responses and standard error is shown as a function of gaze direction: Upper Left vs. Lower Right (UL vs. LR) in one group and Lower Left vs. Upper Right (LL vs. UR) in another group of participants.

Experiment 14

In order to disentangle visual and positional memory stores, we changed the presentation mode of matrices. Observers saw the squares sequentially (see Figure 13B) to specifically request positional memory (Pickering et al., 2001).

Methods

Forty-three female students at the University of Geneva (aged from 17 to 24 years) participated in this experiment for course credit. All participants were strongly right-handed (with a score equal or above 80 on a scale of 100 on the Edinburgh Handedness Inventory). None of them had previously participated in the first experiment. Conditions were the same as in Experiment 13; in the first group, 25 participants saw matrices in the upper left and in the

lower right corners whereas in the second group, 18 participants saw matrices in the lower left and the upper right corners of the screen.

The experimental procedure was also identical to the previous experiment. The only difference was that participants saw the squares sequentially. The presentation time of each square was fixed at one second, resulting in identical total presentation times of the matrices (for the same number of squares) in Experiments 13 and 14.

Results

Figure 14B shows a higher percentage of correct responses for the upper left corner than for the lower right corner in the first group (44% vs. 31%), $F(1, 24) = 11.96$, $p = .002$, $\eta^2_P = .333$. In the second group, there was no difference between the lower left and upper right quadrant (35% vs. 34%), $F(1, 17) = .01$, $p = .907$. As in Experiment 13, a mixed-factors ANOVA revealed a main effect of lateral position, $F(1, 41) = 5.26$, $p = .027$, $\eta^2_P = .114$, and a significant interaction, $F(1, 41) = 4.44$, $p = .041$, $\eta^2_P = .098$, confirming that elevation also played a significant role with better performance in the upper left quadrant.

Discussion

We confirmed the advantage of the upper left quadrant for positional memory that we had already observed for visual memory in Experiment 13. We suggest that gaze direction activates brain areas associated with the respective vertical or horizontal hemifield. Therefore, our results are consistent with studies showing that visual and positional short-term memory are two subsystems that both rely on the right hemisphere. Further, both may be facilitated by the activity of the inferior temporal cortex, which is thought to be involved in attention to the upper visual field (Rapcsak, Cimino, & Heilman, 1988; Shelton, Bowers, & Heilman, 1990).

Experiment 15

Experiments 13 and 14 have revealed that both visual and positional memory stores show an advantage for gaze directed to the left. Based on known hemispheric asymmetries, we expect that object-location binding will be improved with gaze directed to the right as it is associated with functioning of the left hemisphere (Kessels et al., 2002).

Method

Thirty-six female students at the University of Geneva (aged from 18 to 25 years) participated in this experiment for course credit or pay (15 CHF). All participants were strongly right-handed (with a score equal or above 80 on a scale of 100 on the Edinburgh Handedness Inventory). Nobody knew any Japanese. At the beginning of the experiment, the object-location binding span was determined for each of our participants by increasing the number of symbols until participants were unable to provide a correct answer. After the presentation of the stimulus matrix, participants were asked to recall the position of each Japanese symbol (see Figure 15). Blue dots were displayed to indicate the stimulus positions in the test phase and participants had to assign a symbol to each location. To assign a symbol to a location, participants left-clicked on the dot to browse through the different objects (i.e. the image shown at the dot location changed with each click). Right-clicking allowed participants to browse backwards. For each location, the participant could browse all symbols displayed initially. Once satisfied with the response, the participant proceeded to the next trial by clicking on a separate button.

In the experiment proper, the same procedure as in the span test was employed, but the position of the stimulus matrix (and therefore gaze position) was manipulated. As in our previous experiments, participants experienced two counterbalanced conditions (upper left/lower right or lower left/upper right) with 10 trials for each quadrant. There were 18 participants in both groups. In the two conditions, matrices were displayed in random order in two of the four corners of the screen.

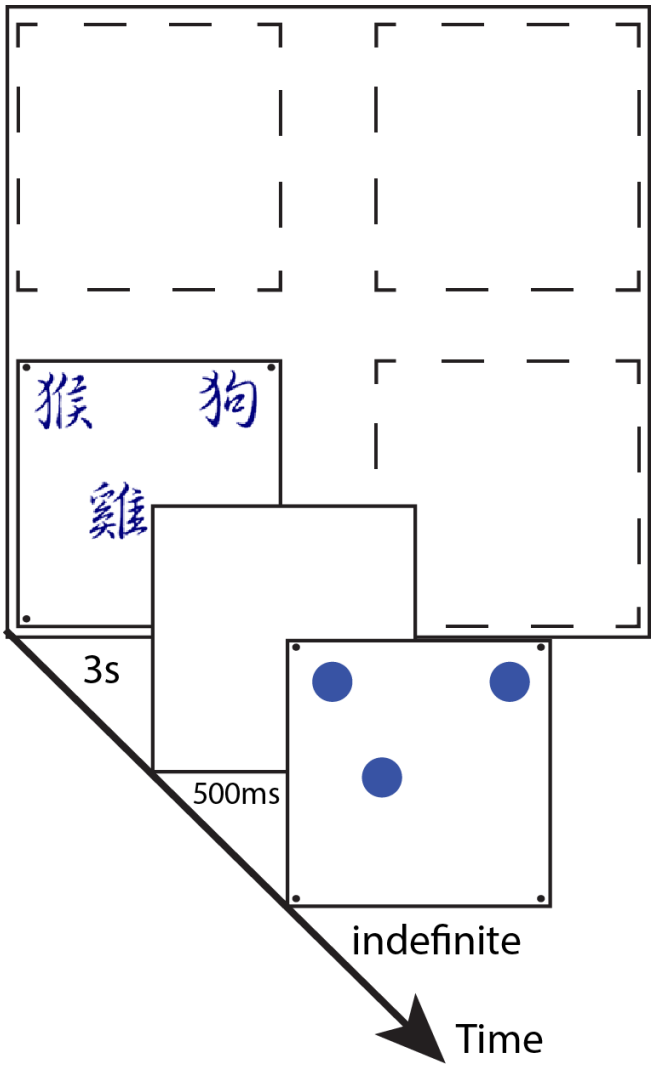

Figure 15. Illustration of the object-location binding paradigm in Experiment 15. The stimulus matrix appeared at once in one of the quadrants for as many seconds as there were Japanese symbols (3 seconds in the example). At the end of the presentation, a response matrix appeared. Dots indicated the positions of previously displayed stimuli. Participants clicked on the dots to browse through all the symbols displayed initially.

Results

Figure 14C shows that percentage of correct responses in the first group was higher in the lower right corner than in the upper left corner (66% vs. 49%), $F(1, 17) = 13.18$, $p = .002$, $\eta^2_P = .437$. In the second group, the percentage of correct responses was higher in the lower left corner than in the upper right corner (61% vs. 47%), $F(1, 17) = 10.49$, $p = .005$, $\eta^2_P = .382$. A mixed-factors ANOVA showed no main effect of lateralization but an interaction, $F(1, 34) = 23.63$, $p < .001$, $\eta^2_P = .410$, confirming better performance with gaze directed downward.

Discussion

Consistent with the hypothesis that vertical eye movements would activate cortical regions responsible for improved visual discrimination in the lower visual field, we observed better performance when gaze was directed downward and participants had to visually discriminate unknown Japanese symbols.

However, we did not find any difference in laterality. We had predicted better performance when observers looked to the right, consistent with the deficit in object-location binding observed after left-hemisphere lesions (Kessels et al., 2002). In our view, this discrepancy is accounted for by our stimuli that discouraged verbal strategies because they could not be named. In contrast, the stimuli in Kessels et al. (2002) were everyday objects that could be easily named. Therefore, Kessel et al.'s conclusion that object-location binding relies on the left hemisphere may arise from the contribution of verbal memory to task performance. Our results suggest that without the involvement of verbal processing, the lateralization to the left hemisphere disappears. However, more work is needed to confirm this conclusion.

Discussion

In this chapter we investigated vertical and horizontal asymmetries on maintenance of information in visuospatial short-term memory using the gaze direction method. In Experiments 10-12, with no control of the strategy used by participants, better performance was observed when gaze was directed to the left than to the right, irrespective of the vertical position. In Experiment 13 and Experiment 14, when investigating visual and positional subcomponents of visuospatial memory, better performance was observed when gaze was directed to the upper left quadrant, suggesting the importance of both horizontal and vertical asymmetries. Finally, investigating object location binding (third component of visuospatial memory) in Experiment 15 revealed that participants performed better when the task was displayed in the lower visual field without any difference between left and right.

Gaze Direction and Quadrant Asymmetries

Our results suggested that manipulating orientation of gaze seems to be an effective method to elicit both horizontal and vertical asymmetries. In this chapter, we used this method as a way to differentiate subcomponents of visuospatial short-term memory. Moreover, our findings support the hypothesis that horizontal gaze increases contralateral hemispheric activation (see Propper et al., 2012) and facilitates cognitive functions associated with the activated hemisphere. We believe that our unilateral gaze method has similar effects to the unilateral visual stimulation method used by Schiffer et al. (2004). When vision was limited to only one hemifield by wearing special glasses, Schiffer et al. observed stronger activation in the contralateral cerebral hemisphere. Based on studies investigating cerebral differences between attention directed to the upper and lower visual field (Rapcsak et al., 1988; Shelton et al., 1990), we claim that vertical ocular movements will activate different parts of the brain. According to this hypothesis, looking up will activate ventral parts of the brain, such as temporal lobes, whereas looking down will activate dorsal parts of the brain such as parietal lobes. More precisely, we postulated that looking to the upper left will facilitate visuospatial short-term memory by the activation of the right inferior temporal cortex (Rapcsak et al., 1988; Shelton et al., 1990). While these hypotheses are in line with the reported effects of gaze direction, they clearly need further neurophysiological testing.

We think that not taking into account vertical asymmetry was the reason why lateral eye movement investigations ceased. Interestingly, as mentioned before, most studies reviewed by Ehrlichman in his meta-analysis on lateral eye movement's literature (Ehrlichman & Weinberger, 1978) reported that participants were looking up while solving spatial problems (see, Ehrlichman, 1977; Ehrlichman, Weiner, & Baker, 1974; Galin & Ornstein, 1974; Kinsbourne, 1972). However, at that time, the model proposed by this literature was unable to explain why vertical saccades were observed. We postulated that some authors did not find the consistent and expected left versus right and upper versus lower advantages because of the validity of questions, the scoring method and the absence of answer control. As we observed in Experiments 10-12, over and above the task used, the strategies set up by participants play an important role. Depending on the strategy used, spontaneous eye movements can therefore be oriented in different directions. Also, as mentioned previously, eye movements may ease cognitive activities but they are not mandatory (Micic et al., 2010).

We can also compare our results to the NLP model which is the only model that makes predictions about eye movements in visual quadrants. As mentioned in the Introduction, Ahmad (2013) tested the entire model but was only able to find some evidence that people tended to look spontaneously to the upper left when involved in visual recall (Figure 10). It is interesting to notice that our results also supported the same assumption that looking to the upper left is a way to increase the retrieval of images from memory. It is more difficult to interpret the results from Experiment 15 in light of NLP theory because there are no specific assumptions for object-location binding.

Horizontal Asymmetries: Right Hemisphere Advantage for Global Processing

The finding of Experiments 10-14 was predicted and is in line with studies mentioned above showing that visual and positional memory tend to be located in the right hemisphere (Kessels et al., 2002). In these experiments, the participant had to remember different positions of the same "object" (i.e. a black square). These tasks do not need any fine discrimination of the displayed matrices but only memorization of simultaneous (visual memory) or consecutive (positional memory) positions. In other words, these tasks involve memory representations in which relations between objects are more important than the visual details of individual objects. As mentioned in the Introduction of Chapter 1, there is behavioral and

neuropsychological evidence that processing global aspects of visual stimuli is facilitated in the left visual field (right hemisphere) compared to the right visual field (left hemisphere) (Fouty et al., 1992; Metcalfe et al., 1995; Robertson & Lamb, 1991; Sergent, 1982). We claim that the matrix task in Experiments 10-14 also involved global visual processing to store spatial relations, which explains why performance was better when gaze was directed to the left and, consequently, the right hemisphere was activated. Furthermore, our finding can be related to that of Gable et al. (2013) who found that contraction of the left hand by activating the contralateral right hemisphere enhanced processing of global visual stimuli. We think that we were also able to increase right hemisphere activity using the gaze direction method and therefore enhance global processing of our stimuli.

In Experiment 15, we did not observe the expected right hemifield advantage consistent with Kessels's finding that deficit in object-location binding occurs after left hemisphere lesions. As mentioned before, we think that this lack of result is due to the fact that the stimuli that we used could not be named and therefore did not lead to a left hemisphere advantage. Further experiments should investigate whether different degrees of stimuli verbalizability could modulate horizontal asymmetry effect for object location binding as seems to be the case in the HERA model discussed earlier (Golby et al., 2001).

Vertical Asymmetries: Visual Exploration versus Sensory Processing

In Experiments 10-12, we did not observe any vertical asymmetry effect whereas we did find an advantage in the upper hemifield in Experiments 13-14. As mentioned previously, we think that we were not able to find the elevation effect on our first set of experiments because we did not control for the participants' strategies. It is more difficult to situate the effect of vertical gaze compared to horizontal gaze. Perhaps the advantage of upward gaze is consistent with Previc's idea that visual search or attention is better in the upper visual field. More attention is definitely beneficial in our paradigm, but it is difficult to reconcile better performance in the upper visual field with previous research on vertical hemifield asymmetries that have used vastly different tasks and obtained mixed results (Carrasco et al., 2001; Genzano, Di Nocera, & Ferlazzo, 2001; He et al., 1996; Rezec & Dobkins, 2004). More specifically, we can postulate that spatial attention is crucial in our task, and then our results are in line with Qu, Song, and Ding (2006) who found a greater P1 component (modulated by spatial selective attention) in the upper visual field. In the same vein, when comparing our results with those of

Niebauer and Christman (1998), one may conclude that the activation of cortical areas involved in categorical judgments of spatial relations improves performance in our task. Possibly, distance information was not as important as categorical relations (left of, right of, etc.) because the grid had only five rows and columns. If we had required our participants to judge distances more accurately, the advantage of upward gaze may have turned into an advantage of downward gaze. This specialization of the upper visual field on spatial processing and visual exploration is corroborated by recent neurophysiological findings mentioned above (Hafed & Chen, 2016; Mayo et al., 2015).

In contrast, we postulate that the lower visual field advantage found in Experiment 15 may be related to the superiority of this hemifield in sensory processing (Carrasco et al., 2001). Portin et al. (1999) confirmed a visual discrimination advantage for the lower field by showing differences in magneto-encephalographic (MEG) activation of occipital regions. Also, Qu et al. (2006) found that the early N1 component was larger in the lower visual field compared to the upper field over the occipito-parietal areas. This is consistent with the lower visual field being associated with the dorsal pathway (Fecteau et al., 2000) and with the anatomical specificity found at the retina and superior colliculus levels (Croner & Kaplan, 1995; Curcio & Allen, 1990; Hafed & Chen, 2016). As mentioned previously, the lower hemifield specialization in motion/sensory processing could be explained by the higher concentration of receptors and ganglion cells far from the fovea in the superior retina and the large receptive fields in the superior colliculus.

General Discussion and Conclusions

Two main sets of experiments were reported in the present work in which we investigated both horizontal and vertical asymmetries. In Chapter 1 we used a traditional unilateral presentation method in order to probe perceptual asymmetries of geometrical figures and faces. In Chapter 2, based on spontaneous eye movement and unilateral actions literature, we suggested using gaze direction as a new method to investigate brain asymmetries. We are aware of the numerous limits of the experiments reported in the present thesis work. We tried to manipulate and control as many variables as possible in order to investigate a relatively little-known field in scientific literature. Our purpose was above all to "pave the way" for future research in this field, which could then use what was found in these experiments.

Limitations

We think that the main limitation of our experiments is that eye movements were not monitored in a systematic way. As reported, in all our experiments, participants were given instructions on how to compute the task correctly by the experimenter. They were not allowed to begin the experimental protocol until they were capable of performing tasks without either moving their eyes (Chapter 1) or making saccades in specific locations (Chapter 2). During the whole duration of the experiment, the participants' eye movements were monitored and the experimenter could intervene if necessary. Most participants had no problems complying with instructions. However, particularly in the experiments detailed in Chapter 1 when we increased task demands, some participants reported that it was difficult to compute the task without any eye movements and we cannot rule out that some trials with eye movements were included in analyses, especially short saccades. To cope with this eventuality, in Experiments 1-9, RTs longer than 2.5 times the standard deviation of the respective condition mean were removed, but we are aware that it is not the best way to proceed. Further experiments should track the exact position of eyes on the screen for each trial with the help of an eye tracker. This method would allow researchers to give immediate feedback to participants when they fail to comply with the instructions and to discard subsequent trials that could distort results.

Another limitation that we want to mention is related to the position of the participant's head, which directly affects the position of their eyes in relation to the computer screen. In all of our experiments, the participant's head was held in place by a chin-rest set up in front of the lab computer. The chin-rest was pre-set so that participant's eyes were facing a fixation cross at the very center of the screen. Participants were instructed to place their forehead against the top of the chin-rest for the duration of the experiment. Again most of the participants were able to follow this instruction without difficulty. However, we noticed that, especially in long experiments, some participants tended to slightly move their head back from the chin-rest, which meant that their eyes were no longer facing the exact center of the screen. As previously, when the experimenter noticed this behavior, he intervened during a break between trials blocks. Again, monitoring eye movements with the eye-tracker may have been one solution to dissuade participants from moving their head.

One huge limitation of our present work concerns the gaze direction method that we used in the experiments reported in chapter 2. It is important to mention that the proposed method is new and that there is currently no research directly related to this method. We built up the gaze direction method based on knowledge of perceptual asymmetries investigated on peripheral vision or with the unilateral gaze method (Chapter 1), and based on literature mentioned in Chapter 2 on the impact of movements and more specifically eye movements on cognition. Our goal was to find a new method in order to investigate non-visual eye movements and their potential effects on cognition. We are aware that, in order to do so, we have made a lot of assumptions about how and why this method may improve cognitive processes. As mentioned before, non-visual eye movements have not aroused a great deal of interest in scientific literature and have been investigated in separate ways under different names (e.g., "random", "spontaneous", "unilateral" eye movements) and different theories. Therefore, there is much still to be learnt about this topic and many years of research will be needed before we might be able to get a full picture of this phenomenon.

Further Directions

Visual Asymmetry

We are currently investigating in more detail horizontal and vertical asymmetries for face processing using only gazes. As mentioned before, gaze processing is crucial in face perception and it is not clear to what extent it contributed to our previous findings. A potential limit in previous experiments was that eyes were not displayed equidistant from the center (but images of faces were). One could argue that they should be because eyes are the most important feature in face processing and our task required above all shifts of attention between the eye regions of faces while the rest of the face was completely irrelevant. Thus, in a series of experiments we wanted to know if we could replicate the reaction time advantage in the upper left quadrant with gaze presented in total isolation and equidistant from the central fixation cross. We jointly studied horizontal and vertical asymmetries by presenting gaze stimuli in each quadrant of the visual field. In the first experiment (Figure 16, A), only eye regions were displayed; we used rectangular cuts from face stimuli used previously. In the second experiment (Figure 16, B), we presented solely eyes, nose and eyebrows were concealed from the eye region. The upper visual field advantage was expected since object recognition is better in the upper visual field, reflecting stronger projections into the ventral stream. Concerning horizontal asymmetry, the left advantage for global processing was expected in the first experiment but not in the second experiment, when the eyes were displayed in complete isolation, because global processing in not needed anymore (Conty et al., 2006). Our preliminary findings suggest that, in both experiments, we were able to replicate our previous finding of an upper left visual field advantage. This result is surprising in particular we were not expecting left visual field advantage for eyes displayed alone. One possible explanation could be that the left hemifield advantage that we observed was caused by elevation, the upper left condition being significantly different from the other three. Instead of comparing quadrants, a control experiment (Figure 16, C) comparing only horizontal (left vs. right) and vertical position (upper vs. lower) may give us more information about the previous observed effects.

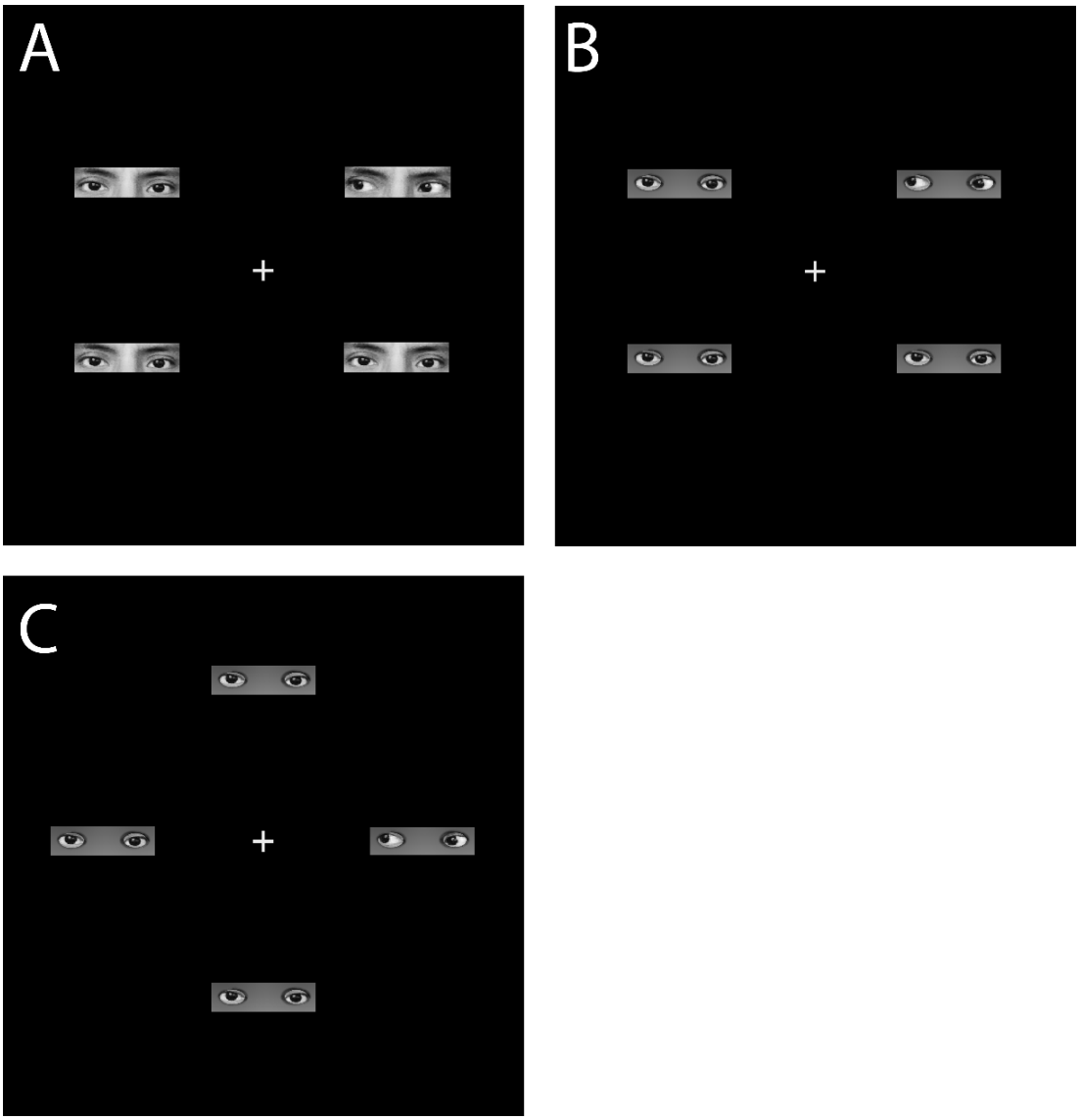

Figure 16. In panel A, four rectangular eye region faces are displayed, one in each quadrant of the subject's visual field, the singleton is on the upper right quadrant. In Panel B, same stimuli as previously but nose and eyebrows are concealed. In panel C, eyes alone are presented on horizontal and vertical axes. NB. For the original stimuli (protected database), the contrast between iris and sclera is less salient.

We are expecting to replicate the upper visual hemifield advantage but as in Conty et al. (2006), to lose the laterality effect. If so it will give us additional evidence suggesting that looking at a quadrant is more than just adding horizontal plus vertical expected simple effects. Again our findings suggest that the display of meaningful stimuli such as faces or gazes in the upper left position lead to a behavioral advantage, presumably because of the activation of the ventral stream of the right hemisphere where specialized modules of processing are located.

In Chapter 1, we investigated horizontal and vertical perceptual asymmetries. For vertical asymmetry, we found a lower visual field advantage for geometrical shapes and an upper visual field advantage for face processing. However, the difference between sensory processing (lower visual field) and object recognition (upper visual field) is not clear in literature. It would be interesting to investigate this difference in greater detail. One way to do so would be to use schematic faces. Schematic faces would be made up of different features; dots for eyes, a vertical line for the nose and horizontal lines for the mouth and eyebrows (Figure 17, A). The participant's task would be to determine the nose orientation of the singleton face which could be slightly tilted (45°) to the left or the right. As schematic faces should normally elicit the same processing as real faces (Maratos, Garner, Hogan, & Karl, 2015), we could predict an upper visual field advantage for object recognition/face perception even if these basic features are similar to the ones used in Experiments 1-6. This experiment would be a good way to test whether vertical asymmetry is material-specific or, as postulated by the literature, relies on object recognition regardless of the type of stimuli used. Furthermore, given that schematic faces should also be treated as global stimuli, a left advantage would also be postulated similarly to Experiments 7-9. Besides the proposed experiment, a control manipulation should present the same features in a scrambled way, in order to confirm that the potential effects observed do indeed rely on one prototypical configuration of features perceived as a face (Figure 17, B). In this experiment, similarly to our experiments on geometric shapes, we would anticipate a lower field advantage (visual discrimination) and a right hemifield advantage because local processing would be required. Finally, a third possible manipulation will be to present schematic faces upside down (Figure 17, C). As in Experiment 8, we would predict that the upper hemifield advantage for object recognition would remain but the left advantage for holistic processing should disappear.

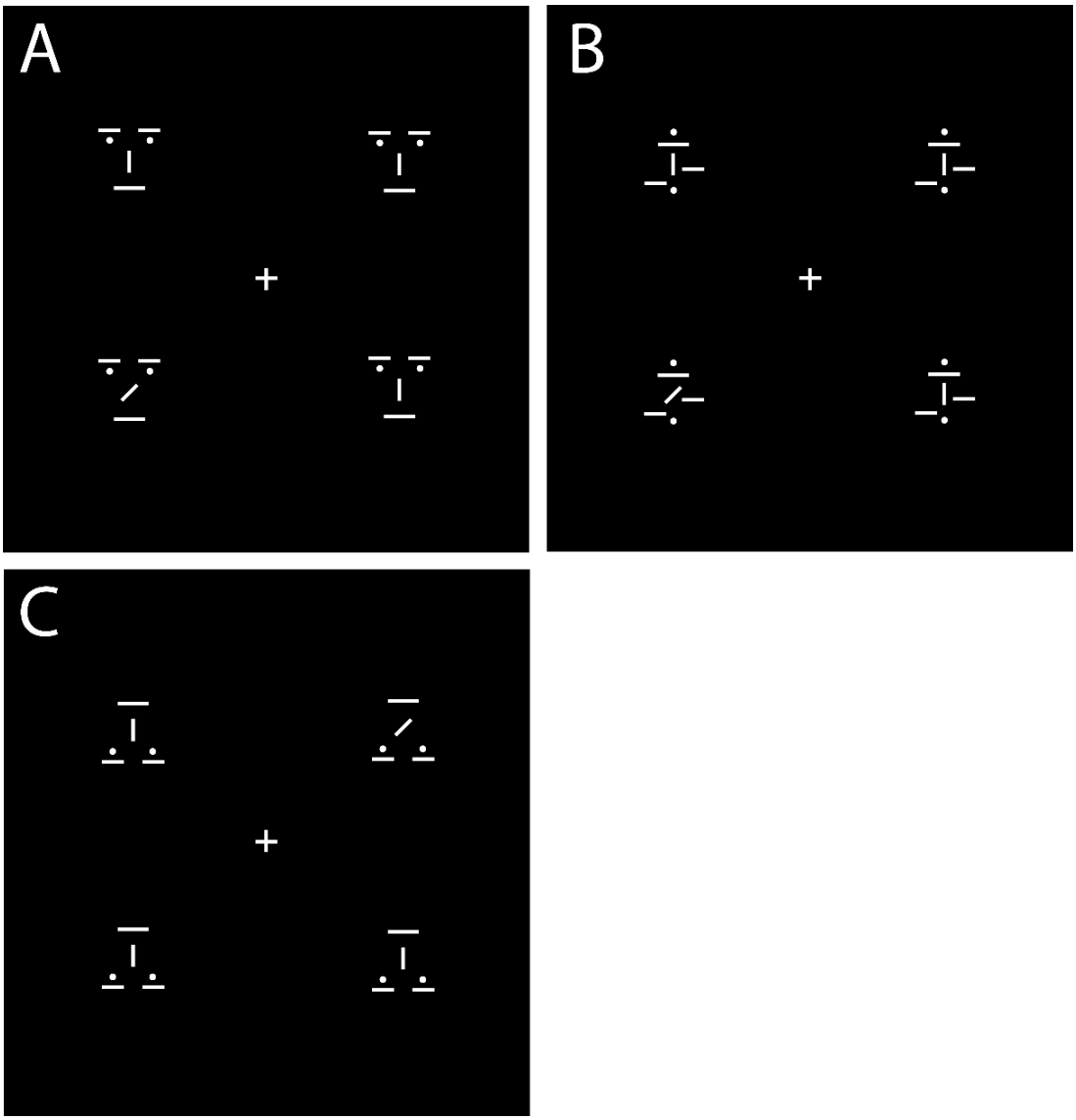

Figure 17. In panel A, four schematic faces are displayed, one in each quadrant of the subject's visual field, the singleton is on the lower left quadrant. In Panel B, the same features as previously but displayed in a scramble way. In panel C, schematic faces are presented upside down.

Our findings did not allow us to conclude about eventual asymmetries in the distribution of attention within our visual field depending on stimuli. One experiment that we are currently preparing will aim to investigate if one type of stimulus (face or geometrical form) causes a stronger attentional capture when displayed in one visual quadrant compared to the other three. Spatial attention capture will be measured by the evoked potential N2pc using electroencephalography (EGG). This electrophysiological component is measured based on the difference of activation between two posterior electrodes (PO7–PO8), one ipsilateral and one contralateral to the target (Eimer, 1996). Consistent with our behavioral results, we could anticipate a stronger N2pc in the upper left quadrant for faces and a stronger N2pc in the lower

right quadrant for visual forms. For sensory processing, previous findings using array items have found a larger N2pc in the lower versus the upper visual field (Luck, Girelli, McDermott, & Ford, 1997) but they only investigated horizontal asymmetries. To our knowledge, no studies have investigated attentional capture for face stimuli using N2pc. Interestingly, Quek and Finkbeiner (2015) manipulating endogenously oriented spatial attention suggested that spatial attention plays a role but is not sufficient to explain the specialization of upper visual field for face processing.

Movement and Cognition

Although it is well known that unilateral motor actions, such as hand clenching, activate contralateral posterior frontal lobe areas (i.e. motor cortex), it is not known whether such activity spreads beyond the precentral gyrus and what happens after motor activation. Relationships between motor actions, cognition, affect, and brain activity are still not clear and are a matter of debate. Two main models are currently competing in literature, a "persistent activity model" proposed by Harmon-Jones (2006) and a "reduced activity model" proposed by Cross-Villasana et al. (2015). The first proposed that unilateral hand clenching induce a contralateral hemisphere activation that will persist even after motor activation, facilitating subsequent behaviors relying on the functions of the involved hemisphere. On the contrary, the latter proposed that motor contraction did not lead to persistent activity in a given hemisphere but instead to a state of reduced cortical activity. Furthermore, this reduction of cortical activity prior to tasks could facilitate performance by facilitating task-specific cortical activation and preventing interference from other non-pertinent cortical regions. Further research is needed to investigate which model is more accurate and to determine the exact locations, timing, and through what mechanisms such movements can have an impact on cognition and emotion. We recently conducted our own EEG experiment in order to investigate this matter; EGG signals were recorded before, during and after hand clenching. We are currently analyzing the data.

Another interrogation raised by our findings is the potential impact of the duration of eye movements. For our findings reported in Chapter 2, the duration of the unilateral eye movement was not fixed. For the encoding phase, the duration of gaze direction depended on the trials and was more pronounced for hard trials given that the presentation time for matrices was 1s per filled square. Further studies should look at the impact of gaze direction duration on memory. Based on spontaneous eye movement literature (Ahmad, 2013; Kinsbourne, 1972;

Micic et al., 2010), we could argue that brief shifts of gaze are sufficient to ease cognition. However, based on unilateral motor activation/gaze literature (Harmon-Jones, 2006; Propper et al., 2012; Propper et al., 2013; Schiffer et al., 2004), we could argue that sustained gaze direction is the cause of the observed advantages. A really simple experiment to perform would be to manipulate the time of the sustained unilateral eye movement prior to the presentation of a stimulus to encode in one quadrant. The gaze duration (Figure 18, 1) could be really short (100 ms), moderate (10 seconds) or long (30 seconds). It would be followed by a fixed encoding phase of 5 seconds (Figure 18, 2) regardless of the difficulty of the trial. Finally, there would be a recall phase (Figure 18, 3) for an unlimited time, as in our previous experiments. If shift of gaze is necessary and sufficient to ease cognitive processes then we would not expect manipulation of matrices duration presentation to further impact the previously observed facilitation effect. On the contrary, if gaze duration has an impact then long periods of directional sustained eye movements prior to encoding should result in better recall performance compared to brief and moderate periods. As in Experiment 13, the phonological loop will be blocked in order to force participants to use a visual strategy.

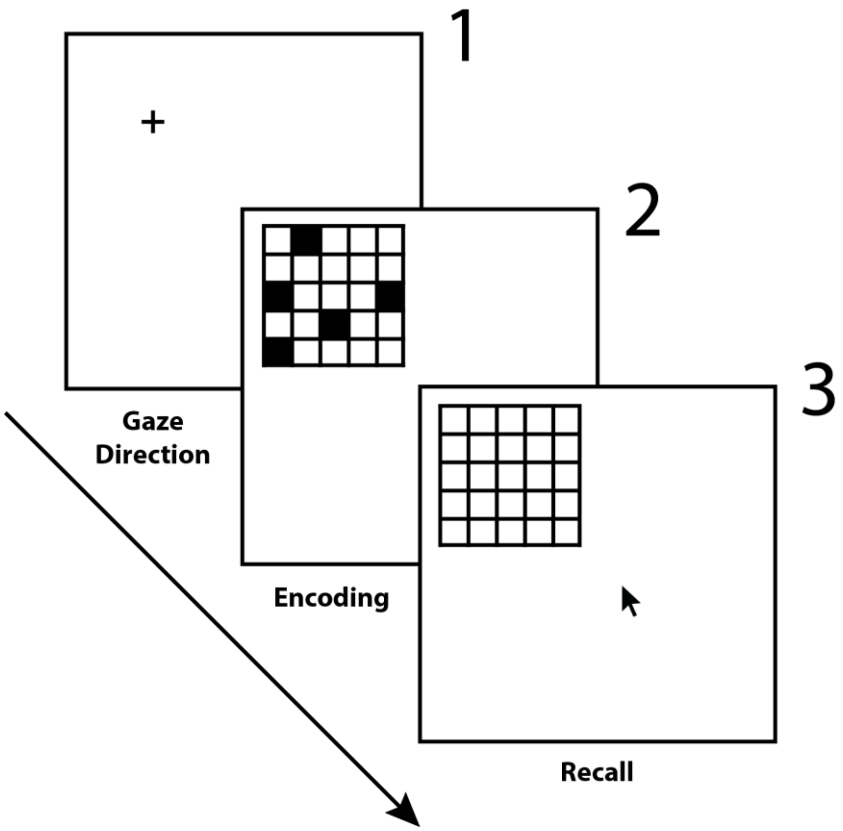

Figure 18. During Phase 1, the participant is invited to shift his gaze within one of the four visual quadrants of his visual field. The duration of this phase could be either brief (100 ms), moderate (10 seconds) or long (30 seconds). Then a visual matrix to encode is displayed within the same quadrant for 5 Second (Phase 2). In Phase 3, a blank matrix appears and the participant is asked to reproduce the encoded pattern in Phase 2 by mouse click.

Based on horizontal asymmetries, we postulated that right shifts of gaze would show an advantage for verbal processing. We have done extensive searches with words and digits as stimuli hoping to find a double dissociation for visuospatial versus verbal material. We used a large panel of decision tasks (lexical, gender, semantic) and memory tasks (free recall, recognition) but we were not able to probe horizontal asymmetry for verbal processing using the gaze direction method. Nevertheless our lack of results is in line with the mixed results obtained in lateral eye movement literature observing spontaneous eye movements for verbal questions (Ehrlichman & Weinberger, 1978; Macdonald & Hiscock, 1992; Raine, 1991). If people are not making spontaneous eye movements to the right when engaged in verbal processing, it seems logical that asking people to look to the right will not improve their performance for verbal processing. On the contrary, consistent with the only assumption of the NLP eye

movement model supported by recent research (Ahmad, 2013) and by early research on lateral eye movements (Ehrlichman, 1977; Ehrlichman et al., 1974; Galin & Ornstein, 1974; Kinsbourne, 1972), people tend to consistently move their eyes spontaneously toward the upper left position when asked visuospatial questions. Therefore, it seems coherent that asking them to look toward this position will ease performance even if we have not yet understand the neural mechanisms behind this. It is hard to explain why this facilitation effect occurs for visuospatial but not for verbal memory. Based on Ehrlichman's work mentioned above, we know that regardless of direction and in comparison with visuospatial questions, verbal questions, require extensive search which is associated with more saccades (on average 1.5-2 times more). Even if we know that gaze fixation does not hinder performance (Micic et al., 2010), we could postulate that forcing shift of gaze in one direction (the same for encoding and recall) is not an optimal method to facilitate verbal recall. Conversely, asking participants to perform saccades in many directions, as was the case in EMDR research with bilateral saccades (Christman et al., 2003), or increasing saccades rate prior to recall should be a better way to improve performance for verbal material.

It is interesting to mention once again that NLP makes specific assumptions on non-visual eye movements for verbal learning that have never been tested. A pedagogical tool called "cognitive learning" has been developed which is already in use in the educational field for learning vocabulary in some English private schools despite the complete lack of scientific research on this topic. New words are presented to children in the top left of their visual field (best mental image of the word) and then they are instructed to perform a visual saccade toward the bottom right ("in order to feel that the word has the correct spelling") (Thiry, 2006). No research has been able to confirm the role of the bottom right position in kinesthetic feeling (Ahmad, 2013; Buckner et al., 1987). However, it is interesting to think that perhaps not just one eye movement but a sequential pattern of eye movements will ease cognitive performance of certain cognitive tasks by facilitating the activation of several specific regions in the brain. For instance, we know that in EMDR bilateral saccades increased episodic memory, so will bilateral saccades occurring only in the upper versus lower hemifield have the same effect? What about diagonal saccades (e.g. upper left to bottom right)? Perhaps ocular saccades in the "cognitive learning" tool used by NLP are, in the end, very similar to those carried out in the EMDR protocol. Bilateral saccades regardless of the elevation meridian could be a way to improve verbal memory.

Just as we write these lines, a new explanation has emerged from literature concerning spontaneous eye movements. Martarelli, Mast, and Hartmann (2016) inspired by "blank screen paradigm" literature (Hartmann, Martarelli, Mast, & Stocker, 2014; Hartmann, Mast, & Fischer, 2015; Spivey & Geng, 2001) has proposed that gaze position could be a way to access spatial-temporal associations. The main finding of this research was that participants tend to shift their gaze more rightwards during future compared to past items during encoding, free recall and recognition. The assumption is that time will be mentally represented on an imaginary line, past associated with the left and future with the right side. It is interesting to note that, even if it is not mentioned in the paper, this new hypothesis is, in a manner of speaking, recycling old PNL assumptions (see Figure 10: The left side was associated with “remembered” whereas the right side was associated with “constructed” sensory representations). However the experimental paradigm is well-designed and goes beyond the NLP model of eye movements which focused on recall. We really hope that this recent research will revive interest on the topic of spontaneous eye movements.

Implications

More research is definitely needed before considering the practical implications of our work. However, considering these rather encouraging results, if unilateral actions do indeed alter brain activity in predictable ways then the scope is broad. Examination of the effects of simple, self-initiated body movements on brain activity may ultimately increase the likely utility of this procedure for practical benefits in applied settings to combat cognitive or impaired regulation of mood. Also, the induction of certain patterns of ocular movements could then be used in the pedagogical field in order to help children to learn new knowledge. In clinical neuropsychology this could be the basis of new rehabilitation techniques, or simply in everyday life as a personal improvement skill to improve one’s memory.

References

Ahmad, K. Z. (2013). Lying eyes: The truth about NLP eye patterns and their relationship with academic performance in business and management studies (MBA). *International Journal of Business and Management, 8*(23), 67-75. doi: 10.5539/ijbm.v8n23p67

Amadeo, M., & Shagass, C. (1963). Eye-movements, attention and hypnosis. *Journal of Nervous and Mental Disease, 136*(2), 139-145. doi: 10.1097/00005053-196302000-00004

Amenedo, E., Pazo-Alvarez, P., & Cadaveira, F. (2007). Vertical asymmetries in pre-attentive detection of changes in motion direction. *International Journal of Psychophysiology, 64*(2), 184-189. doi: 10.1016/j.ijpsycho.2007.02.001

Argyle, M., & Dean, J. (1965). Eye-contact, distance and affiliation. *Sociometry, 28*(3), 289-304. doi: 10.2307/2786027

Argyle, M., & Ingham, R. (1972). Gaze, mutual gaze, and proximity. *Semiotica, 6*(1), 32-49. doi: 10.1515/semi.1972.6.1.32

Argyle, M., Lalljee, M., & Cook, M. (1968). The effects of visibility on interaction in a dyad. *Human Relations, 21*(1), 3-17. doi: 10.1177/001872676802100101

Asanowicz, D., Smigasiewicz, K., & Verleger, R. (2013). Differences between visual hemifields in identifying rapidly presented target stimuli: letters and digits, faces, and shapes. *Frontiers in Psychology, 4*, 452. doi: 45210.3389/Fpsyg.2013.00452

Avidan, G., Tanzer, M., & Behrmann, M. (2011). Impaired holistic processing in congenital prosopagnosia. *Neuropsychologia, 49*(9), 2541-2552. doi: 10.1016/j.neuropsychologia.2011.05.002

Bacon, W. F., & Egeth, H. E. (1994). Overriding stimulus-driven attentional capture. *Perception and Psychophysics, 55*(5), 485-496. doi: 10.3758/Bf03205306

Bakan, P. (1969). Hypnotizability, laterality of eye-movements and functional brain asymmetry. *Perceptual and Motor Skills, 28*, 927-932. doi: 10.2466/pms.1969.28.3.927

Bandler, R., & Grinder, J. (1979). *Frogs into princes* (Vol. 15). Moab, UT: Real People Press.

Bandler, R., & Grinder, J. (1982). *Les secrets de la communication*. Montréal: Le jour.

Barcaro, U., Bonanni, E., Denoth, F., Murri, L., Navona, C., & Stefanini, A. (1989). A study of the interhemispheric correlation during sleep in elderly subjects. *Journal of Clinical Neurophysiology, 6*(2), 191-199. doi: 10.1097/00004691-198904000-00005

Barrowcliff, A. L., Gray, N. S., Freeman, T. C. A., & Macculloch, M. J. (2004). Eye-movements reduce the vividness, emotional valence and electrodermal arousal associated with negative autobiographical memories. *Journal of Forensic Psychiatry & Psychology, 15*(2), 325-345. doi: 10.1080/14789940410001673042

Bartolomeo, P., Thiebaut de Schotten, M., & Chica, A. B. (2012). Brain networks of visuospatial attention and their disruption in visual neglect. *Frontiers in Human Neuroscience, 6*, 110. doi: 10.3389/Fnhum.2012.00110

Baumer, T., Munchau, A., Weiller, C., & Liepert, J. (2002). Fatigue suppresses ipsilateral intracortical facilitation. *Experimental Brain Research, 146*(4), 467-473. doi: 10.1007/s00221-002-1202-x

Bavelas, J. B., Coates, L., & Johnson, T. (2002). Listener responses as a collaborative process: The role of gaze. *Journal of Communication, 52*(3), 566-580. doi: 10.1093/Joc/52.3.566

Beattie, G. W. (1978). Sequential temporal patterns of speech and gaze in dialogue. *Semiotica, 23*(1-2), 29-52. doi: 10.1515/semi.1978.23.1-2.29

Beattie, G. W. (1981). A further investigation of the cognitive interference hypothesis of gaze patterns during conversation. *British Journal of Social Psychology, 20*(4), 243-248. doi: 10.1111/j.2044-8309.1981.tb00493.x

Behrmann, M., Avidan, G., Marotta, J. J., & Kimchi, R. (2005). Detailed exploration of face-related processing in congenital prosopagnosia: 1. Behavioral findings. *Journal of Cognitive Neuroscience, 17*(7), 1130-1149. doi: 10.1162/0898929054475154

Belger, A., Puce, A., Krystal, J. H., Gore, J. C., Goldman-Rakic, P., & McCarthy, G. (1998). Dissociation of mnemonic and perceptual processes during spatial and nonspatial working memory using fMRI. *Human Brain Mapping, 6*(1), 14-32. doi: 10.1002/(SICI)1097-0193(1998)6:1<14::AID-HBM2>3.3.CO;2-2

Benaron, D. A., Hintz, S. R., Villringer, A., Boas, D., Kleinschmidt, A., Frahm, J., . . . Stevenson, D. K. (2000). Noninvasive functional imaging of human brain using light. *Journal of Cerebral Blood Flow and Metabolism, 20*(3), 469-477. doi: 10.1097/00004647-200003000-00005

Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience, 8*(6), 551-565. doi: 10.1162/jocn.1996.8.6.551

Benton, A., Hannay, J., & Varney, N. R. (1975). Visual-perception of line direction in patients with unilateral brain disease. *Neurology, 25*(10), 907-910. doi: 10.1212/WNL.25.10.907

Bergstrom, K. J., & Hiscock, M. (1988). Factors influencing ocular motility during the performance of cognitive tasks. *Canadian Journal of Psychology/Revue Canadienne De Psychologie, 42*(1), 1-23. doi: 10.1037/H0084174

Bilodeau, L., & Faubert, J. (1997). Isoluminance and chromatic motion perception throughout the visual field. *Vision Research, 37*(15), 2073-2081. doi: 10.1016/S0042-6989(97)00012-6

Binetti, N., Harrison, C., Coutrot, A., Johnston, A., & Mareschal, I. (2016). Pupil dilation as an index of preferred mutual gaze duration. *Open Science, 3*(7). doi: 10.1098/rsos.160086

Bisson, J. I., Ehlers, A., Matthews, R., Pilling, S., Richards, D., & Turner, S. (2007). Psychological treatments for chronic post-traumatic stress disorder - Systematic review and meta-analysis. *British Journal of Psychiatry, 190*, 97-104. doi: 10.1192/bjp.bp.106.021402

Bradley, R., Greene, J., Russ, E., Dutra, L., & Westen, D. (2005). A multidimensional meta-analysis of psychotherapy for PTSD. *American Journal of Psychiatry, 162*(2), 214-227. doi: 10.1176/appi.ajp.162.2.214

Bradshaw, J. L., & Gates, E. A. (1978). Visual-Field Differences in Verbal Tasks - Effects of Task Familiarity and Sex of Subject. *Brain and Language, 5*(2), 166-187. doi: 10.1016/0093-934x(78)90016-0

Bradshaw, J. L., & Sherlock, D. (1982). Bugs and faces in the 2 visual-fields - the analytic holistic processing dichotomy and task sequencing. *Cortex, 18*(2), 211-225. doi: 10.1016/S0010-9452(82)80004-X

Brasilneto, J., Pascualleone, A., Vallssole, J., Cammarota, A., Cohen, L. G., & Hallett, M. (1993). Postexercise depression of motor evoked-potentials - a measure of central-nervous-system fatigue. *Experimental Brain Research, 93*(1), 181-184. doi: 10.1007/BF00227794

Buckner, M., Meara, N. M., Reese, E. J., & Reese, M. (1987). Eye-movement as an indicator of sensory components in thought. *Journal of Counseling Psychology, 34*(3), 283-287. doi: 10.1037/0022-0167.34.3.283

Cabeza, R., Dolcos, F., Graham, R., & Nyberg, L. (2002). Similarities and differences in the neural correlates of episodic memory retrieval and working memory. *Neuroimage, 16*(2), 317-330. doi: 10.1006/nimg.2002.1063

Calder, A. J., Beaver, J. D., Winston, J. S., Dolan, R. J., Jenkins, R., Eger, E., & Henson, R. N. (2007). Separate coding of different gaze directions in the superior temporal sulcus and inferior parietal lobule. *Current Biology, 17*(1), 20-25. doi: 10.1016/j.cub.2006.10.052

Cameron, E. L., Tai, J. C., & Carrasco, M. (2002). Covert attention affects the psychometric function of contrast sensitivity. *Vision Research, 42*(8), 949-967. doi: 10.1016/S0042-6989(02)00039-1

Cameron, E. L., Tai, J. C., Eckstein, M. P., & Carrasco, M. (2004). Signal detection theory applied to three visual search tasks - identification, yes/no detection and localization. *Spatial Vision, 17*(4-5), 295-325. doi: 10.1163/1568568041920212

Carey, S., & Diamond, R. (1977). From piecemeal to configurational representation of faces. *Science, 195*(4275), 312-314. doi: 10.1126/science.831281

Carlei, C., & Kerzel, D. (2014). Gaze direction affects visuo-spatial short-term memory. *Brain and Cognition, 90C*, 63-68. doi: 10.1016/j.bandc.2014.06.007

Carlei, C., & Kerzel, D. (2015). The effect of gaze direction on the different components of visuo-spatial short-term memory. *Laterality: Asymmetries of Body, Brain and Cognition, 20*(6), 738-754. doi: 10.1080/1357650X.2015.1047380

Carrasco, M., Mclean, T. L., Katz, S. M., & Frieder, K. S. (1998). Feature asymmetries in visual search: Effects of display duration, target eccentricity, orientation and spatial frequency. *Vision Research, 38*(3), 347-374. doi: 10.1016/S0042-6989(97)00152-1

Carrasco, M., Talgar, C. P., & Cameron, E. L. (2001). Characterizing visual performance fields: effects of transient covert attention, spatial frequency, eccentricity, task and set size. *Spatial Vision, 15*(1), 61-75. doi: 10.1163/15685680152692015

Carrasco, M., Williams, P. E., & Yeshurun, Y. (2002). Covert attention increases spatial resolution with or without masks: Support for signal enhancement. *Journal of Vision, 2*(6). doi: 10.1167/2.6.4

Chambers, K. W., McBeath, M. K., Schiano, D. J., & Metz, E. G. (1999). Tops are more salient than bottoms. *Perception and Psychophysics, 61*(4), 625-635. doi: 10.3758/Bf03205535

Chan, A. W. Y., Kravitz, D. J., Truong, S., Arizpe, J., & Baker, C. I. (2010). Cortical representations of bodies and faces are strongest in commonly experienced configurations. *Nature Neuroscience, 13*(4), 417-418. doi: 10.1038/nn.2502

Christman, S. D., & Garvey, K. (2001). *Bilateral eye movements reduce asymmetries in hemispheric activation*. Paper presented at the EMDR International Association Conference, Austin, TX.

Christman, S. D., Garvey, K. J., Propper, R. E., & Phaneuf, K. A. (2003). Bilateral eye movements enhance the retrieval of episodic memories. *Neuropsychology, 17*(2), 221-229. doi: 10.1037/0894-4105.17.2.221

Christman, S. D., & Niebauer, C. L. (1997). The relation between left–right and upper–lower visual field differences. In S. Christman (Ed.), *Cerebral asymmetries in sensory and perceptual processing*. Amsterdam: Elsevier.

Christman, S. D., Propper, R. E., & Dion, A. (2004). Increased interhemispheric interaction is associated with decreased false memories in a verbal converging semantic associates paradigm. *Brain and Cognition, 56*(3), 313-319. doi: 10.1016/j.bandc.2004.08.005

Coan, J. A., & Allen, J. J. B. (2003). Frontal EEG asymmetry and the behavioral activation and inhibition systems. *Psychophysiology, 40*(1), 106-114. doi: 10.1111/1469-8986.00011

Coan, J. A., & Allen, J. J. B. (2004). Frontal EEG asymmetry as a moderator and mediator of emotion. *Biological Psychology, 67*(1-2), 7-49. doi: 10.1016/j.biopsycho.2004.03.002

Conty, L., Tijus, C., Hugueville, L., Coelho, E., & George, N. (2006). Searching for asymmetries in the detection of gaze contact versus averted gaze under different head views: A behavioural study. *Spatial Vision, 19*(6), 529-545. doi: 10.1163/156856806779194026

Cook, M. (1977). Gaze and mutual gaze in social encounters. *American Scientist, 65*(3), 328-333.

Corballis, M. C., Badzakova-Trajkov, G., & Haberling, I. S. (2012). Right hand, left brain: Genetic and evolutionary bases of cerebral asymmetries for language and manual action. *Wiley Interdisciplinary Reviews: Cognitive Science, 3*(1), 1-17. doi: 10.1002/wcs.158

Corballis, P. M., Funnell, M. G., & Gazzaniga, M. S. (2002). Hemispheric asymmetries for simple visual judgments in the split brain. *Neuropsychologia, 40*(4), 401-410. doi: 10.1016/S0028-3932(01)00100-2

Corbetta, M., Patel, G., & Shulman, G. L. (2008). The reorienting system of the human brain: From environment to theory of mind. *Neuron, 58*(3), 306-324. doi: 10.1016/j.neuron.2008.04.017

Croner, L. J., & Kaplan, E. (1995). Receptive-fields of P-ganglion and M-ganglion cells across the primate retina. *Vision Research, 35*(1), 7-24. doi: 10.1016/0042-6989(94)E0066-T

Cross-Villasana, F., Gropel, P., Doppelmayr, M., & Beckmann, J. (2015). Unilateral left-hand contractions produce widespread depression of cortical activity after their execution. *PloS One, 10*(12). doi: 10.1371/journal.pone.0145867

Crow, T. J., Close, J. P., Dagnall, A. M., & Priddle, T. H. (2009). Where and what is the right shift factor or cerebral dominance gene? A critique of Francks et al. (2007). *Laterality: Asymmetries of Body, Brain and Cognition, 14*(1), 3-10. doi: 10.1080/13576500802574984

Curcio, C. A., & Allen, K. A. (1990). Topography of ganglion-cells in human retina. *Journal of Comparative Neurology, 300*(1), 5-25. doi: 10.1002/cne.903000103

Danckert, J., & Goodale, M. A. (2001). Superior performance for visually guided pointing in the lower visual field. *Experimental Brain Research, 137*(3-4), 303-308. doi: 10.1007/s002210000653

Danckert, J., & Goodale, M. A. (2003). Ups and downs in the visual control of action. In S. H. Johnson-Frey (Ed.), *Taking action: Cognitive neuroscience perspectives on intentional acts* (pp. 29-64). Cambridge: MA: MIT Press.

Darling, S., Della Sala, S., & Logie, R. H. (2009). Dissociation between appearance and location within visuo-spatial working memory. *The Quarterly Journal of Experimental Psychology, 62*(3), 417-425. doi: 10.1080/17470210802321984

Darling, S., Martin, D., Hellmann, J. H., & Memon, A. (2009). Some witnesses are better than others. *Personality and Individual Differences, 47*(4), 369-373. doi: 10.1016/j.paid.2009.04.010

Davidson, P. R., & Parker, K. C. H. (2001). Eye movement desensitization and reprocessing (EMDR): A meta-analysis. *Journal of Consulting and Clinical Psychology, 69*(2), 305-316. doi: 10.1037//0022-006x.69.2.305

Davidson, R. J. (1998). Affective style and affective disorders: Perspectives from affective neuroscience. *Cognition & Emotion, 12*(3), 307-330. doi: 10.1080/026999398379628

Davidson, R. J., Saron, C. D., Senulis, J. A., Ekman, P., & Friesen, W. V. (1990). Approach withdrawal and cerebral asymmetry - emotional expression and brain physiology. *Journal of Personality and Social Psychology, 58*(2), 330-341. doi: 10.1037/0022-3514.58.2.330

Day, M. E. (1964). An eye-movement phenomenon relating to attention, thought and anxiety. *Perceptual and Motor Skills, 19*(2), 443-446. doi: 10.2466/pms.1964.19.2.443

De Renzi, E. (1986). Prosopagnosia in two patients with CT scan evidence of damage confined to the right hemisphere. *Neuropsychologia, 24*(3), 385-389. doi: 10.1016/0028-3932(86)90023-0

De Renzi, E., Perani, D., Carlesimo, G. A., Silveri, M. C., & Fazio, F. (1994). Prosopagnosia can be associated with damage confined to the right hemisphere - an MRI and PET study and a review of the literature. *Neuropsychologia, 32*(8), 893-902. doi: 10.1016/0028-3932(94)90041-8

Dimond, S. J., Bureš, J., Farrington, L. J., & Brouwers, E. Y. M. (1975). The use of contact lenses for the lateralisation of visual input in man. *Acta Psychologica, 39*(5), 341-349. doi: 10.1016/0001-6918(75)90026-8

Distel, H., & Fries, W. (1982). Contralateral cortical projections to the superior colliculus in the macaque monkey. *Experimental Brain Research, 48*(2), 157-162. doi: 10.1007/BF00237210

Doherty-Sneddon, G., Bruce, V., Bonner, L., Longbotham, S., & Doyle, C. (2002). Development of gaze aversion as disengagement from visual information. *Developmental Psychology, 38*(3), 438-445. doi: 10.1037//0012-1649.38.3.438

Doherty-Sneddon, G., & Phelps, F. G. (2005). Gaze aversion: A response to cognitive or social difficulty? *Memory and Cognition, 33*(4), 727-733. doi: 10.3758/Bf03195338

Doi, H., & Ueda, K. (2007). Searching for a perceived stare in the crowd. *Perception, 36*(5), 773-780. doi: 10.1068/p5614

Doi, H., Ueda, K., & Shinohara, K. (2009). Relational property between head and eye regions is the primary determinant of the efficiency in search for a deviant gaze. *The Quarterly Journal of Experimental Psychology, 62*(9), 1723-1737. doi: 10.1080/17470210802596825

Du, F., & Abrams, R. A. (2010). Endogenous orienting is reduced during the attentional blink. *Experimental Brain Research, 205*(1), 115-121. doi: 10.1007/s00221-010-2345-9

Duke, J. D. (1968). Lateral eye movement behavior. *Journal of General Psychology, 78*(2), 189-195. doi: 10.1080/00221309.1968.9710432

Dumermuth, G., & Lehmann, D. (1981). Eeg power and coherence during non-rem and rem phases in humans in all-night sleep analyses. *European Neurology, 20*(6), 429-434. doi: 10.1159/000115274

Dutton, G. N., Saaed, A., Fahad, B., Fraser, R., McDaid, G., McDade, J., . . . Spowart, K. (2004). Association of binocular lower visual field impairment, impaired simultaneous perception, disordered visually guided motion and inaccurate saccades in children with

cerebral visual dysfunction - a retrospective observational study. *Eye, 18*(1), 27-34. doi: 10.1038/sj.eye.6700541

Edwards, M., & Badcock, D. R. (1993). Asymmetries in the sensitivity to motion in-depth - a centripetal bias. *Perception, 22*(9), 1013-1023. doi: 10.1068/P221013

Ehrlichman, H. (1977). Field-dependence-independence and lateral eye-movements following verbal and spatial questions. *Perceptual and Motor Skills, 44*(3), 1229-1230. doi: 10.2466/pms.1977.44.3c.1229

Ehrlichman, H., & Barrett, J. (1983). 'Random' saccadic eye movements during verbal-linguistic and visual-imaginal tasks. *Acta Psychologica, 53*(1), 9-26. doi: 10.1016/0001-6918(83)90013-6

Ehrlichman, H., & Micic, D. (2012). Why do people move their eyes when they think? *Current Directions in Psychological Science, 21*(2), 96-100. doi: 10.1177/0963721412436810

Ehrlichman, H., Micic, D., Sousa, A., & Zhu, J. (2007). Looking for answers: eye movements in non-visual cognitive tasks. *Brain and Cognition, 64*(1), 7-20. doi: 10.1016/j.bandc.2006.10.001

Ehrlichman, H., & Weinberger, A. (1978). Lateral eye movements and hemispheric asymmetry: a critical review. *Psychological Bulletin, 85*(5), 1080-1101. doi: 10.1037/0033-2909.85.5.1080

Ehrlichman, H., Weiner, S. L., & Baker, A. H. (1974). Effects of verbal and spatial questions on initial gaze shifts. *Neuropsychologia, 12*(2), 265-277. doi: 10.1016/0028-3932(74)90012-8

Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity. *Electroencephalography and Clinical Neurophysiology, 99*(3), 225-234. doi: 10.1016/0013-4694(96)95711-9

Emery, N. J. (2000). The eyes have it: The neuroethology, function and evolution of social gaze. *Neuroscience and Biobehavioral Reviews, 24*(6), 581-604. doi: 10.1016/S0149-7634(00)00025-7

Evert, D. L., McGlinchey-Berroth, R., Verfaellie, M., & Milberg, W. P. (2003). Hemispheric asymmetries for selective attention apparent only with increased task demands in healthy participants. *Brain and Cognition, 53*(1), 34-41. doi: 10.1016/S0278-2626(03)00207-0

Exline, R. V., & Messick, D. (1967). The effects of dependency and social reinforcement upon visual behaviour during an interview. *British Journal of Social and Clinical Psychology, 6*(4), 256-266. doi: 10.1111/j.2044-8260.1967.tb00528.x

Farah, M. J., Tanaka, J. W., & Drain, H. M. (1995). What causes the face inversion effect? *Journal of Experimental Psychology: Human Perception and Performance, 21*(3), 628. doi: 10.1037/0096-1523.21.3.628

Fecteau, J. H., Enns, J. T., & Kingstone, A. (2000). Competition-induced visual field differences in search. *Psychological Science, 11*(5), 386-393. doi: 10.1111/1467-9280.00275

Felisberti, F. M., & McDermott, M. R. (2013). Spatial location in brief, free-viewing face encoding modulates contextual face recognition. *I-Perception, 4*(5), 352-360. doi: 10.1068/i0582

Feng, J., & Spence, I. (2014). Upper visual field advantage in localizing a target among distractors. *I-Perception, 5*(2), 97-100. doi: 10.1068/I0625rep

Fioretto, M., Gandolfo, E., Orione, C., Fatone, M., Rela, S., & Sannita, W. G. (1995). Automatic Perimetry and Visual P300 - Differences between Upper and Lower Visual-Fields Stimulation in Healthy-Subjects. *Journal of Medical Engineering and Technology, 19*(2-3), 80-83. doi: 10.3109/03091909509030280

Fouty, H. E., Otto, M. W., Yeo, R. A., & Briggs, C. R. (1992). A novel contact-lens system to assess visual hemispheric asymmetries. *Perceptual and Motor Skills, 74*(2), 567-575. doi: 10.2466/pms.1992.74.2.567

Freire, A., Lee, K., & Symons, L. A. (2000). The face-inversion effect as a deficit in the encoding of configural information: Direct evidence. *Perception, 29*(2), 159-170. doi: 10.1068/P3012

Gable, P. A., Poole, B. D., & Cook, M. S. (2013). Asymmetrical hemisphere activation enhances global-local processing. *Brain and Cognition, 83*(3), 337-341. doi: 10.1016/j.bandc.2013.09.012

Galin, D., & Ornstein, R. (1974). Individual differences in cognitive style-1. Reflective eye-movements. *Neuropsychologia, 12*(3), 367-376. doi: 10.1016/0028-3932(74)90052-9

Ganis, G., Kosslyn, S. M., Stose, S., Thompson, W. L., & Yurgelun-Todd, D. A. (2003). Neural correlates of different types of deception: An fMRI investigation. *Cerebral Cortex, 13*(8), 830-836. doi: 10.1093/cercor/13.8.830

Gauthier, I., Tarr, M. J., Moylan, J., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). The fusiform "face area" is part of a network that processes faces at the individual level. *Journal of Cognitive Neuroscience, 12*(3), 495-504. doi: 10.1162/089892900562165

Gazzaniga, M. S. (2000). Cerebral specialization and interhemispheric communication - Does the corpus callosum enable the human condition? *Brain, 123*(7), 1293-1326. doi: 10.1093/brain/123.7.1293

Genzano, V. R., Di Nocera, F., & Ferlazzo, F. (2001). Upper/lower visual field asymmetry on a spatial relocation memory task. *Neuroreport, 12*(6), 1227-1230. doi: 10.1097/00001756-200105080-00034

George, N., Driver, J., & Dolan, R. J. (2001). Seen gaze-direction modulates fusiform activity and its coupling with other brain areas during face processing. *Neuroimage, 13*(6), 1102-1112. doi: 10.1006/nimg.2001.0769

Godijn, R., & Theeuwes, J. (2002). Programming of endogenous and exogenous saccades: Evidence for a competitive integration model. *Journal of Experimental Psychology: Human Perception and Performance, 28*(5), 1039-1054. doi: 10.1037//0096-1523.28.5.1039

Golby, A. J., Poldrack, R. A., Brewer, J. B., Spencer, D., Desmond, J. E., Aron, A. P., & Gabrieli, J. D. E. (2001). Material-specific lateralization in the medial temporal lobe and prefrontal cortex during memory encoding. *Brain, 124*, 1841-1854. doi: 10.1093/brain/124.9.1841

Goldin-Meadow, S., & Alibali, M. W. (2013). Gesture's Role in Speaking, Learning, and Creating Language. *Annual Review of Psychology, 64*, 257-283. doi: 10.1146/annurev-psych-113011-143802

Goldman-Eisler, F. (1967). Sequential temporal patterns and cognitive processes in speech. *Language and Speech, 10*(2), 122-132. doi: 10.1177/002383096701000205

Goldstein, A., & Babkoff, H. (2001). A comparison of upper vs. lower and right vs. left visual fields using lexical decision. *The Quarterly Journal Of Experimental Psychology Section A, 54*(4), 1239-1259. doi: 10.1080/713756008

Goldstein, A., Revivo, K., Kreitler, M., & Metuki, N. (2010). Unilateral muscle contractions enhance creative thinking. *Psychonomic Bulletin & Review, 17*(6), 895-899. doi: 10.3758/Pbr.17.6.895

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences, 15*(1), 20-25. doi: 10.1016/0166-2236(92)90344-8

Gordon, J., Shapley, R., Patel, P., Pastagia, J., & Truong, C. (1997). The lower visual field is better than the upper visual field at red/green recognition. *Investigative Ophthalmology and Visual Science, 38*(4), 4199-4199.

Grabowska, A., Herman, A., Nowicka, A., Szatkowska, I., & Szelag, E. (1994). Individual-differences in the functional asymmetry of the human brain. *Acta Neurobiologiae Experimentalis, 54*(2), 155-162.

Greenberg, J. H., Reivich, M., Alavi, A., Hand, P., Rosenquist, A., Rintelmann, W., . . . Wolf, A. (1981). Metabolic mapping of functional activity in human subjects with the [18F] fluorodeoxyglucose technique. *Science, 212*(4495), 678-680. doi: 10.1126/science.6971492

Greene, D. J., & Zaidel, E. (2011). Hemispheric differences in attentional orienting by social cues. *Neuropsychologia, 49*(1), 61-68. doi: 10.1016/j.neuropsychologia.2010.11.007

Gross, M. M. (1972). Hemispheric specialization for processing of visually presented verbal and spatial stimuli. *Perception and Psychophysics, 12*(4), 357-363. doi: 10.3758/Bf03207222

Gunter, R. W., & Bodner, G. E. (2008). How eye movements affect unpleasant memories: Support for a working-memory account. *Behaviour Research and Therapy, 46*(8), 913-931. doi: 10.1016/j.brat.2008.04.006

Gur, R. E. (1975). Conjugate lateral eye-movements as an index of hemispheric activation. *Journal of Personality and Social Psychology, 31*(4), 751-757. doi: 10.1037/0022-3514.31.4.751

Habib, R., Nyberg, L., & Tulving, E. (2003). Hemispheric asymmetries of memory: The HERA model revisited. *Trends in Cognitive Sciences, 7*(6), 241-245. doi: 10.1016/S1364-6613(03)00110-4

Hafed, Z. M., & Chen, C. Y. (2016). Sharper, stronger, faster upper visual field representation in primate superior colliculus. *Current Biology, 26*(13), 1647-1658. doi: 10.1016/j.cub.2016.04.059

Hagenbeek, R. F., & Van Strien, J. W. (2002). Left-right and upper-lower visual field asymmetries for face matching, letter naming, and lexical decision. *Brain and Cognition, 49*(1), 34-44. doi: 10.1006/brcg.2001.1481

Hannay, H. J., & Malone, D. R. (1976). Visual-field effects and short-term-memory for verbal material. *Neuropsychologia, 14*(2), 203-209. doi: 10.1016/0028-3932(76)90049-X

Hansotia, P., Broste, S., So, E., Ruggles, K., Wall, R., & Friske, M. (1990). Eye-movement patterns in rem-sleep. *Electroencephalography and Clinical Neurophysiology, 76*(5), 388-399. doi: 10.1016/0013-4694(90)90093-Y

Harmon-Jones, E. (2006). Unilateral right-hand contractions cause contralateral alpha power suppression and approach motivational affective experience. *Psychophysiology, 43*(6), 598-603. doi: 10.1111/j.1469-8986.2006.00465.x

Harmon-Jones, E., Gable, P. A., & Peterson, C. K. (2010). The role of asymmetric frontal cortical activity in emotion-related phenomena: A review and update. *Biological Psychology, 84*(3), 451-462. doi: 10.1016/j.biopsycho.2009.08.010

Harmon-Jones, E., Peterson, C. K., & Harris, C. R. (2009). Jealousy: Novel methods and neural correlates. *Emotion, 9*(1), 113-117. doi: 10.1037/a0014117

Harmon-Jones, E., & Sigelman, J. (2001). State anger and prefrontal brain activity: Evidence that insult-related relative left-prefrontal activation is associated with experienced anger and aggression. *Journal of Personality and Social Psychology, 80*(5), 797-803. doi: 10.1037/0022-3514.80.5.797

Harmon-Jones, E., Sigelman, J., Bohlig, A., & Harmon-Jones, C. (2003). Anger, coping, and frontal cortical activity: The effect of coping potential on anger-induced left frontal activity. *Cognition & Emotion, 17*(1), 1-24. doi: 10.1080/02699930302278

Hartmann, M., Martarelli, C. S., Mast, F. W., & Stocker, K. (2014). Eye movements during mental time travel follow a diagonal line. *Consciousness and Cognition, 30*, 201-209. doi: 10.1016/j.concog.2014.09.007

Hartmann, M., Mast, F. W., & Fischer, M. H. (2015). Spatial biases during mental arithmetic: Evidence from eye movements on a blank screen. *Frontiers in Psychology, 6*, 12. doi: 10.3389/Fpsyg.2015.00012

Hauser, M. D., Chomsky, N., & Fitch, W. T. (2002). The faculty of language: What is it, who has it, and how did it evolve? *Science, 298*(5598), 1569-1579. doi: 10.1126/science.298.5598.1569

He, S., Cavanagh, P., & Intriligator, J. (1996). Attentional resolution and the locus of visual awareness. *Nature, 383*(6598), 334-337. doi: 10.1038/383334a0

Heilman, K. M., & Valenstein, E. (1979). Mechanisms underlying hemispatial neglect. *Annals of Neurology, 5*(2), 166-170. doi: 10.1002/ana.410050210

Herve, P. Y., Zago, L., Petit, L., Mazoyer, B., & Tzourio-Mazoyer, N. (2013). Revisiting human hemispheric specialization with neuroimaging. *Trends in Cognitive Sciences, 17*(2), 69-80. doi: 10.1016/j.tics.2012.12.004

Hillger, L. A., & Koenig, O. (1991). Separable mechanisms in face processing - evidence from hemispheric-specialization. *Journal of Cognitive Neuroscience, 3*(1), 42-58. doi: 10.1162/jocn.1991.3.1.42

Hiscock, M., & Bergstrom, K. J. (1981). Ocular motility as an indicator of

verbal and visuospatial processing. *Memory and Cognition, 9*(3), 332-338. doi: 10.3758/Bf03196967

Iturria-Medina, Y., Fernandez, A. P., Morris, D. M., Canales-Rodriguez, E. J., Haroon, H. A., Penton, L. G., . . . Melie-Garcia, L. (2011). Brain hemispheric structural efficiency and interconnectivity rightward asymmetry in human and nonhuman primates. *Cerebral Cortex, 21*(1), 56-67. doi: 10.1093/cercor/bhq058

Jensen-Campbell, L. A., Knack, J. M., Waldrip, A. M., & Campbell, S. D. (2007). Do Big Five personality traits associated with self-control influence the regulation of anger and aggression? *Journal of Research in Personality, 41*(2), 403-424. doi: 10.1016/j.jrp.2006.05.001

Jokisch, D., & Jensen, O. (2007). Modulation of gamma and alpha activity during a working memory task engaging the dorsal or ventral stream. *Journal of Neuroscience, 27*(12), 3244-3251. doi: 10.1523/Jneurosci.5399-06.2007

Jones, N. A., & Fox, N. A. (1992). Electroencephalogram asymmetry during emotionally evocative films and its relation to positive and negative affectivity. *Brain and Cognition, 20*(2), 280-299. doi: 10.1016/0278-2626(92)90021-D

Jonides, J., Smith, E. E., Koeppe, R. A., Awh, E., Minoshima, S., & Mintun, M. A. (1993). Spatial working-memory in humans as revealed by PET. *Nature, 363*(6430), 623-625. doi: 10.1038/363623a0

Jordan, T. R., & Patching, G. R. (2004). What do lateralized displays tell us about visual word perception? A cautionary indication from the word-letter effect. *Neuropsychologia, 42*(11), 1504-1514. doi: 10.1016/j.neuropsychologia.2004.03.010

Jordan, T. R., Patching, G. R., & Thomas, S. M. (2003). Assessing the role of hemispheric specialisation, serial-position processing, and retinal eccentricity in lateralised word

recognition. *Cognitive Neuropsychology, 20*(1), 49-71. doi: 10.1080/02643290244000185

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience, 17*(11), 4302-4311.

Kelley, W. M., Miezin, F. M., McDermott, K. B., Buckner, R. L., Raichle, M. E., Cohen, N. J., . . . Petersen, S. E. (1998). Hemispheric specialization in human dorsal frontal cortex and medial temporal lobe for verbal and nonverbal memory encoding. *Neuron, 20*(5), 927-936. doi: 10.1016/S0896-6273(00)80474-2

Kendon, A. (1967). Some functions of gaze-direction in social interaction. *Acta Psychologica, 26*(1), 22-63. doi: 10.1016/0001-6918(67)90005-4

Kendon, A., & Cook, M. (1969). The consistency of gaze patterns in social interaction. *British Journal of Psychology, 60*(4), 481-494. doi: 10.1111/j.2044-8295.1969.tb01222.x

Kessels, R. P. C., Kappelle, L. J., de Haan, E. H. F., & Postma, A. (2002). Lateralization of spatial-memory processes: evidence on spatial span, maze learning, and memory for object locations. *Neuropsychologia, 40*(8), 1465-1473. doi: 10.1016/S0028-3932(01)00199-3

Kessler, K., & Tipper, S. P. (2004). Retrieval of implicit inhibitory processes: The impact of visual field, object-identity, and memory dynamics. *Visual Cognition, 11*(8), 965-995. doi: 10.1080/13506280444000012

Khan, M. A., & Lawrence, G. P. (2005). Differences in visuomotor control between the upper and lower visual fields. *Experimental Brain Research, 164*(3), 395-398. doi: 10.1007/s00221-005-2325-7

Kinsbourne, M. (1972). Eye and head turning indicates cerebral lateralization. *Science, 176*(4034), 539-541. doi: 10.1126/science.176.4034.539

Kirchhoff, B. A., Wagner, A. D., Maril, A., & Stern, C. E. (2000). Prefrontal-temporal circuitry for episodic encoding and subsequent memory. *Journal of Neuroscience, 20*(16), 6173-6180.

Kitterle, F. L., Christman, S., & Hellige, J. B. (1990). Hemispheric-differences are found in the identification, but not the detection, of low versus high spatial-frequencies. *Perception and Psychophysics, 48*(4), 297-306. doi: 10.3758/Bf03206680

Kocel, K., Galin, D., Ornstein, R., & Merrin, E. L. (1972). Lateral eye movement and cognitive mode. *Psychonomic Science, 27*(4), 223-224. doi: 10.3758/BF03328944

Kremlacek, J., Kuba, M., Chlubnova, J., & Kubova, Z. (2004). Effect of stimulus localisation on motion-onset VEP. *Vision Research, 44*(26), 2989-3000. doi: 10.1016/j.visres.2004.07.002

Krigolson, O., & Heath, M. (2006). A lower visual field advantage for endpoint stability but no advantage for online movement precision. *Experimental Brain Research, 170*(1), 127-135. doi: 10.1007/s00221-006-0386-x

Kuiken, D., Chudleigh, M., & Racher, D. (2010). Bilateral eye movements, attentional flexibility and metaphor comprehension: The substrate of REM dreaming? *Dreaming, 20*(4), 227-247. doi: 10.1037/a0020841

Laeng, B., Overvoll, M., & Steinsvik, O. O. (2007). Remembering 1500 pictures: The right hemisphere remembers better than the left. *Brain and Cognition, 63*(2), 136-144. doi: 10.1016/j.bandc.2006.10.009

Lakha, L., & Humphreys, G. (2005). Lower visual field advantage for motion segmentation during high competition for selection. *Spatial Vision, 18*(4), 447-460. doi: 10.1163/1568568054389570

Lamb, M. R., Robertson, L. C., & Knight, R. T. (1990). Component mechanisms underlying the processing of hierarchically organized patterns - inferences from patients with unilateral cortical-lesions. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 16*(3), 471-483. doi: 10.1037/0278-7393.16.3.471

Land, M. F., & Tatler, B. W. (2009). *Looking and acting: Vision and eye movements in natural behaviour*. Oxford, UK: Oxford University Press.

Lecerf, T., & de Ribaupierre, A. (2005). Recognition in a visuospatial memory task: The effect of presentation. *European Journal of Cognitive Psychology, 17*(1), 47-75. doi: 10.1080/09541440340000420

Lee, B., Kaneoke, Y., Kakigi, R., & Sakai, Y. (2009). Human brain response to visual stimulus between lower/upper visual fields and cerebral hemispheres. *International Journal of Psychophysiology, 74*(2), 81-87. doi: 10.1016/j.ijpsycho.2009.07.005

Lee, C. W., & Cuijpers, P. (2013). A meta-analysis of the contribution of eye movements in processing emotional memories. *Journal of Behavior Therapy and Experimental Psychiatry, 44*(2), 231-239. doi: 10.1016/j.jbtep.2012.11.001

Levick, S. E., Wexler, B. E., Lorig, T., Gur, R. E., Gur, R. C., & Schwartz, G. E. (1993). Asymmetrical visual deprivation - a technique to differentially influence lateral hemispheric function. *Perceptual and Motor Skills, 76*(3), 1363-1382. doi: 10.2466/pms.1993.76.3c.1363

Levine, M. W., & McAnany, J. J. (2005). The relative capabilities of the upper and lower visual hemifields. *Vision Research, 45*(21), 2820-2830. doi: 10.1016/j.visres.2005.04.001

Logie, R. H. (2003). Spatial and visual working memory: A mental workspace. In D. E. Irwin & B. H. Ross (Eds.), *Psychology of Learning and Motivation : Vol. 42. Cognitive vision* (pp. 37-78). New York: Academic Press.

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*(1), 64-87. doi: 10.1006/cogp.1997.0660

Lyle, K. B., Hanaver-Torrez, S. D., Hacklander, R. P., & Edlin, J. M. (2012). Consistency of handedness, regardless of direction, predicts baseline memory accuracy and potential for memory enhancement. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 38*(1), 187-193. doi: 10.1037/A0024831

Lyle, K. B., Logan, J. M., & Roediger, H. L. (2008). Eye movements enhance memory for individuals who are strongly right-handed and harm it for individuals who are not. *Psychonomic Bulletin & Review, 15*(3), 515-520. doi: 10.3758/Pbr.15.3.515

Lynch, J. C. (1980). The functional-organization of posterior parietal association cortex. *Behavioral and Brain Sciences, 3*(4), 485-499. doi: 10.1017/S0140525X00006324

Macaluso, E., Driver, J., & Frith, C. D. (2003). Multimodal spatial representations engaged in human parietal cortex during both saccadic and manual spatial orienting. *Current Biology, 13*(12), 990-999. doi: 10.1016/S0960-9822(03)00377-4

Macdonald, B. H., & Hiscock, M. (1992). Direction of lateral eye-movements as an index of cognitive mode and emotion - a reappraisal. *Neuropsychologia, 30*(8), 753-755. doi: 10.1016/0028-3932(92)90044-M

Mann, S., Vrij, A., Nasholm, E., Warmelink, L., Leal, S., & Forrester, D. (2012). The direction of deception: Neuro-linguistic programming as a lie detection tool. *Journal of Police and Criminal Psychology, 27*(2), 160-166. doi: 10.1007/s11896-011-9097-8

Maratos, F. A., Garner, M., Hogan, A. M., & Karl, A. (2015). When is a face a face? Schematic faces, emotion, attention and the N170. *AIMS Neuroscience, 2*(3), 172-182. doi: 10.3934/Neuroscience.2015.3.172

Martarelli, C. S., Mast, F. W., & Hartmann, M. (2016). Time in the eye of the beholder: Gaze position reveals spatial-temporal associations during encoding and memory retrieval of future and past. *Memory and Cognition*. doi: 10.3758/s13421-016-0639-2

Martinez, A., Moses, P., Frank, L., Buxton, R., Wong, E., & Stiles, J. (1997). Hemispheric asymmetries in global and local processing: Evidence from fMRI. *Neuroreport, 8*(7), 1685-1689. doi: 10.1097/00001756-199705060-00025

Mayo, J. P., DiTomasso, A. R., Sommer, M. A., & Smith, M. A. (2015). Dynamics of visual receptive fields in the macaque frontal eye field. *Journal of Neurophysiology, 114*(6), 3201-3210. doi: 10.1152/jn.00746.2015

McCarthy, G., Puce, A., Gore, J. C., & Allison, T. (1997). Face-specific processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience, 9*(5), 605-610. doi: 10.1162/jocn.1997.9.5.605

McDermott, K. B., Buckner, R. L., Petersen, S. E., Kelley, W. M., & Sanders, A. L. (1999). Set- and code-specific activation in the frontal cortex: An fMRI study of encoding and retrieval of faces and words. *Journal of Cognitive Neuroscience, 11*(6), 631-640. doi: 10.1162/089892999563698

McNally, R. J. (1999). EMDR and mesmerism: A comparative historical analysis. *Journal of Anxiety Disorders, 13*(1-2), 225-236. doi: 10.1016/S0887-6185(98)00049-8

Metcalfe, J., Funnell, M., & Gazzaniga, M. S. (1995). Right-hemisphere memory superiority - studies of a split-brain patient. *Psychological Science, 6*(3), 157-164. doi: 10.1111/j.1467-9280.1995.tb00325.x

Meunier, H., Vauclair, J., & Fagard, J. (2012). Human infants and baboons show the same pattern of handedness for a communicative gesture. *PloS One, 7*(3). doi: 10.1371/journal.pone.0033959

Michael, G. A., & Ojeda, N. (2005). Visual field asymmetries in selective attention: Evidence from a modified search paradigm. *Neuroscience Letters, 388*(2), 65-70. doi: 10.1016/j.neulet.2005.06.027

Micic, D., Ehrlichman, H., & Chen, R. (2010). Why do we move our eyes while trying to remember? The relationship between non-visual gaze patterns and memory. *Brain and Cognition, 74*(3), 210-224. doi: 10.1016/j.bandc.2010.07.014

Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. New York: Oxford University Press.

Morgan, A. H., Mcdonald, P. J., & Macdonal, H. (1971). Differences in bilateral alpha activity as a function of experimental task, with a note on lateral eye movements and hypnotizability. *Neuropsychologia, 9*(4), 459-469. doi: 10.1016/0028-3932(71)90011-X

Munoz, D. P. (2002). Commentary: Saccadic eye movements: overview of neural circuitry. *Progress in Brain Research, 140*, 89-96. doi: 10.1016/S0079-6123(02)40044-1

Munoz, D. P., & Everling, S. (2004). Look away: The anti-saccade task and the voluntary control of eye movement. *Nature Reviews Neuroscience, 5*(3), 218-228. doi: 10.1038/nrn1345

Navon, D. (1977). Forest before trees - precedence of global features in visual perception. *Cognitive Psychology, 9*(3), 353-383. doi: 10.1016/0010-0285(77)90012-3

Niebauer, C. L., & Christman, S. D. (1998). Upper and lower visual field differences in categorical and coordinate judgments. *Psychonomic Bulletin & Review, 5*(1), 147-151. doi: 10.3758/Bf03209471

Nieuwenhuis, S., Elzinga, B. M., Ras, P. H., Berends, F., Duijs, P., Samara, Z., & Slagter, H. A. (2013). Bilateral saccadic eye movements and tactile stimulation, but not auditory stimulation, enhance memory retrieval. *Brain and Cognition, 81*(1), 52-56. doi: 10.1016/j.bandc.2012.10.003

Nyberg, L., Cabeza, R., & Tulving, E. (1996). PET studies of encoding and retrieval: The HERA model. *Psychonomic Bulletin & Review, 3*(2), 135-148. doi: 10.3758/Bf03212412

Nyberg, L., Persson, J., Habib, R., Tulving, E., McIntosh, A. R., Cabeza, R., & Houle, S. (2000). Large scale neurocognitive networks underlying episodic memory. *Journal of Cognitive Neuroscience, 12*(1), 163-173. doi: 10.1162/089892900561805

Ocklenburg, S., & Güntürkün, O. (2012). Hemispheric asymmetries: The comparative view. *Frontiers in Psychology, 3*, 5. doi: 10.3389/fpsyg.2012.00005

Oldfield, R. C. (1971). The assessment and analysis of handedness: The edinburgh inventory. *Neuropsychologia, 9*(1), 97-113. doi: 10.1016/0028-3932(71)90067-4

Ottes, F. P., Vangisbergen, J. A. M., & Eggermont, J. J. (1986). Visuomotor fields of the superior colliculus - a quantitative model. *Vision Research, 26*(6), 857-873. doi: 10.1016/0042-6989(86)90144-6

Palanica, A., & Itier, R. J. (2011). Searching for a perceived gaze direction using eye tracking. *Journal of Vision, 11*(2). doi: 10.1167/11.2.19

Parker, A., Buckley, S., & Dagnall, N. (2009). Reduced misinformation effects following saccadic bilateral eye movements. *Brain and Cognition, 69*(1), 89-97. doi: 10.1016/j.bandc.2008.05.009

Pelizzon, L., Brandimonte, M. A., & Favretto, A. (1999). Imagery and recognition: Dissociable measures of memory? *European Journal of Cognitive Psychology, 11*(3), 429-443. doi: 10.1080/713752323

Perkins, B. R., & Rouanzoin, C. C. (2002). A critical evaluation of current views regarding eye movement desensitization and reprocessing (EMDR): Clarifying points of confusion. *Journal of Clinical Psychology, 58*(1), 77-97. doi: 10.1002/jclp.1130

Peterson, C. K., Shackman, A. J., & Harmon-Jones, E. (2008). The role of asymmetrical frontal cortical activity in aggression. *Psychophysiology, 45*(1), 86-92. doi: 10.1111/j.1469-8986.2007.00597.x

Petit, L., Clark, V. P., Ingeholm, J., & Haxby, J. V. (1997). Dissociation of saccade-related and pursuit-related activation in human frontal eye fields as revealed by fMRI. *Journal of Neurophysiology, 77*(6), 3386-3390.

Pickering, S. J., Gathercole, S. E., Hall, M., & Lloyd, S. A. (2001). Development of memory for pattern and path: Further evidence for the fractionation of visuo-spatial memory. *The Quarterly Journal Of Experimental Psychology Section A, 54*(2), 397-420. doi: 10.1080/02724980042000174

Pierrot-Deseilligny, C., Muri, R. M., Nyffeler, T., & Milea, D. (2005). The role of the human dorsolateral prefrontal cortex in ocular motor behavior. *Annals of the New York Academy of Sciences, 1039*, 239-251. doi: 10.1196/annals.1325.023

Pitman, R. K., Orr, S. P., Altman, B., Longpre, R. E., Poire, R. E., & Macklin, M. L. (1996). Emotional processing during eye movement desensitization and reprocessing therapy of Vietnam veterans with chronic posttraumatic stress disorder. *Comprehensive Psychiatry, 37*(6), 419-429. doi: 10.1016/S0010-440x(96)90025-5

Polich, J. (1984). Hemispheric patterns in visual-search. *Brain and Cognition, 3*(2), 128-139. doi: 10.1016/0278-2626(84)90012-5

Polich, J., DeFrancesco, D. P., Garon, J. F., & Cohen, W. (1990). Hemispheric differences in visual search of simple line arrays. *Psychological Research, 52*(1), 54-61. doi: 10.1007/BF00867212

Portin, K., Vanni, S., Virsu, V., & Hari, R. (1999). Stronger occipital cortical activation to lower than upper visual field stimuli - neuromagnetic recordings. *Experimental Brain Research, 124*(3), 287-294. doi: 10.1007/s002210050625

Posner, M. I., Walker, J. A., Friedrich, F. J., & Rafal, R. D. (1984). Effects of parietal injury on covert orienting of attention. *Journal of Neuroscience, 4*(7), 1863-1874.

Poynter, W., & Roberts, C. (2012). Hemispheric asymmetries in visual search. *Laterality: Asymmetries of Body, Brain and Cognition, 17*(6), 711-726. doi: 10.1080/1357650x.2011.626558

Previc, F. H. (1990). Functional specialization in the lower and upper visual-fields in humans - its ecological origins and neurophysiological implications. *Behavioral and Brain Sciences, 13*(3), 519-541. doi: 10.1017/S0140525X00080018

Previc, F. H., & Naegele, P. D. (2001). Target-tilt and vertical-hemifield asymmetries in free-scan search for 3-D targets. *Perception and Psychophysics, 63*(3), 445-457. doi: 10.3758/BF03194411

Propper, R. E., Brunyé, T. T., Christman, S. D., & Januszewskia, A. (2012). Look over there! Unilateral gaze increases geographical memory of the 50 United States. *Brain and Cognition, 78*(1), 59-62. doi: 10.1016/j.bandc.2011.10.002

Propper, R. E., McGraw, S. E., Brunye, T. T., & Weiss, M. (2013). Getting a grip on memory: Unilateral hand clenching alters episodic recall. *PloS One, 8*(4), e62474. doi: 10.1371/journal.pone.0062474

Propper, R. E., Pierce, J., Geisler, M. W., Christman, S. D., & Bellorado, N. (2007). Effect of bilateral eye movements on frontal interhemispheric gamma EEG coherence: Implications for EMDR therapy. *The Journal of Nervous and Mental Disease, 195*(9), 785-788. doi: 10.1097/NMD.0b013e318142cf73

Puce, A., Allison, T., Bentin, S., Gore, J. C., & McCarthy, G. (1998). Temporal cortex activation in humans viewing eye and mouth movements. *Journal of Neuroscience, 18*(6), 2188-2199.

Qu, Z., Song, Y., & Ding, Y. L. (2006). Asymmetry between the upper and lower visual fields: An event-related potential study. *Chinese Science Bulletin, 51*(5), 536-541. doi: 10.1007/s11434-006-0536-3

Quek, G. L., & Finkbeiner, M. (2014a). Face-sex categorization is better above fixation than below: Evidence from the reach-to-touch paradigm. *Cognitive Affective & Behavioral Neuroscience, 14*(4), 1407-1419. doi: 10.3758/s13415-014-0282-y

Quek, G. L., & Finkbeiner, M. (2014b). Gaining the upper hand: Evidence of vertical asymmetry in sex-categorisation of human hands. *Advances in Cognitive Psychology, 10*(4), 131-143. doi: 10.5709/acp-0164-8

Quek, G. L., & Finkbeiner, M. (2015). The upper-hemifield advantage for masked face processing: Not just an attentional bias. *Attention, Perception, & Psychophysics, 78*(1), 52-68. doi: 10.3758/s13414-015-0965-7

Raine, A. (1991). Are lateral eye-movements a valid index of functional hemispheric asymmetries? *British Journal of Psychology, 82 (Pt 2)*, 129-135. doi: 10.1111/j.2044-8295.1991.tb02388.x

Rapcsak, S. Z., Cimino, C. R., & Heilman, K. M. (1988). Altitudinal neglect. *Neurology, 38*(2), 277-281. doi: 10.1212/WNL.38.2.277

Raymond, J. E. (1994). Directional anisotropy of motion sensitivity across the visual-field. *Vision Research, 34*(8), 1029-1037. doi: 10.1016/0042-6989(94)90007-8

Renfrey, G., & Spates, C. R. (1994). Eye-movement desensitization - a partial dismantling study. *Journal of Behavior Therapy and Experimental Psychiatry, 25*(3), 231-239. doi: 10.1016/0005-7916(94)90023-X

Rezec, A. A., & Dobkins, K. R. (2004). Attentional weighting: A possible account of visual field asymmetries in visual search? *Spatial Vision, 17*(4-5), 269-293. doi: 10.1163/1568568041920203

Ricciardelli, P., Ro, T., & Driver, J. (2002). A left visual field advantage in perception of gaze direction. *Neuropsychologia, 40*(7), 769-777. doi: 10.1016/S0028-3932(01)00190-7

Richler, J. J., Cheung, O. S., & Gauthier, I. (2011). Holistic processing predicts face recognition. *Psychological Science, 22*(4), 464-471. doi: 10.1177/0956797611401753

Robertson, L. C., & Lamb, M. R. (1991). Neuropsychological contributions to theories of part whole organization. *Cognitive Psychology, 23*(2), 299-330. doi: 10.1016/0010-0285(91)90012-D

Rogers, S., & Silver, S. M. (2002). Is EMDR an exposure therapy? A review of trauma protocols. *Journal of Clinical Psychology, 58*(1), 43-59. doi: 10.1002/jclp.1128

Ross, R. J., Ball, W. A., Dinges, D. F., Kribbs, N. B., Morrison, A. R., Silver, S. M., & Mulvaney, F. D. (1994). Rapid eye movement sleep disturbance in posttraumatic stress disorder. *Biological Psychiatry, 35*(3), 195-202. doi: 10.1016/0006-3223(94)91152-5

Rossion, B., Dricot, L., Devolder, A., Bodart, J. M., Crommelinck, M., de Gelder, B., & Zoontjes, R. (2000). Hemispheric asymmetries for whole-based and part-based face processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience, 12*(5), 793-802. doi: 10.1162/089892900562606

Rubin, N., Nakayama, K., & Shapley, R. (1996). Enhanced perception of illusory contours in the lower versus upper visual hemifields. *Science, 271*(5249), 651-653. doi: 10.1126/science.271.5249.651

Samar, V. J. (1983). Multidimensional influences of cerebral asymmetries on visual half-field asymmetries and cognitive skills. *Brain and Cognition, 2*(4), 355-382. doi: 10.1016/0278-2626(83)90019-2

Samara, Z., Elzinga, B. M., Slagter, H. A., & Nieuwenhuis, S. (2011). Do horizontal saccadic eye movements increase interhemispheric coherence? Investigation of a hypothesized neural mechanism underlying EMDR. *Frontiers in psychiatry, 2*, 4. doi: 10.3389/fpsyt.2011.00004

Sasson, N., Tsuchiya, N., Hurley, R., Couture, S. M., Penn, D. L., Adolphs, R., & Piven, J. (2007). Orienting to social stimuli differentiates social cognitive impairment in autism and schizophrenia. *Neuropsychologia, 45*(11), 2580-2588. doi: 10.1016/j.neuropsychologia.2007.03.009

Schacter, D. L., & Wagner, A. D. (1999). Medial temporal lobe activations in fMRI and PET studies of episodic encoding and retrieval. *Hippocampus, 9*(1), 7-24. doi: 10.1002/(SICI)1098-1063(1999)9:1<7::AID-HIPO2>3.0.CO;2-K

Schiff, B. B., Kenwood, C., Guirguis, M., & Herman, C. P. (1998). Asymmetrical hemispheric activation and behavioral persistence: Effects of unilateral muscle contractions. *Neuropsychology, 12*(4), 526-532. doi: 10.1037/0894-4105.12.4.526

Schiffer, F. (1997). Affect changes observed with right versus left lateral visual field stimulation in psychotherapy patients: Possible physiological, psychological, and therapeutic implications. *Comprehensive Psychiatry, 38*(5), 289-295. doi: 10.1016/S0010-440x(97)90062-6

Schiffer, F., Anderson, C. M., & Teicher, M. H. (1999). Electroencephalogram, bilateral ear temperature, and affect changes induced by lateral visual field stimulation. *Comprehensive Psychiatry, 40*(3), 221-225. doi: 10.1016/S0010-440x(99)90007-X

Schiffer, F., Mottaghy, F. M., Vimal, R. L. P., Renshaw, P. E., Cowan, R., Pascual-Leone, A., . . . Rohan, M. (2004). Lateral visual field stimulation reveals extrastriate cortical activation in the contralateral hemisphere: An fMRl study. *Psychiatry Research: Neuroimaging, 131*(1), 1-9. doi: 10.1016/j.pscychresns.2004.01.0020

Schiffer, F., Stinchfield, Z., & Pascual-Leone, T. (2002). Prediction of clinical response to transcranial magnetic stimulation for depression by baseline lateral visual-field stimulation. *Neuropsychiatry Neuropsychology and Behavioral Neurology, 15*(1), 18-27.

Schwartz, G. E., Davidson, R. J., & Maer, F. (1975). Right hemisphere lateralization for emotion in the human brain: Interactions with cognition. *Science, 190*(4211), 286-288. doi: 10.1126/science.1179210

Seidler, G. H., & Wagner, F. E. (2006). Comparing the efficacy of EMDR and trauma-focused cognitive-behavioral therapy in the treatment of PTSD: A meta-analytic study. *Psychological Medicine, 36*(11), 1515-1522. doi: 10.1017/S0033291706007963

Senju, A., Hasegawa, T., & Tojo, Y. (2005). Does perceived direct gaze boost detection in adults and children with and without autism? The stare-in-the-crowd effect revisited. *Visual Cognition, 12*(8), 1474-1496. doi: 10.1080/13506280444000797

Sergent, J. (1982). The cerebral balance of power: Confrontation or cooperation? *Journal of Experimental Psychology: Human Perception and Performance, 8*(2), 253-272. doi: 10.1037/0096-1523.8.2.253

Sergent, J. (1984). Configural processing of faces in the left and the right cerebral hemispheres. *Journal of Experimental Psychology: Human Perception and Performance, 10*(4), 554-572. doi: 10.1037/0096-1523.10.4.554

Servan-Schreiber, D., Schooler, J., Dew, M. A., Carter, C., & Bartone, P. (2006). Eye movement desensitization and reprocessing for posttraumatic stress disorder: A pilot blinded, randomized study of stimulation type. *Psychotherapy and Psychosomatics, 75*(5), 290-297. doi: 10.1159/000093950

Shapiro, F. (1996). Eye movement desensitization and reprocessing (EMDR): Evaluation of controlled PTSD research. *Journal of Behavior Therapy and Experimental Psychiatry, 27*(3), 209-218. doi: 10.1016/S0005-7916(96)00029-8

Shapiro, F. (2001). *Eye movement desensitization and reprocessing: Basic principles, protocols and procedures*. New York: Guilford Press.

Shapiro, F. (2012). EMDR therapy: An overview of current and future research foreword. *European Review of Applied Psychology, 62*(4), 193-195. doi: 10.1016/j.erap.2012.09.005

Shapiro, F., & Laliotis, D. (2011). EMDR and the adaptive information processing model: Integrative treatment and case conceptualization. *Clinical Social Work Journal, 39*(2), 191-200. doi: 10.1007/s10615-010-0300-7

Shelton, P. A., Bowers, D., & Heilman, K. M. (1990). Peripersonal and vertical neglect. *Brain, 113*(1), 191-205. doi: 10.1093/brain/113.1.191

Shen, K., Bezgin, G., Selvam, R., McIntosh, A. R., & Ryan, J. D. (2016). An anatomical interface between memory and oculomotor systems. *Journal of Cognitive Neuroscience, 1*(12). doi: 10.1162/jocn_a_01007

Shulman, G. L., & Corbetta, M. (2012). Two attentional networks. Identification and function within a larger cognitive architecture. In M. I. Posner (Ed.), *Cognitive Neuroscience of Attention* (pp. 113–128). London: Guilford Press.

Silberman, E. K., & Weingartner, H. (1986). Hemispheric lateralization of functions related to emotion. *Brain and Cognition, 5*(3), 322-353. doi: 10.1016/0278-2626(86)90035-7

Sivak, B., Sivak, J. G., & Mackenzie, C. L. (1985). Contact-lens design for lateralizing visual input. *Neuropsychologia, 23*(6), 801-803. doi: 10.1016/0028-3932(85)90086-7

Smigasiewicz, K., Weinrich, J., Reinhardt, B., & Verleger, R. (2014). Deployment and release of interhemispheric inhibition in dual-stream rapid serial visual presentation. *Biological Psychology, 99*, 47-59. doi: 10.1016/j.biopsycho.2014.02.008

Sparks, D. L. (2002). The brainstem control of saccadic eye movements. *Nature Reviews Neuroscience, 3*(12), 952-964. doi: 10.1038/nrn986

Sparks, D. L., & Nelson, J. S. (1987). Sensory and motor maps in the mammalian superior colliculus. *Trends in Neurosciences, 10*(8), 312-317. doi: 10.1016/0166-2236(87)90085-3

Spivey, M. J., & Geng, J. J. (2001). Oculomotor mechanisms activated by imagery and memory: Eye movements to absent objects. *Psychological Research, 65*(4), 235-241. doi: 10.1007/s004260100059

Squire, L. R., Stark, C. E. L., & Clark, R. E. (2004). The medial temporal lobe. *Annual Review of Neuroscience, 27*, 279-306. doi: 10.1146/annurev.neuro.27.070203.144130

Stickgold, R. (2002). EMDR: A putative neurobiological mechanism of action. *Journal of Clinical Psychology, 58*(1), 61-75. doi: 10.1002/Jclp.1129

Stickgold, R. (2005). Sleep-dependent memory consolidation. *Nature, 437*(7063), 1272-1278. doi: 10.1038/nature04286

Stickgold, R. (2008). Sleep-dependent memory processing and EMDR action. *Journal of EMDR practice and research, 2*(4), 289-299. doi: 10.1891/1933-3196.2.4.289

Stickgold, R., & Walker, M. P. (2013). Sleep-dependent memory triage: Evolving generalization through selective processing. *Nature Neuroscience, 16*(2), 139-145. doi: 10.1038/nn.3303

Takao, H., Hayashi, N., & Ohtomo, K. (2011). White matter asymmetry in healthy individuals: A diffusion tensor imaging study using tract-based spatial statistics. *Neuroscience, 193*, 291-299. doi: 10.1016/j.neuroscience.2011.07.041

Tebecis, A. K., & Provins, K. A. (1975). Hypnosis and eye-movements. *Biological Psychology, 3*(1), 31-47. doi: 10.1016/0301-0511(75)90004-6

Theeuwes, J. (2010). Top-down and bottom-up control of visual selection. *Acta Psychologica, 135*(2), 77-99. doi: 10.1016/j.actpsy.2010.02.006

Thiebaut de Schotten, M., Ffytche, D. H., Bizzi, A., Dell'Acqua, F., Allin, M., Walshe, M., . . . Catani, M. (2011). Atlasing location, asymmetry and inter-subject variability of white matter tracts in the human brain with MR diffusion tractography. *Neuroimage, 54*(1), 49-59. doi: 10.1016/j.neuroimage.2010.07.055

Thiry, A. (2006). *Ça y est, j'ai compris Méthodes d'études et de stratégies d'apprentissage avec la PNL*. Bruxelles: De Boeck et Larcier.

Thiry, A., & Lellouche, Y. (2007). *Apprendre à apprendre avec la PNL*. Bruxelles: De Boeck.

Treisman, A., & Gormican, S. (1988). Feature analysis in early vision: Evidence from search asymmetries. *Psychological Review, 95*(1), 15-48. doi: 10.1037/0033-295X.95.1.15

Tulving, E., Kapur, S., Craik, F. I., Moscovitch, M., & Houle, S. (1994). Hemispheric encoding/retrieval asymmetry in episodic memory: Positron emission tomography findings. *Proceedings of the National Academy of Sciences, 91*(6), 2016-2020. doi: 10.1073/pnas.91.6.2016

Turken, A. U., & Dronkers, N. F. (2011). The neural architecture of the language comprehension network: Converging evidence from lesion and connectivity analyses. *Frontiers in Systems Neuroscience, 5*, 1. doi: 10.3389/fnsys.2011.00001

Tzourio-Mazoyer, N., Petit, L., Razafimandimby, A., Crivello, F., Zago, L., Jobard, G., . . . Mazoyer, B. (2010). Left hemisphere lateralization for language in right-handers is controlled in part by familial sinistrality, manual preference strength, and head size. *Journal of Neuroscience, 30*(40), 13314-13318. doi: 10.1523/Jneurosci.2593-10.2010

van den Hout, M. A., Engelhard, I. M., Rijkeboer, M. M., Koekebakker, J., Hornsveld, H., Leer, A., . . . Akse, N. (2011). EMDR: Eye movements superior to beeps in taxing working memory and reducing vividness of recollections. *Behaviour Research and Therapy, 49*(2), 92-98. doi: 10.1016/j.brat.2010.11.003

van den Hout, M. A., Muris, P., Salemink, E., & Kindt, M. (2001). Autobiographical memories become less vivid and emotional after eye movements. *British Journal of Clinical Psychology, 40*, 121-130. doi: 10.1348/014466501163571

Vankleeck, M. H. (1989). Hemispheric-differences in global versus local processing of hierarchical visual-stimuli by normal subjects - new data and a meta-analysis of previous studies. *Neuropsychologia, 27*(9), 1165-1178. doi: 10.1016/0028-3932(89)90099-7

Verona, E., Sadeh, N., & Curtin, J. J. (2009). Stress-induced asymmetric frontal brain activity and aggression risk. *Journal of Abnormal Psychology, 118*(1), 131-145. doi: 10.1037/a0014376

Vigneau, M., Beaucousin, V., Herve, P. Y., Duffau, H., Crivello, F., Houde, O., . . . Tzourio-Mazoyer, N. (2006). Meta-analyzing left hemisphere language areas: Phonology, semantics, and sentence processing. *Neuroimage, 30*(4), 1414-1432. doi: 10.1016/j.neuroimage.2005.11.002

von Grunau, M., & Anston, C. (1995). The detection of gaze direction: A stare-in-the-crowd effect. *Perception, 24*(11), 1297-1313. doi: 10.1068/p241297

Vrij, A., Oliveira, J., Hammond, A., & Ehrlichman, H. (2015). Saccadic eye movement rate as a cue to deceit. *Journal of Applied Research in Memory and Cognition, 4*(1), 15-19. doi: 10.1016/j.jarmac.2014.07.005

Wacker, J., Chavanon, M. L., Leue, A., & Stemmler, G. (2008). Is running away right? The behavioral activation-behavioral inhibition model of anterior asymmetry. *Emotion, 8*(2), 232-249. doi: 10.1037/1528-3542.8.2.232

Wagner, A. D., Poldrack, R. A., Eldridge, L. L., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. E. (1998). Material-specific lateralization of prefrontal activation during episodic encoding

and retrieval. *Neuroreport, 9*(16), 3711-3717. doi: 10.1097/00001756-199811160-00026

Weiner, S. L., & Ehrlichman, H. (1976). Ocular motility and cognitive process. *Cognition, 4*(1), 31-43. doi: 10.1016/0010-0277(76)90009-3

Weitzenhoffer, A. M., & Brockmeier, J. D. (1970). Attention and eye movements. *Journal of Nervous and Mental Disease, 151*(2), 130-142.

Wicker, B., Michel, F., Henaff, M. A., & Decety, J. (1998). Brain regions involved in the perception of gaze: A PET study. *Neuroimage, 8*(2), 221-227. doi: 10.1006/nimg.1998.0357

Wilson, D. L., Silver, S. M., Covi, W. G., & Foster, S. (1996). Eye movement desensitization and reprocessing: Effectiveness and autonomic correlates. *Journal of Behavior Therapy and Experimental Psychiatry, 27*(3), 219-229. doi: 10.1016/S0005-7916(96)00026-2

Wiseman, R., Watt, C., ten Brinke, L., Porter, S., Couper, S. L., & Rankin, C. (2012). The eyes don't have it: Lie detection and neuro-linguistic programming. *PloS One, 7*(7). doi: 10.1371/journal.pone.0040259

Witkowski, T. (2010). Thirty-five years of research on Neuro-Linguistic Programming. NLP research data base. State of the art or pseudoscientific decoration? *Polish Psychological Bulletin, 41*(2), 58-66. doi: 10.2478/v10059-010-0008-0

Young, A. W., & Ellis, A. W. (1985). Different methods of lexical access for words presented in the left and right visual hemifields. *Brain and Language, 24*(2), 326-358. doi: 10.1016/0093-934x(85)90139-7

Young, L. R., & Sheena, D. (1975). Survey of eye-movement recording methods. *Behavior Research Methods & Instrumentation, 7*(5), 397-429. doi: 10.3758/Bf03201553

Zanette, G., Bonato, C., Polo, A., Tinazzi, M., Manganotti, P., & Fiaschi, A. (1995). Long-lasting depression of motor-evoked potentials to transcranial magnetic stimulation following exercise. *Experimental Brain Research, 107*(1), 80-86. doi: 10.1007/BF00228019

Annexes

Brain and Cognition 90 (2014) 63–68

Contents lists available at ScienceDirect

Brain and Cognition

journal homepage: www.elsevier.com/locate/b&c

Gaze direction affects visuo-spatial short-term memory

Christophe Carlei, Dirk Kerzel *

Faculté de Psychologie et des Sciences de l'Éducation, Université de Genève, Switzerland

ARTICLE INFO

Article history:
Accepted 10 June 2014

Keywords:
Hemispheric asymmetries
Gaze direction
Unilateral gaze
Visuo-spatial working memory
Visuo-spatial short-term memory

ABSTRACT

Hemispheric asymmetries were investigated by changing the horizontal position of stimuli that had to be remembered in a visuo-spatial short-term memory task. Observers looked at matrices containing a variable number of filled squares on the left or right side of the screen center. At stimulus offset, participants reproduced the positions of the filled squares in an empty response matrix. Stimulus and response matrices were presented in the same quadrant. We observed that memory performance was better when the matrices were shown on the left side of the screen. We distinguished between recall strategies that relied on visual or non-visual (verbal) cues and found that the effect of gaze position occurred more reliably in participants using visual recall strategies. Overall, the results show that there is a solid enhancement of visuo-spatial short-term memory when observers look to the left. In contrast, vertical position had no influence on performance. We suggest that unilateral gaze to the left activates centers in the right hemisphere contributing to visuo-spatial memory.

1. Introduction

It is generally assumed that the left hemisphere is more involved in verbal processing, whereas the right hemisphere is more involved in visuo-spatial processing (Gazzaniga, 2000). For instance, it has been confirmed that lesions to the right parietal cortex produce stronger perturbations of spatial memory than lesions of the left parietal cortex (e.g., Warrington & Rabin, 1970), which may be related to the frequent occurrence of attentional deficits after lesions of the right hemisphere (Milner & McIntosh, 2005). Interestingly, activity of the right intraparietal sulcus (IPS) reflects the stimulation of both visual hemi-fields in a visual short-term memory (VSTM) task, while the left IPS responded only to stimuli in the contralateral hemi-field (Sheremata, Bettencourt, & Somers, 2010). This asymmetry further underlines the dominance of the right hemisphere in visuo-spatial processing.

Behaviorally, the hemispheric asymmetries can be tested by restricting the presentation of stimuli to one hemi-field, thereby forcing initial processing in the contralateral cortical hemisphere. For instance, Gross (1972) and Samar (1983) demonstrated that responses in categorization or lexical decision tasks were faster when verbal stimuli were presented in the right visual field. Similarly, performance in naming tasks was better when words (vs. non-words) were presented in the right visual field (Jordan & Patching, 2004; Jordan, Patching, & Thomas, 2003). In contrast, spatial stimuli are processed faster when the visual input is initially directed at the right hemisphere. Laeng, Peters, and McCabe (1998) found that pictures were better remembered when they were displayed in the left visual field and Fouty, Otto, Yeo, and Briggs (1992) found higher accuracy and shorter reaction times with left hemi-field presentation when participants were asked to match line orientations to a response set and to make same-different judgments of faces.

Studies using lateralized presentation rely on the fact that the initial processing of the stimuli occurs in the opposite hemisphere. Additionally, there is strong contra-lateral activation when a single hemi-field is stimulated continuously (Schiffer et al., 2004) despite the connections between the two hemispheres. Another method to induce relatively greater activation in one hemisphere than the other relies on spreading activation from motor centers. Harmon-Jones (2006) observed that contraction of one hand increased the activation over contralateral frontal cortices (i.e., alpha suppression). Presumably, the contralateral activation of motor cortex resulting from unilateral hand contraction spread to more frontal areas. At the same time, clenching the right hand (i.e., left hemisphere activation) led to increased approach affect compared to clenching the left hand. In previous work, approach motivated states have been related to activity of the left frontal cortex (Harmon-Jones, Sigelman, Bohlig, & Harmon-Jones, 2003; Jones & Fox, 1992). More relevant to the present paper, it has recently been

* Corresponding author. Address: Faculté de Psychologie et des Sciences de l'Éducation, Université de Genève, 40 Boulevard du Pont d'Arve, CH-1205 Genève, Switzerland.
E-mail address: dirk.kerzel@unige.ch (D. Kerzel).

http://dx.doi.org/10.1016/j.bandc.2014.06.007
0278-2626/

shown that contraction of one hand affects episodic memory of word lists (Propper, McGraw, Brunye, & Weiss, 2013). Consistent with the presumed mode of processing of each hemisphere (Habib, Nyberg, & Tulving, 2003), memory performance improved when participants clenched the right hand before encoding and the left hand before recall. Thus, unilateral motor action activates the contralateral hemisphere and facilitates behavior associated with that hemisphere.

In the present contribution, we will investigate the effect of unilateral gaze on visuo-spatial short-term memory. Up to date, there is no direct evidence showing that looking to one side activates the contralateral hemisphere. However, there is some reason to believe that this is the case. Propper, Brunyé, Christman, and Januszewskia (2012) presented participants with a blank map of the United States and asked them to name the states, point to states when the names were read to them, or to name and point simultaneously. Importantly, participants wore glasses that forced them to look at the map with gaze directed to the left, center, or right. With gaze directed towards the left or center, performance was best in the naming condition, decreased with pointing and even further with both tasks simultaneously. In contrast, the difference between naming and pointing was absent when gaze was directed to the right. The interpretation was that gaze directed to the right improved recall in the pointing task by increasing activation of the left hemisphere. This result is consistent with a specialization of the left hemisphere for retrieval of both spatial and verbal information from semantic memory (Habib et al., 2003). In contrast, it does not support the specialization of the right hemisphere for the retrieval of only spatial information from semantic memory (Belger et al., 1998; Jonides et al., 1993).

In light of these results, we set out to explore the effect of unilateral gaze in a task that involved visuo-spatial information. In contrast to Propper et al. (2012), we do not focus on semantic long-term memory, but on visuo-spatial short-term memory (VSTM). Intuitively, VSTM tasks are closer to the perceptual tasks reviewed above that consistently showed better performance for visuo-spatial information directed at the left hemisphere by right hemi-field presentation. Our basic assumption is that gaze directed to the left or right will increase contralateral cortical activity. As the right hemisphere is more strongly associated with visuo-spatial processing, we expect better performance on VSTM tasks when gaze is directed to the left.

2. Overview of experiments

Our experimental task required observers to memorize the positions of filled squares in a five-by-five matrix (see Fig. 1). Immediately after stimulus presentation, they had to reproduce the positions by mouse click in a response matrix that was shown at the same position as the stimulus matrix. To avoid ceiling or floor effects, the session started by a pre-test of the visual span and the number of filled squares in the experiment was adjusted according to individual performance on the span test.

In all experiments, we compared memory performance with gaze directed to the left to memory performance with gaze directed to the right. In addition, we varied the vertical position of the stimuli by presenting the stimuli in opposite quadrants. We opposed the upper left and lower right quadrant in Experiments 1 and 2, and the lower left and the upper right quadrant in Experiment 3. Consistent with the mixed effects of vertical hemifield in previous studies (cf. Introduction to Experiment 3), we did not observe changes in performance depending on vertical position. Therefore, we will focus our discussion on effects of horizontal gaze direction.

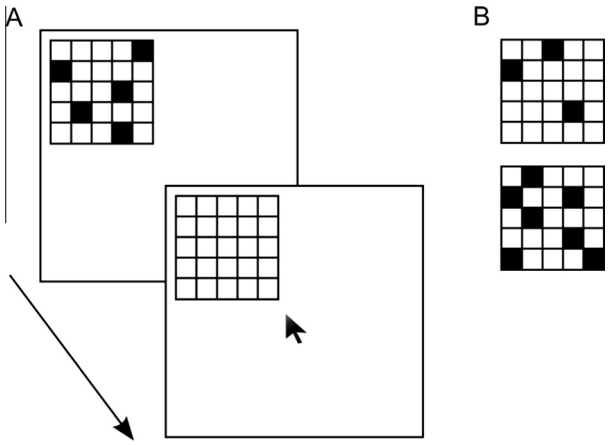

Fig. 1. Illustration of stimuli and procedure. (A) Sample trial with the stimulus matrix in the upper left quadrant of the screen (not drawn to scale). The presentation time was 1 s for each filled square. Then, the response matrix appeared at the same position as the stimulus matrix, together with a mouse cursor in the center. Participants clicked on the remembered cells in the response matrix. Participants using a counting strategy may encode the number of cells from the left edge for each row, resulting in the code 5, 1, 4, 2, 4 from top to bottom. When more than one square was presented per row or rows were empty, this had to be remembered in addition to the square positions. (B) Two sample matrices with three and seven filled squares, respectively.

In Experiment 2, we replicated the basic findings from Experiment 1 and additionally measured individual strategies used to solve the task. We distinguished between strategies based on visual images and strategies based on verbal codes. Individual strategies were also measured in Experiment 3.

3. Experiment 1

3.1. Method

3.1.1. Participants

Participants were twenty-one right-handed students (9 female, aged from 18 to 35) at the University of Geneva. Handedness was measured by self-report. It has been reported that memory for verbal material of consistent right-/left-handers improves when they make saccadic eye movements for 30 s before the memory test (Lyle, Hanaver-Torrez, Hacklander, & Edlin, 2012; Lyle, Logan, & Roediger, 2008). Presumably, consistent left-/right-handed individuals benefit from the saccade task because their relatively weaker hemispheric interaction increases when saccades are made. Because we tested visuo-spatial memory and our hypotheses do not relate to the strength of hemispheric interactions, we had no apriori reason to exclude inconsistent left-/right-handers in the current task. If anything, this decision made our study more conservative because the less homogenous sample increased the random error. The data of one participant was lost due to computer failure. At their arrival, subjects participated in a lottery to win 50 Swiss Francs.

3.1.2. Stimuli and apparatus

Observers' head movements were restrained by a chin/forehead rest at 118 cm from the ground. The experiment was controlled by E-Prime (v1.2) and the stimuli were generated by a video-projector. The visual stimulus was a five-by-five matrix of 50 × 50 cm (or 17.4° × 17.4° of visual angle, width × height) shown on a projection screen (170 × 130 cm, or 46.7° × 39.1°) at a distance of 160 cm. When the matrix was shown in a quadrant, there was a margin of 2 cm (0.7°) to the edge of the screen. The eyes were approximately at the horizontal and vertical center of the screen.

A variable number of cells in the matrix were filled. The presentation time was 1 s per filled square (e.g., for a matrix with three filled squares, the presentation time was 3 s). The filled squares marked positions that had to be remembered. Fig. 1 shows three sample stimuli. For each number of squares, there were 10 different matrices that were randomly assigned to the experimental conditions. The matrices had been created to avoid patterns that were easy to remember, such as clusters, lines, or geometric figures. Because of the small number of trials, it was important to make sure that all matrices hat the same difficulty. This was confirmed by one-way ANOVAs on the percent correct responses of matrices containing the same number of squares, which did not produce any significant results.

3.1.3. Procedure and span evaluation

In the first part of the experimental session, we determined the visuo-spatial span for each subject (see Lecerf & de Ribaupierre, 2005). The matrix was presented in the center of the screen. Immediately after presentation of the stimulus matrix, the screen went blank for 150 ms. Then, an empty response matrix appeared at the same position as the stimulus matrix. We hoped that the brief flicker introduced by the blank period would erase an iconic image of the stimulus matrix. At the same time as the response matrix, the mouse cursor appeared in the center of the screen. Then, participants indicated the remembered positions by clicking on the cells of the matrix. Response time was unlimited and it was possible to reset the response matrix after response errors. A response was considered correct if all square positions were correctly reproduced.

After seven practice trials, the span evaluation started with two filled squares. There were three consecutive repetitions for each number of squares. When at least one trial of the three repetitions was correct, the number of squares was subsequently increased by one. When the participant failed all three repetitions, the procedure stopped and the previous number of squares with at least two correct responses was considered the participant's memory span. The maximal span was limited to seven because otherwise, it was more likely that participants encoded the empty spaces rather than the filled squares.

3.1.4. Experimental task

The procedure was as in the span evaluation with the following exceptions. Participants worked through ten trials with a number of squares corresponding to the memory span, followed by ten trials with an additional square (span + 1). In both blocks, stimulus matrices were presented randomly either in the upper left or in the lower right quadrant. On each trial, the response matrix was presented at the same position as the stimulus matrix. Presentation times and response acquisition were as in the span test. Overall, there were 20 experimental trials resulting from the combination of the two numbers of squares (span, span + 1), two stimulus positions (upper left, lower right), and five repetitions. A new pattern of filled squares was presented on each trial. It took about 20 min to complete the experiment (including practice trials and span procedure).

3.2. Results and discussion

The mean memory span, the range of the span, and memory performance as a function of gaze direction (Experiments 1–3) and strategy (Experiments 2 and 3) are shown in Table 1. A response was counted as correct if the positions of all filled squares in the matrix were reproduced correctly. As presentation of the squares was simultaneous, the order of mouse clicks in the matrix was not taken into account. We calculated the mean percentage of correct responses for each location and number of squares. A repeated-measures ANOVA (2 matrix positions: upper left, lower right; 2 number of squares: span and span + 1) showed that the percentage of correct responses was higher when the number of squares corresponded to the memory span than when one square was added (64% vs. 53%), $F(1,19) = 8.88$, $p = .008$, $\eta^2_P = .32$. We were surprised by the very good performance on trials with span + 1 squares (53% correct responses). Apparently, our procedure underestimated the span in the experimental trials. While the term "span" seems inappropriate with such a high level of performance, we nonetheless keep it for lack of a better term. When the matrix was shown in the upper left corner, performance was better than when it was shown in the lower right corner (63% vs. 54%), $F(1,19) = 5.52$, $p = .029$, $\eta^2_P = .23$. The effect of stimulus position is consistent with our hypothesis that looking to the left activates the right hemisphere, which is experienced as facilitation of the respective lateralized cognitive function (i.e., visuo-spatial memory). The interaction of matrix position and number of squares was not significant, $p = .150$.

Table 1
Results from Experiments 1 to 3. The span refers to the number of squares participants were able to memorize (see text). In Experiment 1, individual strategies were not measured. In Experiment 3, the interaction between strategy and gaze direction was not significant, but we nonetheless report the means as a function of gaze direction and strategy.

Experiment	Span		Memory performance gaze left vs. right		
	Mean	Range	Overall	Visual strategy	Verbal strategy
1	5.55	4–7	64% vs. 53%	–	–
2	5.29	3–7	63% vs. 58%	82% vs. 50%	45% vs. 62%
3	5.57	3–7	59% vs. 49%	66% vs. 61%	60% vs. 38%

4. Experiment 2

In order to explain the inter-individual variability in the effect of gaze direction, we examined the modulating effect of strategies used to solve the task. After informal questioning of the participants, we discerned two main strategies. The visual strategy involved remembering the complete image or the shape created by the squares. The counting strategy involved remembering the position of individual squares by counting the number of empty cells relative to some reference point. For instance, participants may recall the number of empty cells from the left edge for each row containing a filled square (cf. Fig. 1).

We expected that participants relying on the counting strategy would be differently influenced by gaze direction. Looking to the left is expected to facilitate performance when a visual strategy is used because of the right hemisphere's greater involvement in visuo-spatial memory. In contrast, the counting strategy involves mental repetition of words or numbers, which depends on verbal rather than visuo-spatial memory. Therefore, looking to the right may facilitate performance when a counting strategy is used because of the left hemisphere's specialization for verbal stimuli.

4.1. Method

Thirty-five students at the University of Geneva (25 female, 4 left-handed, aged from 20 to 35 years) participated in this experiment. The experimental procedure was the same as in Experiment 1 with the following exceptions. Trials with a number of squares corresponding to the span and trials with span + 1 squares were presented in random order. Further, the position of the subject relative to the screen was slightly changed. The screen was closer to the participant (144 cm instead of 160 cm). Therefore, the visual angle subtended by the matrix increased from 17.4° to 20.9°. The

height of the chin rest was raised by 4 cm (now at 122 cm from the ground), which brought the eyes closer to the center of the screen.

In order to determine the strategy, we asked participants at the end of the experiment to describe their strategy. Participants were classified according to their reports during debriefing. Individuals who reported having counted the black squares on every trial in order to remember the position of squares were classified into the counting strategy. Individuals who reported having tried to remember matrices as a whole were classified into the visual strategy. Participants who reported having used both strategies depending on the pattern of filled squares were classified into the mixed strategy.

4.2. Results

The results are presented in Fig. 2. There were 10 participants using the visual strategy, 13 participants using counting, and 12 participants alternating between the two. Because the number of squares had not interacted with the effect of gaze direction in Experiment 1, we collapsed across this factor. A mixed-factors ANOVA (2 gaze directions: upper left, lower right; 3 strategies: visual, counting, mixed) confirmed better performance when participants looked at the upper left compared to the lower right (63% vs. 58%), $F(1,32) = 7.95$, $p = .008$, $\eta^2_P = .20$. There was no main effect of strategy, $F(2,32) = 1.07$, $p = .353$, but an interaction between gaze direction and strategy, $F(2,32) = 37.79$, $p < .001$, $\eta^2_P = .70$ (see Fig. 2). To follow up on this interaction, we compared the upper left and the lower right for the three groups. A t-test showed that there were more correct answers for matrices in the upper left than in the lower right quadrant for participants with a visual strategy (82% vs. 50%), $t(9) = 7.69$ $p < .001$, confirming the results of the first experiment. On the other hand, there was an opposite effect with the counting strategy (45% vs. 62%), $t(12) = 16.01$, $p = .002$, and no effect with a mixed strategy, (65% vs. 61%), $t(11) = 1.45$, $p = .175$.

4.3. Discussion

We replicated the effect of gaze direction with a larger sample and found a strong modulation by strategy. Participants using a visual strategy showed better performance with gaze directed at the upper left quadrant. We suggest that the visual strategy relies on visuo-spatial memory, which improves when the right hemisphere is activated by directing gaze to the left. The results from the group using the counting strategy are also interesting. Under the assumption that these participants transformed the visual stimulus into a verbal code, activation of the left hemisphere would have been beneficial. Consistent with this idea, better performance was observed when gaze was directed to the right. Participants using a mixed strategy showed no effect of gaze direction, which makes sense when considering that a given gaze direction either facilitates or degrades performance depending on the strategy.

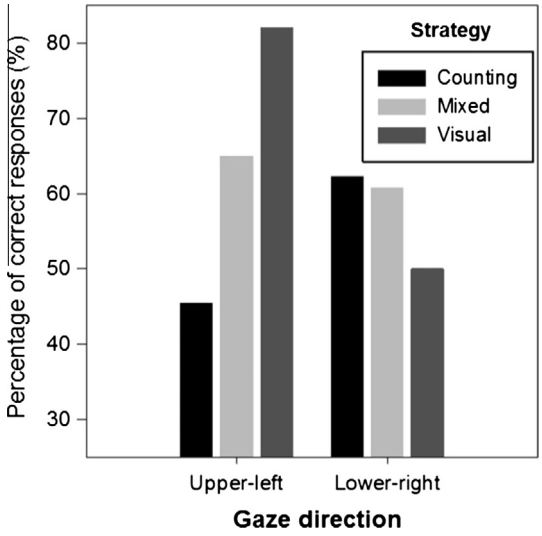

Fig. 2. Results from Experiment 2. Percentage of correct responses is shown as a function of gaze direction and strategy.

5. Experiment 3

In Experiments 1 and 2, a difference was observed between gaze directed at the upper left quadrant and gaze directed at the lower right quadrant, which we attributed to activation of the contralateral hemisphere. However, the two gaze directions examined so far confound laterality (left, right) and elevation (up, down). Beyond the dichotomy between left and right, there are also studies focusing on differences between the upper and lower visual field. For example, attentional resolution was found to be enhanced in the lower visual field (He, Cavanagh, & Intriligator, 1996), which may be explained by enhanced visual discrimination (Carrasco, Talgar, & Cameron, 2001). Similarly, the segmentation of an image into figure and background (Rubin, Nakayama, & Shapley, 1996) and goal-directed actions (Danckert & Goodale, 2001; Khan & Lawrence, 2005; Krigolson & Heath, 2006) are performed better in the lower than the upper visual field. While most studies point to an advantage of processing in the lower visual field (overview in Danckert and Goodale (2003)), visual search (Previc & Naegele, 2001), letter naming (Hagenbeek & Van Strien, 2002), and distance judgments (Niebauer & Christman, 1998) were found to be better in the upper visual field. Given the complexity of the literature on this topic, it is difficult to predict whether there would be an advantage of the upper or lower visual field for the VSTM task of Experiments 1 and 2. Therefore, we do not have any predictions about whether looking upwards or downwards would facilitate performance.

To examine whether laterality or elevation caused the asymmetry observed in Experiments 1 and 2, we examined the lower left and the upper right quadrant (instead of the upper left and lower right). If presentation above and not presentation to the left explained the facilitation in Experiments 1–2, we should find better performance for the upper right than for the lower left quadrant in the current experiment. In addition, we developed questions to allow for a more objective classification of participants. As in the previous experiment, the visual and counting strategies should lead to opposite effects, because they rely on different hemispheres.

5.1. Method

Thirty students at the University of Geneva (25 female, 2 left-handed, aged from 19 to 27), participated. All subjects received a voucher for a lunch at MacDonald's worth 11.30 Swiss Francs.

The same procedure was used as in the second experiment with the following exceptions. The matrices were shown in the upper right quadrant of the screen or in the lower left quadrant (i.e., vertical positions were inverted relative to Experiment 1). Further, participants filled in a questionnaire at the end of the session in order to determine the strategy. Participants rated how often they used each strategy on a scale from zero to three: 0 = never, 1 = sometimes, 2 = often, 3 = every time. Four questions were administered in French. Here, we report the English translation.

For the visual strategy, we asked "I imagined a global shape to better remember the position of squares" and "I imagined isolated shapes to better remember the position of certain squares". For the counting strategy, we asked "I counted the total number of squares displayed in the grid" and "I mentally repeated numbers corresponding to positions of squares (lines and/or columns)". If a participant had a score equal or superior to four on two questions of the same strategy, the participant was categorized into the respective strategy, except if his score on the other strategy was equal or superior to three. In this case, the participant was categorized into the "mixed" strategy. A participant having scores inferior to four on both sets of questions was also categorized into "mixed". The criterion of four was selected *apriori* because it indicated that the participant had indicated at least "often" (score of 2) on both questions or "every time" (score of 3) on one question. Therefore, a total score of 4 indicated that the participant had used the respective strategy frequently. Unless the participant obtained a similar score on the other strategy, we think it was justified to classify the participant into the respective strategy. Some additional questions unrelated to strategies were administered but these are not reported.

5.2. Results

A mixed-factors ANOVA (2 gaze directions: lower left, upper right; strategy: visual $n = 14$, counting $n = 4$, mixed $n = 12$) confirmed a significant effect of gaze direction with better performance when gaze was directed at the lower left than at the upper right quadrant (59% vs. 49%), $F(1,27) = 6.74$, $p = .015$, $\eta^2_P = .20$. Performance depended also on strategy and was better with the visual (63%) than with the counting or mixed strategies (49% and 45%, respectively), $F(2,27) = 3.65$, $p = .039$, $\eta^2_P = .21$. The interaction was not significant, $p = .420$.

5.3. Discussion

Performance was better when gaze was directed at the lower left vs. upper right quadrant. This result confirms our hypothesis that looking to the left increases activation of the right hemisphere, which facilitates performance on VSTM tasks. Comparison of Experiment 3 with Experiments 1–2 suggests that the elevation of the stimuli does not play a role. Further, there was no interaction with strategy. Rather, the advantage of the lower left position was independent of strategy, which may be due to the small number of participants using a counting strategy (only 4).

6. General discussion

Our results show that in a task involving maintenance of information in visuo-spatial short-term memory, it mattered where gaze was directed. Across Experiments 1–3, better performance was observed when gaze was directed to the left than to the right. This finding is in line with the hypothesis that unilateral gaze increases contralateral hemispheric activation (cf. Propper et al., 2012). Accordingly, looking to the left increases activation of the right hemisphere. As the right hemisphere is specialized in spatial memory, performance on the visuo-spatial memory task improved. In contrast, Propper et al. (2012) had concluded that gaze directed to the right (i.e., left hemisphere activation) improves performance in a spatial relative to a verbal task. Their results are consistent with the lateralization of retrieval from semantic memory to the left hemisphere, but not with the lateralization of visuo-spatial processing to the right hemisphere. Thus, unilateral gaze affects short-term and long-term memory differently, which is not surprising given the distinct neural substrates (Tulving, Kapur, Craik, Moscovitch, & Houle, 1994).

Further, there was some evidence in Experiment 2 that performance improves with gaze directed at the lower right when participants use a verbal strategy. This would be consistent with activation of the left hemisphere, which is specialized in the processing and production of language. However, this result was not replicated in Experiment 3, possibly because of the small number of participants using the verbal strategy. In addition, it is possible that strategy and the consistency of handedness were confounded. We did not measure the consistency of handedness and the sample size for verbal strategy was very small ($n = 4$). Thus, it may have been possible that among the few individuals who were using the verbal strategy there were more inconsistent than consistent right-handers. However, only consistent right-handers show improvement of memory performance after the execution of saccades (Lyle et al., 2012; Lyle et al., 2008). Consequently, future studies would need to better distinguish between effects of handedness and encoding strategy.

While our results show a robust advantage in a VSTM task when gaze was directed to the left, we would nonetheless like to mention some limitations of the present study. For example, we did not monitor the direction of gaze by means of an eyetracker. We assumed that participants would look at the stimuli in order to perform the task properly. Actually, we think it is very unlikely that participants would encode the stimuli extrafoveally, for instance by keeping their eyes directed at the empty center of the screen. Moreover, the unequal distribution of subjects in the different strategy groups reduced statistical significance in the last experiment. In future experiments, it would be preferable to identify experimental tasks that exclusively tap into one type of memory.

Further, more research is needed to confirm that directing gaze at one quadrant actually does produce more activation in the respective contralateral cortical centers. Recent research suggests that links between asymmetric hemispheric activation and behavior are strong. For instance, temperature in the ear is correlated with activation in the ipsilateral hemisphere and it has been shown that higher temperature in the left ear is associated with more impulsive behavior in a go-nogo task (Helton, 2010), which is consistent with theories about the lateralization of approach and avoidance (Gray, 1990). Similarly, our research suggests a link between asymmetric brain activation and behavior, but our research remains inconclusive with respect to the underlying neurophysiology. If the effect was mediated by cortical centers of oculomotor control, such as the frontal eye fields, it may be possible to measure differences in the distribution of alpha power between the left and right frontal cortices (cf. Harmon-Jones, 2006). Moreover, our task involves only one component of working memory, the maintenance of information. Future studies should investigate tasks that also require the manipulation of information (reviewed in Barrouillet and Camos (2012)).

Further, it remains unclear whether there is a link between effects of unilateral gaze that we observed in the current study and "non-visual eye movements". Until now, the literature on non-visual eye movements focused on the frequency of saccadic eye movements, but similar to our research, it was also interested in the link between eye movements and memory (e.g. Ehrlichman & Micic, 2012; Ehrlichman, Micic, Sousa, & Zhu, 2007). In contrast to our research, however, there was no systematic investigation of directional patterns. The main finding of these studies was that looking for information in long-term memory increases, whereas maintenance of information in working memory decreases eye movement rate. We also know that the frequency of saccadic eye movements depended on the task. They are more frequent for verbal than for spatial tasks, regardless of visual stimulation (Ehrlichman & Barrett, 1983).

We speculate that we unconsciously make non-visual saccades at a certain frequency in order to activate specific areas in the brain to facilitate the recruitment of some cognitive abilities. For instance, in a task involving visuo-spatial memory in which people can freely move their eyes, the best performance will result when participants make non-visual saccadic eye movements oriented to the left at a certain frequency. However, another direction may be beneficial for verbal tasks and the frequency may be different.

In sum, we find that gaze direction may play a functional role in cognitive processing. Looking to the left increases performance in a task involving visuo-spatial short-term memory.

However, the exact neural causes remain to be investigated.

Acknowledgments

We wish to thank MacDonald's Geneva for their generous support (lunch vouchers) and Catherine Thevenot and Thierry Lecerf for their helpful comments.

References

Barrouillet, P., & Camos, V. (2012). As time goes by temporal constraints in working memory. *Current Directions in Psychological Science, 21*(6), 413–419. http://dx.doi.org/10.1177/0963721412459513.

Belger, A., Puce, A., Krystal, J. H., Gore, J. C., Goldman-Rakic, P., & McCarthy, G. (1998). Dissociation of mnemonic and perceptual processes during spatial and nonspatial working memory using fMRI. *Human Brain Mapping, 6*(1), 14–32. http://dx.doi.org/10.1002/(SICI)1097-0193(1998)6:1<14::AID-HBM2>3.3.CO;2-2.

Carrasco, M., Talgar, C. P., & Cameron, E. L. (2001). Characterizing visual performance fields: Effects of transient covert attention, spatial frequency, eccentricity, task and set size. *Spatial Vision, 15*(1), 61–75. http://dx.doi.org/10.1163/15685680152692015.

Danckert, J., & Goodale, M. A. (2001). Superior performance for visually guided pointing in the lower visual field. *Experimental Brain Research, 137*(3–4), 303–308. http://dx.doi.org/10.1007/s002210000653.

Danckert, J., & Goodale, M. A (2003). Ups and downs in the visual control of action. In S. H. Johnson-Frey (Ed.), *Taking action: Cognitive neuroscience perspectives on intentional acts* (pp. 29–64). Cambridge, MA: MIT Press.

Ehrlichman, H., & Barrett, J. (1983). 'Random' saccadic eye movements during verbal-linguistic and visual-imaginal tasks. *Acta Psychologica, 53*(1), 9–26. http://dx.doi.org/10.1016/0001-6918(83)90013-6.

Ehrlichman, H., & Micic, D. (2012). Why do people move their eyes when they think? *Current Directions in Psychological Science, 21*(2), 96–100. http://dx.doi.org/10.1177/0963721412436810.

Ehrlichman, H., Micic, D., Sousa, A., & Zhu, J. (2007). Looking for answers: Eye movements in non-visual cognitive tasks. *Brain and Cognition, 64*(1), 7–20. http://dx.doi.org/10.1016/j.bandc.2006.10.001.

Fouty, H. E., Otto, M. W., Yeo, R. A., & Briggs, C. R. (1992). A novel contact-lens system to assess visual hemispheric asymmetries. *Perceptual and Motor Skills, 74*(2), 567–575. http://dx.doi.org/10.2466/pms.1992.74.2.567.

Gazzaniga, M. S. (2000). Cerebral specialization and interhemispheric communication – Does the corpus callosum enable the human condition? *Brain, 123*(7), 1293–1326. http://dx.doi.org/10.1093/brain/123.7.1293.

Gray, J. A. (1990). Brain systems that mediate both emotion and cognition. *Cognition & Emotion, 4*(3), 269–288. http://dx.doi.org/10.1080/02699939008410799.

Gross, M. M. (1972). Hemispheric specialization for processing of visually presented verbal and spatial stimuli. *Perception and Psychophysics, 12*(4), 357–363. http://dx.doi.org/10.3758/Bf03207222.

Habib, R., Nyberg, L., & Tulving, E. (2003). Hemispheric asymmetries of memory: The HERA model revisited. *Trends in Cognitive Sciences, 7*(6), 241–245. http://dx.doi.org/10.1016/S1364-6613(03)00110-4.

Hagenbeek, R. F., & Van Strien, J. W. (2002). Left-right and upper-lower visual field asymmetries for face matching, letter naming, and lexical decision. *Brain and Cognition, 49*(1), 34–44. http://dx.doi.org/10.1006/brcg.2001.1481.

Harmon-Jones, E. (2006). Unilateral right-hand contractions cause contralateral alpha power suppression and approach motivational affective experience. *Psychophysiology, 43*(6), 598–603. http://dx.doi.org/10.1111/j.1469-8986.2006.00465.x.

Harmon-Jones, E., Sigelman, J., Bohlig, A., & Harmon-Jones, C. (2003). Anger, coping, and frontal cortical activity: The effect of coping potential on anger-induced left frontal activity. *Cognition & Emotion, 17*(1), 1–24. http://dx.doi.org/10.1080/02699930302278.

He, S., Cavanagh, P., & Intriligator, J. (1996). Attentional resolution and the locus of visual awareness. *Nature, 383*(6598), 334–337. http://dx.doi.org/10.1038/383334a0.

Helton, W. S. (2010). The relationship between lateral differences in tympanic membrane temperature and behavioral impulsivity. *Brain and Cognition, 74*(2), 75–78. http://dx.doi.org/10.1016/j.bandc.2010.06.008.

Jones, N. A., & Fox, N. A. (1992). Electroencephalogram asymmetry during emotionally evocative films and its relation to positive and negative affectivity. *Brain and Cognition, 20*(2), 280–299. http://dx.doi.org/10.1016/0278-2626(92)90021-D.

Jonides, J., Smith, E. E., Koeppe, R. A., Awh, E., Minoshima, S., & Mintun, M. A. (1993). Spatial working-memory in humans as revealed by PET. *Nature, 363*(6430), 623–625. http://dx.doi.org/10.1038/363623a0.

Jordan, T. R., & Patching, G. R. (2004). What do lateralized displays tell us about visual word perception? A cautionary indication from the word–letter effect. *Neuropsychologia, 42*(11), 1504–1514. http://dx.doi.org/10.1016/j.neuropsychologia.2004.03.010.

Jordan, T. R., Patching, G. R., & Thomas, S. M. (2003). Assessing the role of hemispheric specialisation, serial-position processing, and retinal eccentricity in lateralised word recognition. *Cognitive Neuropsychology, 20*(1), 49–71. http://dx.doi.org/10.1080/02643290244000185.

Khan, M. A., & Lawrence, G. P. (2005). Differences in visuomotor control between the upper and lower visual fields. *Experimental Brain Research, 164*(3), 395–398. http://dx.doi.org/10.1007/s00221-005-2325-7.

Krigolson, O., & Heath, M. (2006). A lower visual field advantage for endpoint stability but no advantage for online movement precision. *Experimental Brain Research, 170*(1), 127–135. http://dx.doi.org/10.1007/s00221-006-0386-x.

Laeng, B., Peters, M., & McCabe, B. (1998). Memory for locations within regions: Spatial biases and visual hemifield differences. *Memory and Cognition, 26*(1), 97–107. http://dx.doi.org/10.3758/Bf03211373.

Lecerf, T., & de Ribaupierre, A. (2005). Recognition in a visuospatial memory task: The effect of presentation. *European Journal of Cognitive Psychology, 17*(1), 47–75. http://dx.doi.org/10.1080/09541440340000420.

Lyle, K. B., Hanaver-Torrez, S. D., Hacklander, R. P., & Edlin, J. M. (2012). Consistency of handedness, regardless of direction, predicts baseline memory accuracy and potential for memory enhancement. *Journal of Experimental Psychology-Learning Memory and Cognition, 38*(1), 187–193. http://dx.doi.org/10.1037/A0024831.

Lyle, K. B., Logan, J. M., & Roediger, H. L. (2008). Eye movements enhance memory for individuals who are strongly right-handed and harm it for individuals who are not. *Psychonomic Bulletin & Review, 15*(3), 515–520. http://dx.doi.org/10.3758/Pbr.15.3.515.

Milner, A. D., & McIntosh, R. D. (2005). The neurological basis of visual neglect. *Current Opinion in Neurology, 18*(6), 748–753. http://dx.doi.org/10.1097/01.wco.0000191512.60368.ee.

Niebauer, C. L., & Christman, S. D. (1998). Upper and lower visual field differences in categorical and coordinate judgments. *Psychonomic Bulletin & Review, 5*(1), 147–151. http://dx.doi.org/10.3758/BF03209471.

Previc, F. H., & Naegele, P. D. (2001). Target-tilt and vertical-hemifield asymmetries in free-scan search for 3-D targets. *Perception and Psychophysics, 63*(3), 445–457. http://dx.doi.org/10.3758/BF03194411.

Propper, R. E., Brunyé, T. T., Christman, S. D., & Januszewskia, A. (2012). Look over there! Unilateral gaze increases geographical memory of the 50 United States. *Brain and Cognition, 78*(1), 59–62. http://dx.doi.org/10.1016/j.bandc.2011.10.002.

Propper, R. E., McGraw, S. E., Brunye, T. T., & Weiss, M. (2013). Getting a grip on memory: Unilateral hand clenching alters episodic recall. *PLoS One, 8*(4), e62474. http://dx.doi.org/10.1371/journal.pone.0062474.

Rubin, N., Nakayama, K., & Shapley, R. (1996). Enhanced perception of illusory contours in the lower versus upper visual hemifields. *Science, 271*(5249), 651–653. http://dx.doi.org/10.1126/science.271.5249.651.

Samar, V. J. (1983). Multidimensional influences of cerebral asymmetries on visual half-field asymmetries and cognitive skills. *Brain and Cognition, 2*(4), 355–382. http://dx.doi.org/10.1016/0278-2626(83)90019-2.

Schiffer, F., Mottaghy, F. M., Vimal, R. L. P., Renshaw, P. E., Cowan, R., & Pascual-Leone, A. (2004). Lateral visual field stimulation reveals extrastriate cortical activation in the contralateral hemisphere: An fMRI study. *Psychiatry Research-Neuroimaging, 131*(1), 1–9. http://dx.doi.org/10.1016/j.pscychresns.2004.01.0020.

Sheremata, S. L., Bettencourt, K. C., & Somers, D. C. (2010). Hemispheric asymmetry in visuotopic posterior parietal cortex emerges with visual short-term memory load. *Journal of Neuroscience, 30*(38), 12581–12588. http://dx.doi.org/10.1523/Jneurosci.2689-10.2010.

Tulving, E., Kapur, S., Craik, F. I., Moscovitch, M., & Houle, S. (1994). Hemispheric encoding/retrieval asymmetry in episodic memory: Positron emission tomography findings. *Proceedings of the National Academy of Sciences, 91*(6), 2016–2020. http://dx.doi.org/10.1073/pnas.91.6.2016.

Warrington, E. K., & Rabin, P. (1970). Perceptual matching in patients with cerebral lesions. *Neuropsychologia, 8*(4), 475–487. http://dx.doi.org/10.1016/0028-3932(70)90043-6.

Laterality, 2015
http://dx.doi.org/10.1080/1357650X.2015.1047380

Routledge
Taylor & Francis Group

The effect of gaze direction on the different components of visuo-spatial short-term memory

Christophe Carlei and Dirk Kerzel

Faculté de Psychologie et des Sciences de l'Éducation, Université de Genève, Genève, Switzerland

(*Received 4 March 2015; accepted 27 April 2015*)

Cerebral asymmetries and cortical regions associated with the upper and lower visual field were investigated using shifts of gaze. Earlier research suggests that gaze shifts to the left or right increase activation of specific areas of the contralateral hemisphere. We asked whether looking at one quadrant of the visual field facilitates the recall in various visuo-spatial tasks. The different components of visuo-spatial memory were investigated by probing memory for a stimulus matrix in each quadrant of the screen. First, memory for visual images or patterns was probed with a matrix of squares that was simultaneously presented and had to be reconstructed by mouse click. Better memory performance was found in the upper left quadrant compared to the three other quadrants indicating that both laterality and elevation are important. Second, positional memory was probed by subsequently presenting squares which prevented the formation of a visual image. Again, we found that gaze to the upper left facilitated performance. Third, memory for object-location binding was probed by asking observers to associate objects to particular locations. Higher performance was found with gaze directed to the lower quadrants irrespective of lateralization, confirming that only some components of visual short-term memory have shared neural substrates.

Keywords: Hemispheric asymmetries; Gaze direction; Unilateral gaze; Object-location binding; Visuo-spatial short-term memory; Positional memory.

Unilateral actions (e.g., looking to the right or contracting the right hand) are thought to activate the contralateral hemisphere. As a result, lateralized cognitive processes associated with the activated hemisphere are facilitated (Carlei & Kerzel,

Address correspondence to: Christophe Carlei, Faculté de Psychologie et des Sciences de l'Éducation, Université de Genève, 40 Boulevard du Pont d'Arve, CH – 1205 Genève, Switzerland. E-mail: christophe.carlei@unige.ch

We wish to thank our research assistants: Alina Miny, Céline Lucken and Ludivine Jargy.
No potential conflict of interest was reported by the authors.
The authors were supported by the Swiss National Foundation [SNF 100014_156487].

2014; Harmon-Jones, 2006; Propper, Brunyé, Christman, & Januszewskia, 2012; Propper, McGraw, Brunye, & Weiss, 2013). The present study is concerned with effects of gaze direction on memory. Previously, Propper et al. (2012) concluded that gaze directed to the right facilitated retrieval of verbal and spatial information from semantic memory, which has been associated with left hemisphere functioning (Habib, Nyberg, & Tulving, 2003). Using a different paradigm, Carlei and Kerzel (2014) concluded that looking to the left facilitates visuo-spatial memory because of right-hemisphere activation. In the present study, we investigated the effect of vertical and horizontal gaze direction on different components of visuo-spatial working memory.

Asymmetries between the upper and lower hemifields

As we are interested in differences between upward and downward gaze direction, it is useful to look at differences between the upper and lower visual hemifield. Investigations of gaze direction and visual hemifield have in common that the stimuli are presented in eccentric parts of the screen (above, below, left or right of the centre). To investigate effects of visual hemifield, the eyes are directed at the centre of the screen so that different parts of the retina are stimulated. In studies on gaze direction, however, observers directly look at the eccentric stimuli, which results mostly in foveal stimulation.

Previc (1990) argued that sensory processing of low spatial and high temporal frequencies is best in the lower visual field, whereas higher-level perceptual processing and attention are better in the upper visual field. However, the evaluation of Previc's hypothesis is mixed, in particular with respect to attentional asymmetries. For instance, He, Cavanagh, and Intriligator (1996) claimed that attentional resolution was better in the lower visual field by showing lower visual field advantages in difficult search tasks, but no differences in basic search tasks. In contrast, Carrasco, Talgar, and Cameron (2001) showed that attention, as measured by the effects of exogenous cueing, were similar in the upper and lower visual field, whereas perceptual performance was better in the lower visual field. Further, Rezec and Dobkins (2004) showed that discrimination of basic visual features was better in the lower visual field when search involved the complete visual field, suggesting an attentional bias to the lower visual field, whereas discrimination at cued locations in the upper or lower visual field were equal, suggesting that perceptual performance was about equal. Despite the mixed results for attentional asymmetries, Previc's hypothesis that sensory processing is improved in the lower visual field has been supported by more recent research (Carrasco et al., 2001; Gordon, Shapley, Patel, Pastagia, & Truong, 1997; Levine & McAnany, 2005). In particular, the discrimination of colour is improved in the lower visual field (Gordon et al., 1997; Levine & McAnany, 2005). Finally, there is some evidence that the upper visual field is specialized in conscious perception and object recognition. For instance,

localizing a target among distractors (Feng & Spence, 2014), discrimination between words and non-words (Goldstein & Babkoff, 2001), naming letters in a trigram (Hagenbeek & Van Strien, 2002) or categorical judgements of spatial relationships (i.e., above vs. below, Niebauer & Christman, 1998) were better in the upper visual field.

ASYMMETRIES BETWEEN UPWARD AND DOWNWARD GAZE

The reported differences between the upper and lower visual field may arise from the participation of different brain areas in the processing of stimuli from the upper and lower visual field (Rapcsak, Cimino, & Heilman, 1988; Shelton, Bowers, & Heilman, 1990). Here, our question is whether looking upward or downward activates brain areas that are also involved in treating stimuli from the respective vertical hemifields. We do not expect differences in sensory processing, but differences in higher-level processes, such as attention or object recognition, may occur. However, the advantage of the upper visual field for object recognition mostly concerns letters or words (Goldstein & Babkoff, 2001; Hagenbeek & Van Strien, 2002), whereas we investigate short-term memory for non-verbal stimuli. Thus, the mixed findings on attentional asymmetries and the novel nature of our stimuli make it difficult to derive precise predictions for effects of vertical gaze direction on visuo-spatial memory.

DIFFERENT COMPONENTS OF VISUAL SHORT-TERM MEMORY

In the present study, we will investigate the effects of vertical and horizontal gaze direction on visuo-spatial memory. Visuo-spatial working memory can be subdivided into at least two separable storage systems (Logie, 2003). One for maintaining visual information (such as appearance) and the other for maintaining spatial information (such as the location of objects). Darling, Della Sala, and Logie (2009) provided evidence for these two distinct subsystems in visuo-spatial working memory by selectively disrupting memory in the retention interval. While dynamic noise selectively disrupted visual memory for the appearance of letters, a manual tapping task selectively disrupted location memory for the position of squares.

In our current study, we opted for another technique to selectively investigate visual and positional memory. Pickering, Gathercole, Hall, and Lloyd (2001) asked participants to remember the position of black squares that were either shown simultaneously as a black-and-white pattern or one after the other in an empty matrix. The assumption was that the simultaneously presented squares were stored in the visual subsystem whereas the sequentially presented squares were stored in the positional subsystem.

Finally, Kessels, Kappelle, de Haan, and Postma (2002) argued for a third subsystem of spatial memory with separate brain structures, which they referred to as object-location binding. Based on a study with patients after ischemic stroke, they concluded that the left hemisphere was more involved in binding object identities to known positions, whereas the right hemisphere was critical for positional memory.

PRESENT OBJECTIVES AND OVERVIEW OF EXPERIMENTS

To summarize, our goal is to investigate effects of gaze direction on three distinct types of short-term memory: visual memory, positional memory and object-location binding. Our main prediction is that gaze directed to the left activates centres in the right hemisphere, which improves performance on tasks involving visual and positional memory. In contrast, directing gaze to the right activates centres in the left hemisphere, which improves performance on tasks involving object-location binding (cf. Kessels et al., 2002).

In all our experiments, we compared opposing quadrants in separate groups of participants to disentangle effects of laterality and elevation. We presented the matrices in the upper left or the lower right in one group, and in the lower left or the upper right in the other group.

In the first experiment, we focused on visual memory and attempted to replicate previous results (Carlei & Kerzel, 2014) with improved methods (cf. Discussion). We asked participants to memorize the position of black squares in a matrix that was presented simultaneously and to reproduce the square positions after stimulus offset (see Figure 1A). The main manipulation concerned the position of the matrix on the computer screen and the corresponding gaze direction. The matrix was presented in one of the four quadrants. To prevent verbal coding of the square positions, the phonological loop was blocked (Pelizzon, Brandimonte, & Favretto, 1999). We hope to replicate better performance when participants look to the left, which we attributed to right-hemisphere activation (Carlei & Kerzel, 2014). For elevation, we do not have precise expectations. While categorical judgements of position (i.e., below vs. above) were better in the upper visual field, judgements of distance (i.e., close vs. far) were better in the lower visual field (Niebauer & Christman, 1998). Encoding the matrix positions involves judgements of both categorical spatial relations and distances. Therefore, it is not clear what to expect when gaze is directed upwards or downwards.

In the second experiment, we investigated the positional subcomponent of spatial memory. The squares were presented sequentially instead of simultaneously to prevent subjects from encoding the global shape of the pattern (see Figure 1B). We expect to replicate findings observed for visual memory with better performance when gaze is directed to the left.

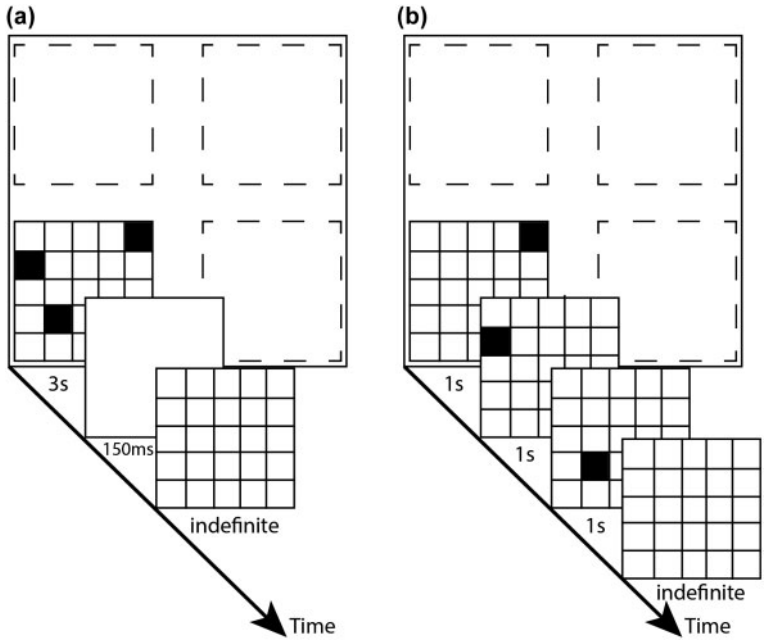

Figure 1. Simultaneous and sequential presentation modes in Experiments 1 and 2 are illustrated in panels A and B, respectively. With simultaneous presentation, presentation time was increased by one second for each square. With sequential presentation, each square was shown for one second. At the end of stimulus presentation, a response matrix appeared in the same location. Participants clicked on the cells to respond. There was no time constraint.

In the third experiment, we investigated object-location binding in a variant of our matrix task that was similar to Kessels et al. (2002). Participants were asked to memorize Japanese symbols at their respective locations. Subsequently, blue dots replaced the Japanese symbols and participants had to recall the Japanese symbol at each dot location. Given that the selected Japanese symbols are visually complex, the capacity to discriminate may play a significant role. As there is some evidence that visual discrimination, as well as attentional and spatial resolution, are better in the lower visual field, we expect better performance when gaze is directed to the lower quadrants.

EXPERIMENT 1

Methods

Participants. Participants were 35 right-handed female students (aged from 17 to 35) at the University of Geneva. All participated for course credit. Handedness of all students was assessed by the Edinburgh Handedness Inventory (Oldfield,

1971), but only strongly right-handed participants with a score equal or above 80 on a scale of 100 participated in the present experiment (see Christman, Propper, & Dion, 2004). We chose to restrict our sample to right-handed women because gender and laterality influence cerebral specialization (Grabowska, Herman, Nowicka, Szatkowska, & Szelag, 1994; Tzourio-Mazoyer et al., 2010). Furthermore, we also chose strongly right-handed participants because we know that their memory performance is more affected by eye movements (Lyle, Logan, & Roediger, 2008). By doing so, we hope to create a more uniform sample and increase our chances of finding reliable differences. Following consent, participants were randomly assigned to one of the two groups. We had 17 participants for the first and 18 participants in the second group.

Stimuli and apparatus. Participants' head position was stabilized with a chin rest at 40 cm from the screen centre in a dimly lit room. The experiment was controlled by E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA). Eye movements were monitored by the experimenter from outside the experimental booth with the help of the image of the eye provided by an EyeLink 1000 eye-tracker (SR-Research, Ontario, Canada). Eye movements were not recorded or analysed, but the experimenter assured that participants followed the instructions to look at the stimulus matrix. No deviations from the instructions were noted, probably because it was very difficult to perform the task in peripheral vision.

The visual stimulus was a five-by-five matrix of 8 × 8 cm (or 11.3° × 11.3° of visual angle, width × height) shown on a computer screen (30 × 39 cm, or 36.9° × 44.3°). When the matrix was shown in a quadrant, there was a margin of 0.4 cm (0.6°) to the edge of the screen. A variable number of cells in the matrix were filled depending on the visual span of each participant.

The filled squares marked positions that had to be remembered. In order to avoid patterns that were easy to remember such as clusters, lines or geometric figures, matrices had been created and selected previously. The same 20 matrices were used for all participants, but their assignment to the experimental conditions was random.

Procedure and span evaluation. The procedure was almost the same as the one we used in a recent paper (Carlei & Kerzel, 2014), but this time the phonological loop was blocked in order to force visual encoding. Participants had to repeat two nonsense syllables throughout the experiment (e.g., badabada), which prevented participants from re-coding the matrices as a series of numbers (e.g., one number for each column containing a square). The syllables were presented via headphones and participants had to repeat the syllables at the same tempo (1 syllable/second) and approximate volume. Compliance in the articulatory suppression task was monitored by the experimenter. A failure to comply was

to miss a syllable, to not respect the tempo or to be inaudible to the experimenter. All our participants managed to follow this instruction.

In the first part of the experimental session, we determined the visual span for each participant (see Lecerf & de Ribaupierre, 2005). For the span evaluation, matrices were always displayed at the centre of the screen. The presentation time was one second per filled square (e.g., for a matrix with three filled squares, the presentation time was three seconds). Subsequently, the screen went blank for 150 ms and finally, an empty response matrix was displayed. The blank period between the stimulus and the response matrix created a flicker that erased the iconic image of the stimulus matrix. When the response matrix was shown, the mouse cursor was available, so that the participant could indicate the remembered positions by clicking on the respective squares. There was no time limit during the response period. Once the participant was satisfied with the response, she confirmed it by clicking on a separate button. A trial was considered correct if all square positions were correctly reproduced. At the beginning of the experiment, participants went through seven practice trials followed by immediate performance feedback. Then, the span evaluation started with two filled squares. For each number of squares, three consecutive repetitions were performed. When at least one trial of the three repetitions was correct, the number of squares on the next trial was increased by one. When the participant failed all three repetitions, the procedure stopped and the previous number of squares with at least two correct responses was considered the participant's memory span.

Experimental task. The procedure was as in the span evaluation with the following exceptions. Stimulus and response matrix were not shown in the centre, but in one of the quadrants. Before presentation of the stimulus matrix, the fixation cross was replaced for 250 ms by an arrow guiding participants to the quadrant of the upcoming matrix. No feedback was given. The duration of the experiment was about 20 minutes (including practice trials and span procedure).

Participants worked through 20 trials following from a 2 (number of squares: span, span + 1) × 2 (diagonally opposed quadrants) × 5 (repetitions) design. Participants in the first group saw matrices in the upper left and in the lower right quadrants, whereas participants in the second group saw matrices in the lower left and the upper right quadrants of the screen.

Results and discussion

The mean memory span and the range of the span for Experiments 1–3 are shown in Table 1. The mean percentage of correct responses for each condition collapsed across span and span + 1 is shown in Figure 2A. For the first group, the percentage of correct responses was higher in the upper left corner than in the lower right corner (68% vs. 53%), $F(1, 16) = 24.27$, $p < .001$, $\eta_p^2 = .60$. This result confirms that activation of the right hemisphere by looking towards the left

TABLE 1
Results from Experiments 1–3

	Span	
Experiment	*Mean*	*Range*
1	5.4	3–7
2	4.6	3–7
3	4.6	3–7

The span refers to the number of squares participants were able to memorize.

improves visuo-spatial short-term memory (Carlei & Kerzel, 2014). For the second group, there was no difference between the lower left and the upper right corner (50% vs. 50%), $F(1, 17) = 0$, $p = 1$. Further, we performed a mixed-design analysis of variance (ANOVA) with one within-subjects (2 matrix positions: left, right) and one between-subjects factor (2 vertical positions: upper left/lower right, lower left/upper right). We found a main effect of matrix position, $F(1, 33) = 5.99$, $p = .020$, $\eta_p^2 = .154$, and an interaction effect, $F(1, 33) = 5.99$, $p = .020$, $\eta_p^2 = .154$, showing that only the upper left was better than the remaining conditions.

Thus, the advantage of stimuli on the left, which we had observed previously (Carlei & Kerzel, 2014), only occurred when the stimuli were presented in the upper left corner. This discrepancy may be explained by differences in the procedure and sample. In our previous research (Carlei & Kerzel, 2014), we separated participants according to the strategy they used to perform the task. We suspected that participants who transformed the visual stimulus into a visual code (i.e., a mental image) relied on visual memory, whereas participants who transformed the visual stimulus into a verbal code (i.e., numbers representing positions) relied on verbal memory. However, the classification of participants was post hoc and possibly unreliable because there was no way of knowing whether a certain coding strategy had been consistently applied. Blocking the phonological loop is a more reliable way to disengage verbal memory. Also, the sample size for either strategy was small in our previous study, which may have prevented a significant interaction to emerge. Further, the current sample was selected with respect to gender (only women) and laterality (only strongly right-handed), whereas the previous sample was completely random. Thus, our present methods reduced the measurement error, which may explain why the effect of gaze direction was confined to a smaller area of space (upper left quadrant vs. entire left side).

EXPERIMENT 2

In order to disentangle visual and positional memory stores, we changed the presentation mode of the matrices. Observers saw the squares sequentially (see Figure 1B) to specifically request positional memory (Pickering et al., 2001).

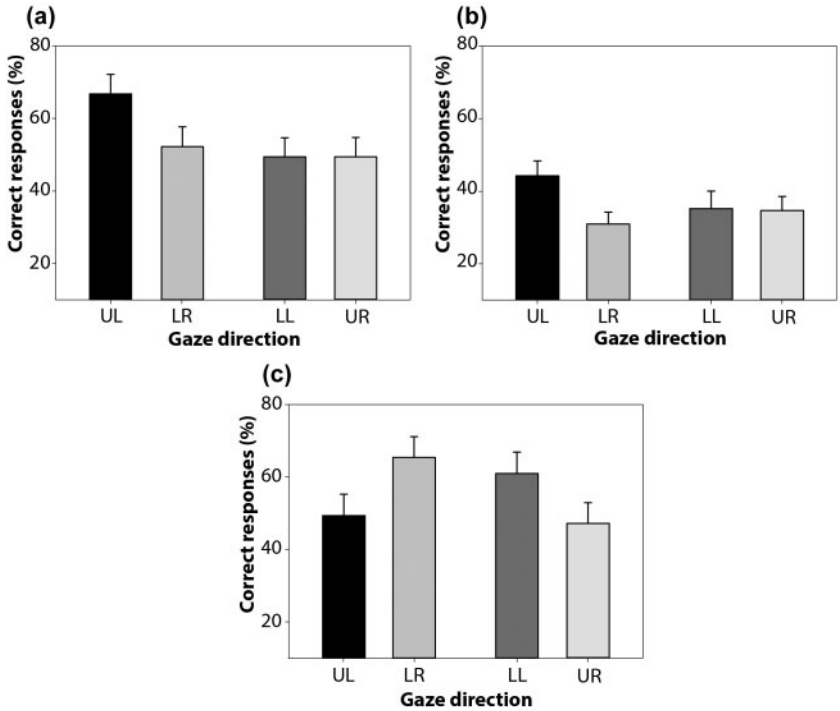

Figure 2. Results from Experiments 1, 2 and 3 are shown in panels A, B and C, respectively. Percentage of correct responses and standard error is shown as a function of gaze direction: Upper Left vs. Lower Right (UL vs. LR) in one group and Lower Left vs. Upper Right (LL vs. UR) in another group of participants.

Methods

Forty-three female students at the University of Geneva (aged from 17 to 24 years) participated in this experiment for course credit. All participants were strongly right-handed (with a score equal or above 80 on a scale of 100 on the Edinburgh Handedness Inventory). None of them had previously participated in the first experiment. Conditions were the same as in Experiment 1; in the first group, 25 participants saw matrices in the upper left and in the lower right corners whereas in the second group, 18 participants saw matrices in the lower left and the upper right corners of the screen.

The experimental procedure was also identical to the first experiment. The only difference was that participants saw the squares sequentially. The presentation time of each square was fixed at one second, resulting in identical total presentation times of the matrices (for the same number of squares) in Experiments 1 and 2.

Results

Figure 2B shows higher percentage of correct responses for the upper left corner than for the lower right corner in the first group (44% vs. 31%), $F(1, 24) = 11.96$, $p = .002$, $\eta_p^2 = .333$. In the second group, there was no difference between the lower left and upper right quadrant (35% vs. 34%), $F(1, 17) = .01$, $p = .907$. As in Experiment 1, a mixed-factors ANOVA revealed a main effect of lateral position, $F(1, 41) = 5.26$, $p = .027$, $\eta_p^2 = .114$, and a significant interaction, $F(1, 41) = 4.44$, $p = .041$, $\eta_p^2 = .098$, confirming that elevation also played a significant role with better performance in the upper left quadrant.

Discussion

We confirmed the advantage of the upper left quadrant for positional memory that we had already observed for visual memory in Experiment 1. We suggest that gaze direction activates brain areas associated with the respective vertical or horizontal hemifield. Therefore, our results are consistent with studies showing that visual and positional short-term memory are two subsystems that both rely on the right hemisphere. Further, both may be facilitated by the activity of the inferior temporal cortex, which is thought to be involved in attention to the upper visual field (Rapcsak et al., 1988; Shelton et al., 1990).

EXPERIMENT 3

The first two experiments have revealed that both visual and positional memory stores show an advantage for gaze directed to the left. Based on known hemispheric asymmetries, we expect that object-location binding will be improved with gaze directed to the right as it is associated with functioning of the left hemisphere (Kessels et al., 2002).

Method

Thirty-six female students at the University of Geneva (aged from 18 to 25 years) participated in this experiment for course credit or pay (15 CHF). All participants were strongly right-handed (with a score equal or above 80 on a scale of 100 on the Edinburgh Handedness Inventory). Nobody knew any Japanese.

At the beginning of the experiment, the object-location binding span was determined for each of our subjects by increasing the number of symbols until participants were unable to provide a correct answer. After the presentation of the stimulus matrix, participants were asked to recall the position of each Japanese symbol (see Figure 3). Blue dots were displayed to indicate the stimulus positions in the test phase and participants had to assign a symbol to each

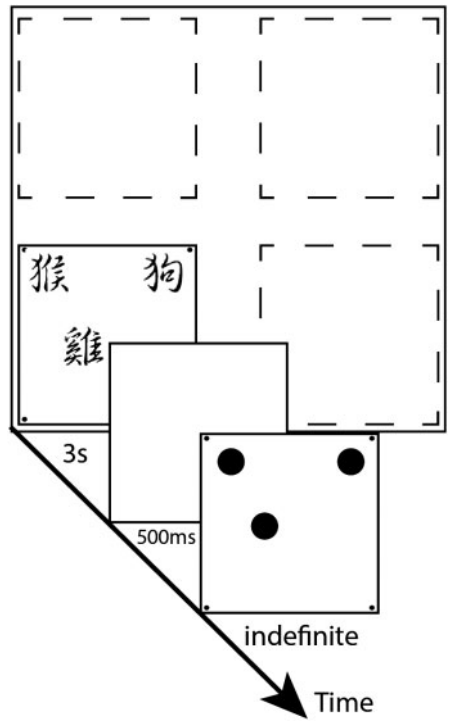

Figure 3. Illustration of the object-location binding paradigm in Experiment 3. The stimulus matrix appeared at once in one of the quadrants for as many seconds as there were Japanese symbols (3 seconds in the example). At the end of the presentation, a response matrix appeared. Dots indicated the positions of previously displayed stimuli. Participants clicked on the dots to browse through all the symbols displayed initially.

location. To assign a symbol to a location, participants left-clicked on the dot to browse through the different objects (i.e., the image shown at the dot location changed with each click). Right-clicking allowed the participants to browse backwards. For each location, the participant could browse all symbols displayed initially. Once satisfied with the response, the participant proceeded to the next trial by clicking on a separate button.

In the experiment proper, the same procedure as in the span test was employed, but the position of the stimulus matrix (and therefore gaze position) was manipulated. As in our previous experiments, participants experienced two counterbalanced conditions (upper left/lower right or lower left/upper right) with 10 trials for each quadrant. There were 18 participants in both groups. In the two conditions, matrices were displayed in random order in two of the four corners of the screen.

Results

Figure 2C shows that percentage of correct responses in the first group was higher in the lower right corner than in the upper left corner (66% vs. 49%), $F(1, 17) = 13.18$, $p = .002$, $\eta_p^2 = .437$. In the second group, the percentage of correct responses was higher in the lower left corner than in the upper right corner (61% vs. 47%), $F(1, 17) = 10.49$, $p = .005$, $\eta_p^2 = .382$. A mixed-factors ANOVA showed no main effect of lateralization but an interaction, $F(1, 34) = 23.63$, $p < .001$, $\eta_p^2 = .410$, confirming better performance with gaze directed downwards.

Discussion

Consistent with the hypothesis that vertical eye movements would activate cortical regions responsible for improved visual discrimination in the lower visual field, we observed better performance when gaze was directed downwards and participants had to visually discriminate unknown Japanese symbols.

However, we did not find any difference in laterality. We had predicted better performance when observers looked to the right, consistent with the deficit in object-location binding observed after right-hemisphere lesions (Kessels et al., 2002). In our view, this discrepancy is accounted for by our stimuli that discouraged verbal strategies because they could not be named. In contrast, the stimuli in Kessels et al. (2002) were everyday objects that could be easily named. Therefore, Kessel et al.'s conclusion that object-location binding relies on the left hemisphere may arise from the contribution of verbal memory to task performance. Our results suggest that without the involvement of verbal processing, the lateralization to the left hemisphere disappears. However, more work is needed to confirm this conclusion.

GENERAL DISCUSSION

In Experiments 1 and 2, better performance was observed when gaze was directed to the upper left quadrant. In Experiment 3, subjects performed better when the task was performed in the lower visual field without any difference between left and right.

The finding of Experiments 1–2 was predicted and is in line with studies mentioned above showing that visual and positional memory tend to be located in the right hemisphere (Kessels et al., 2002) and may be facilitated by the activation of the inferior temporal cortex (Rapcsak et al., 1988; Shelton et al., 1990) when the stimuli are presented in the upper visual field. In the first two tasks, the participant had to remember different positions of the same "object" (i.e., a black square). These tasks do not need any fine discrimination of the displayed matrices but only memorization of simultaneous (visual memory) or consecutive (positional memory) positions. In other words, these tasks involve

memory representations in which relations between objects are more important than the visual details of individual objects. There is evidence that processing global aspects of visual stimuli is facilitated in the left visual field compared to the right visual field (Sergent, 1982). We claim that the matrix task in Experiments 1–2 also involved global visual processing to store spatial relations, which explains why performance was better when gaze was directed to the left and consequently, the right hemisphere was activated.

It is more difficult to situate the effect of vertical gaze position (i.e., advantage in the upper left quadrant) in the literature. Perhaps the advantage with upwards gaze is consistent with Previc's (1990) idea that visual search or attention is better in the upper visual field. More attention is definitely beneficial in our paradigm, but it is difficult to reconcile better performance in the upper visual field with previous research on vertical hemifield asymmetries that have used vastly different tasks and obtained mixed results (Carrasco et al., 2001; Genzano, Di Nocera, & Ferlazzo, 2001; He et al., 1996; Rezec & Dobkins, 2004). When comparing our results with those of Niebauer and Christman (1998), one may conclude that the activation of cortical areas involved in categorical judgements of spatial relations improves performance in our task. Possibly, distance information was not as important as categorical relations (left of, right of, etc.) because the grid had only five rows and columns. If we had required our participants to judge distances more accurately, the advantage of upward gaze may have turned into an advantage of downward gaze.

Neural substrates

Our results showed that manipulating orientation of gaze is a way to differentiate subcomponents of visuo-spatial short-term memory. Moreover, our findings support the hypothesis that horizontal gaze increases contralateral hemispheric activation (cf. Propper et al., 2012) and facilitates cognitive functions associated with the activated hemisphere (cf. introduction). We believe that our unilateral gaze method has similar effects as the unilateral visual stimulation method used by Schiffer et al. (2004). When vision was limited to only one hemifield by wearing special glasses, Schiffer et al. observed stronger activation in the contralateral cerebral hemisphere.

In addition to the distinction between the left and right hemisphere, there is also neurophysiological evidence for the dichotomy between the lower and upper visual field. For instance, Portin, Vanni, Virsu, and Hari (1999) have confirmed the visual discrimination advantage for the lower field by showing differences in magneto-encephalographic activation of occipital regions. Also, Qu, Song, and Ding (2006) found that the early N1 component was larger in the lower visual field compared to the upper field over the occipito-parietal areas while the P1 component, which is modulated by spatial selective attention, was more pronounced for the upper visual field.

Based on studies investigating cerebral differences between attention directed to the upper and lower visual field (Rapcsak et al., 1988; Shelton et al., 1990), we claim that vertical ocular movements will activate different parts of the brain. According to this hypothesis, looking up will activate ventral parts of the brain such as temporal lobes whereas looking down will activate dorsal parts of the brain such as parietal lobes. While these hypotheses are in line with the reported effects of gaze direction, they clearly need further testing in neurophysiological experiments.

Non-visual eye movements

It is interesting to note that research on eye movements has mostly focused on visually triggered saccades (Land & Tatler, 2009). The main purpose of saccadic eye movements is to place the projection of a visual stimulus on the part of the retina with the highest spatial resolution (Young & Sheena, 1975). Far less research has been conducted on non-visual saccades that occur when a person is not looking at a specific visual stimulus, but is engaged in some internal cognitive processing such as thought or imagination. Unlike visual saccades, they are devoid of a visual purpose, occur independently of visual stimulation and are not consciously controlled.

Non-visual saccades have been described as "random", "spontaneous" or as "waking ocular rapid movements" (Lynch, 1980; Weitzenhoffer & Brockmeier, 1970). They are often not even noticed by the person performing them, suggesting that non-visual eye movements are rather automatic and do not require conscious attention.

While most studies agree that non-visual eye movements are an epiphenomenon of mental processes, there is some recent evidence that the execution of eye movements changes cognitive functioning. Christman, Garvey, Propper, and Phaneuf (2003) asked participants to make large ocular movements from left to right during 30 seconds before recalling a list of words or autobiographical events. The authors found that horizontal saccades improved recall, while vertical saccades did not have any effect. The authors hypothesized that lateral saccades resulted in sequential activation of the left and right hemispheres, which improved hemispheric interaction (Christman & Garvey, 2001) and subsequently improved episodic memory. Consistent with our assumptions, changes of gaze direction are thought to result in changes of cortical activation. From our perspective, it would be interesting to investigate whether lateral eye movements also affect visual short-term memory, which we found to be improved when observers looked at the upper left.

Neurolinguistic programming

Further claims of a causal link between gaze direction and behaviour come from Neuro-Linguistic Programming (NLP). NLP is a set of models and techniques

aimed at improving communication skills (Bandler & Grinder, 1979). This discipline is currently considered as a pseudo-science by most researchers (Witkowski, 2010). Nevertheless, it is interesting to note that NLP holds that non-visual eye movements ("ocular access") reflects our way of thinking and that gaze direction may unconsciously help us to retrieve existing mental representations or to create new ones (Buckner, Meara, Reese, & Reese, 1987). The NLP model on eye movements claims that looking to the upper left is a way to increase the retrieval of images from memory. The findings of Experiments 1 and 2 with better performances when gaze was directed to the upper left quadrant for visual and positional memory support the model. It is more difficult to interpret the results from Experiment 3 in light of NLP theory because there are no specific assumptions for object-location binding.

Conclusion

We investigated the effects of gaze direction on the different components of visual short-term memory. Our findings demonstrate the functional role of gaze direction in cognitive processing and contribute to a better understand of hemispheric asymmetries and the cortical specialization. Further, our insights may be useful in everyday life. For instance, looking to the left may increase performance in tasks involving visual short-term memory.

REFERENCES

Bandler, R., & Grinder, J. (1979). *Frogs into princes: Neuro linguistic programming*. Moab: Real People Press.

Buckner, M., Meara, N. M., Reese, E. J., & Reese, M. (1987). Eye-movement as an indicator of sensory components in thought. *Journal of Counseling Psychology*, *34*, 283–287. doi:10.1037/0022-0167.34.3.283

Carlei, C., & Kerzel, D. (2014). Gaze direction affects visuo-spatial short-term memory. *Brain and Cognition*, *90*, 63–68. doi:10.1016/j.bandc.2014.06.007

Carrasco, M., Talgar, C. P., & Cameron, E. L. (2001). Characterizing visual performance fields: effects of transient covert attention, spatial frequency, eccentricity, task and set size. *Spatial Vision*, *15*(1), 61–75. doi:10.1163/15685680152692015

Christman, S. D., & Garvey, K. (2001). *Bilateral eye movements reduce asymmetries in hemispheric activation*. Paper presented at the EMDR International Association Conference, Austin, TX.

Christman, S. D., Garvey, K. J., Propper, R. E., & Phaneuf, K. A. (2003). Bilateral eye movements enhance the retrieval of episodic memories. *Neuropsychology*, *17*, 221–229. doi:10.1037/0894-4105.17.2.221

Christman, S. D., Propper, R. E., & Dion, A. (2004). Increased interhemispheric interaction is associated with decreased false memories in a verbal converging semantic associates paradigm. *Brain and Cognition*, *56*, 313–319. doi:10.1016/j.bandc.2004.08.005

Darling, S., Della Sala, S., & Logie, R. H. (2009). Dissociation between appearance and location within visuo-spatial working memory. *Quarterly Journal of Experimental Psychology*, *62*, 417–425. doi:10.1080/17470210802321984

Feng, J., & Spence, I. (2014). Upper visual field advantage in localizing a target among distractors. *I-Perception*, *5*(2), 97–100. doi:10.1068/I0625rep

Genzano, V. R., Di Nocera, F., & Ferlazzo, F. (2001). Upper/lower visual field asymmetry on a spatial relocation memory task. *Neuroreport*, *12*, 1227–1230. doi:10.1097/00001756-200105080-00034

Goldstein, A., & Babkoff, H. (2001). A comparison of upper vs. lower and right vs. left visual fields using lexical decision. *Quarterly Journal of Experimental Psychology. A: Human Experimental Psychology*, *54*, 1239–1259. doi:10.1080/713756008

Gordon, J., Shapley, R., Patel, P., Pastagia, J., & Truong, C. (1997). The lower visual field is better than the upper visual field at red/green recognition. *Investigative Ophthalmology and Visual Science*, *38*, 4199–4199.

Grabowska, A., Herman, A., Nowicka, A., Szatkowska, I., & Szelag, E. (1994). Individual-differences in the functional asymmetry of the human brain. *Acta Neurobiologiae Experimentalis*, *54*, 155–162.

Habib, R., Nyberg, L., & Tulving, E. (2003). Hemispheric asymmetries of memory: The HERA model revisited. *Trends in Cognitive Sciences*, *7*, 241–245. doi:10.1016/S1364-6613(03)00110-4

Hagenbeek, R. F., & Van Strien, J. W. (2002). Left-right and upper-lower visual field asymmetries for face matching, letter naming, and lexical decision. *Brain and Cognition*, *49*(1), 34–44. doi:10.1006/brcg.2001.1481

Harmon-Jones, E. (2006). Unilateral right-hand contractions cause contralateral alpha power suppression and approach motivational affective experience. *Psychophysiology*, *43*, 598–603. doi:10.1111/j.1469-8986.2006.00465.x

He, S., Cavanagh, P., & Intriligator, J. (1996). Attentional resolution and the locus of visual awareness. *Nature*, *383*, 334–337. doi:10.1038/383334a0

Kessels, R. P. C., Kappelle, L. J., de Haan, E. H. F., & Postma, A. (2002). Lateralization of spatial-memory processes: evidence on spatial span, maze learning, and memory for object locations. *Neuropsychologia*, *40*, 1465–1473. doi:10.1016/S0028-3932(01)00199-3

Land, M. F., & Tatler, B. W. (2009). *Looking and acting: Vision and eye movements in natural behaviour*. Oxford: Oxford University Press.

Lecerf, T., & de Ribaupierre, A. (2005). Recognition in a visuospatial memory task: The effect of presentation. *European Journal of Cognitive Psychology*, *17*(1), 47–75. doi:10.1080/09541440340000420

Levine, M. W., & McAnany, J. J. (2005). The relative capabilities of the upper and lower visual hemifields. *Vision Research*, *45*, 2820–2830. doi:10.1016/j.visres.2005.04.001

Logie, R. H. (2003). Spatial and visual working memory: A mental workspace. In D. E. Irwin & B. H. Ross (Eds.), *Psychology of learning and motivation: Cognitive vision* (Vol. 42, pp. 37–78). New York: Academic Press.

Lyle, K. B., Logan, J. M., & Roediger, H. L. (2008). Eye movements enhance memory for individuals who are strongly right-handed and harm it for individuals who are not. *Psychonomic Bulletin & Review*, *15*, 515–520. doi:10.3758/Pbr.15.3.515

Lynch, J. C. (1980). The functional-organization of posterior parietal association cortex. *Behavioral and Brain Sciences*, *3*, 485–499. doi:10.1017/S0140525X00006324

Niebauer, C. L., & Christman, S. D. (1998). Upper and lower visual field differences in categorical and coordinate judgments. *Psychonomic Bulletin & Review*, *5*(1), 147–151. doi:10.3758/Bf03209471

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*(1), 97–113. doi:10.1016/0028-3932(71)90067-4

Pelizzon, L., Brandimonte, M. A., & Favretto, A. (1999). Imagery and recognition: Dissociable measures of memory? *European Journal of Cognitive Psychology*, *11*, 429–443. doi:10.1080/713752323

Pickering, S. J., Gathercole, S. E., Hall, M., & Lloyd, S. A. (2001). Development of memory for pattern and path: Further evidence for the fractionation of visuo-spatial memory. *Quarterly*

Journal of Experimental Psychology Section A – Human Experimental Psychology, *54*, 397–420. doi:10.1080/02724980042000174

Portin, K., Vanni, S., Virsu, V., & Hari, R. (1999). Stronger occipital cortical activation to lower than upper visual field stimuli – Neuromagnetic recordings. *Experimental Brain Research*, *124*, 287–294. doi:10.1007/s002210050625

Previc, F. H. (1990). Functional specialization in the lower and upper visual-fields in humans – Its ecological origins and neurophysiological implications. *Behavioral and Brain Sciences*, *13*, 519–541. doi:10.1017/S0140525X00080018

Propper, R. E., Brunyé, T. T., Christman, S. D., & Januszewskia, A. (2012). Look over there! Unilateral gaze increases geographical memory of the 50 United States. *Brain and Cognition*, *78* (1), 59–62. doi:10.1016/j.bandc.2011.10.002

Propper, R. E., McGraw, S. E., Brunye, T. T., & Weiss, M. (2013). Getting a grip on memory: Unilateral hand clenching alters episodic recall. *PLoS ONE*, *8*, e62474. doi:10.1371/journal.pone.0062474

Qu, Z., Song, Y., & Ding, Y. L. (2006). Asymmetry between the upper and lower visual fields: An event-related potential study. *Chinese Science Bulletin*, *51*, 536–541. doi:10.1007/s11434-006-0536-3

Rapcsak, S. Z., Cimino, C. R., & Heilman, K. M. (1988). Altitudinal neglect. *Neurology*, *38*, 277–281. doi:10.1212/WNL.38.2.277

Rezec, A. A., & Dobkins, K. R. (2004). Attentional weighting: A possible account of visual field asymmetries in visual search? *Spatial Vision*, *17*, 269–293. doi:10.1163/1568568041920203

Schiffer, F., Mottaghy, F. M., Vimal, R. L. P., Renshaw, P. E., Cowan, R., Pascual-Leone, A., … Rohan, M. (2004). Lateral visual field stimulation reveals extrastriate cortical activation in the contralateral hemisphere: An fMRI study. *Psychiatry Research-Neuroimaging*, *131*(1), 1–9. doi:10.1016/j.pscychresns.2004.01.0020

Sergent, J. (1982). The cerebral balance of power: Confrontation or cooperation? *Journal of Experimental Psychology: Human Perception and Performance*, *8*, 253.

Shelton, P. A., Bowers, D., & Heilman, K. M. (1990). Peripersonal and vertical neglect. *Brain*, *113*, 191–205. doi:10.1093/brain/113.1.191

Tzourio-Mazoyer, N., Petit, L., Razafimandimby, A., Crivello, F., Zago, L., Jobard, G., … Mazoyer, B. (2010). Left hemisphere lateralization for language in right-handers is controlled in part by familial sinistrality, manual preference strength, and head size. *Journal of Neuroscience*, *30*, 13314–13318. doi:10.1523/Jneurosci.2593-10.2010

Weitzenhoffer, A. M., & Brockmeier, J. D. (1970). Attention and eye movements. *The Journal of Nervous and Mental Disease*, *151*(2), 130–142.

Witkowski, T. (2010). Thirty-five years of research on neuro-linguistic programming. NLP research data base. State of the art or pseudoscientific decoration? *Polish Psychological Bulletin*, *41*(2), 58–66. doi:10.2478/v10059-010-0008-0

Young, L. R., & Sheena, D. (1975). Survey of eye-movement recording methods. *Behavior Research Methods & Instrumentation*, *7*, 397–429. doi:10.3758/Bf03201553