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THINKING EYES

Why do we move our eyes when we think?

– Looking for a neural signature using EEG

Dissertação no âmbito do Mestrado Inter-universitário em Neuropsicologia Clínica e Experimental, orientada pelo Doutor Artur Pilacinski e pelo Doutor Gabriel Alexandre Baptiste Besson e apresentada à Faculdade de Psicologia e Ciências da Educação de Coimbra.

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Why do we move our eyes when we think?

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Maria João Lourenço de Matos

Thesis submitted for the Interuniversity Master's in Clinical and Experimental Neuropsychology, supervised by Doctor Artur Pilacinski and by Doctor Gabriel Alexandre Baptiste Besson and presented to the Faculty of Psychology and Educational Sciences of University of Coimbra.

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Resumo

Título: Thinking eyes - porque mexemos os olhos quando pensamos? - em busca de uma assinatura neuronal utilizando EEG

Palavras-chave: movimentos oculares não visuais; memória a longo prazo verbal; EEG; eye-tracking.

Qual é o maior país na África? Quantas plantas tens no teu apartamento? Provavelmente reparaste que quando tentas responder a essas questões mexes os teus olhos. Há uma ligação clara entre movimentos oculomotores e a memória, dado que para onde olhamos influencia a nossa memória e a nossa memória influencia para onde olhamos. No entanto, este fenómeno ainda não é bem compreendido. Recentemente, foi proposto que utilizamos navegações computacionais para organizar domínios não espaciais, entre os quais, a memória declarativa, e que a busca pela memória a longo prazo pode ter evoluído a partir do circuito responsável pela procura de informação no ambiente, enquanto o foco e manipulação da informação pode ter evoluído a partir do circuito responsável pelo foco em estímulos visuais relevantes. Nós estudámos movimentos oculares não visuais (MOnV) na evocação de informação na memória verbal a longo prazo, e como a procura pelo sistema de memória a longo prazo verbal é traduzida em MOnV, onde manipulamos o tipo de busca pelo sistema mnésico, e o nível de abstração dos estímulos em dois estudos com o mesmo paradigma, o primeiro com eye-tracking e o segundo com EEG. Os nossos resultados de ambos os estudos sugerem que os MOnV são um subproduto de mudanças atencionais que necessariamente envolvem a o circuito parieto-frontal responsável pelo planeamento de movimentos sacádicos, e que, quando pensamentos, nós mapeamos os mapas conceptuais tal como se estivéssemos a olhar para objetos. Este é o primeiro estudo sobre os mecanismos neuronais que suportam o movimento oculomotor enquanto pensamos. Apesar de não ser evidente em princípio, as suas implicações ajudam a explicar a evolução da inteligência humana a partir dos sistemas sensório-motores.

Abstract/ Summary

Title: Thinking Eyes: Why do we move our eyes when we think? – Looking for a neural signature using EEG

Keywords: non-visual eye-movements (NEMs); verbal long term memory; electroencephalogram (EEG); eye-tracking.

What is the largest country in Africa? How many plants do you have in your flat? You probably noticed that when trying to answer those questions your eyes move. There is a clear link between eye movements and memory, as where we look influences our memory and our memory influences where we look. However, this phenomenon is not yet well understood. It was recently proposed that we use the navigational computations to organize non-spatial domains, among them, declarative memory and that searching in long term memory might have evolved from the circuitry responsible for searching in the visual environment, whereas focusing on and manipulating information might have evolved from the network involved in focusing on relevant visual stimuli. We studied NEMs in verbal long term memory retrieval, and how mental search through the verbal long term memory system is translated into NEMs. We studied the retrieval of verbal long term memory, where we manipulated the type of search through the memory system and the abstractness of the stimuli in two studies, the first with eye-tracker, and the second with EEG. Our results from both experiments suggest that NEMs are a byproduct of attentional shifts that necessarily engage parieto-frontal saccadic planning network and that, when thinking, we scan the activated concept space just as if we were looking at the objects. This is the first study on the neural underpinnings of the phenomenon of eye movements while thinking. While unobvious at first, its implications shed new light on the evolution of human intelligence from sensorimotor systems.

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List of Abbreviations

DLPFC	Dorsolateral Pre-Frontal Cortex
EEG	Electroencephalography
EMR	Eye Movement Rate
fMRI	Functional Magnetic Resonance Imaging
ITI	Inter-Trial Interval
IPL	Inferior Parietal Lobe
LTM	Long-Term Memory
MTL	Medial Temporal Lobe
NEMs	Non-Visual Eye Movements
PEF	Pre-Frontal Eye Fields
PM	Pre-motor
PPC	Posterior Parietal Cortex
ROIs	Regions of Interest
SEF	Supplementary Eye Field
SCs	Superior Colliculus
WM	Working Memory

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"…people who think differently also, to some extent, see differently."

(Yarbus,1967, p. 211)

Introduction

There is an old and tight interplay between memory and oculomotor systems. In fact, you have probably noticed it yourself, you move your eyes around when retelling that old story your grandfather used to tell every winter or diving deep down your memory trying to remember the answers to a cursed test, or, maybe, just your grocery list. Because these eye movements do not subserve vision, they are called non-visual eye movements (NEMs). Such interaction cannot be accounted for by visual processing or acquired through experience, as the congenitally blind with no ocular nerve damage show NEMs (Kömpf & Piper, 1987). Moreover, these NEMs are involuntary and necessary: restricting eye movements during recall causes neural, functional, and mnemonic alterations (Liu, Rosenbaum, & Ryan, 2020). Although this is a phenomenon we experience in our everyday lives, it remains unclear why it occurs and if it has any hidden role.

In the current work we studied NEMs in verbal long term memory retrieval, and how mental search through the memory system is translated into NEMs. For that, we used behavioral and electrophysiologic data to study NEMs in three dimensions: memory performance, NEMs rate, and neural activity. We conducted two experiments, a behavioral one, with Eyetracking, and, built on the results and limitations of the former, a second experiment, using both eye-tracking and electroencephalography (EEG).

In the first section, Background, we start by discussing NEMs in cognition, with particular emphasis on memory. Then, we go over the oculomotor system and the tight link between oculomotor and memory systems. We briefly go over the spatial navigation system, as it is relevant to explain some core concepts to understand the next part of this section, on cognitive maps and how we navigate our memory, followed by the mechanism by which these might interact. At last, we introduce the EEG signals relevant to this study. In each experiment we go through Methods, Results and Discussion. Then, we present a General Discussion, where we integrate the results of both experiments with the previous knowledge. Finally, we conclude with the contributions of the study and propose promising

future studies, along with the limitations of our study, to be controlled in the following experiments.

1. Background

1.1 Non-visual Eye Movements

The repertoire of eye movements involves a variety of fixational and rotational eye movements that are central to vision. Some of those are particularly informative of cognitive processes, namely saccades, blinks, and pupil reflex.

Blinking acts as a protective measure, as it not only moistens the front surface of the eye but also protects the eye against approaching objects, while pupil reflex regulates the exposure of the retina to the light. Both regulate the amount of information processed by the visual system, therefore serving as an index of mental load/effort (Colzato et al., 2007; Joshi & Gould, 2020; Knapen, 2016; Liu et al., 2019; Pajkossy, Szőllősi, & Racsmány, 2020; Ptok, Hannah, & Watter, 2021) as the greater the mental effort the greater the pupil diameter; and longer and more frequent the blinks. The rationale behind this is that blinks block incoming information from the external world (Rosenbaum, 2009), which may serve as a mechanism to reduce the processing of irrelevant external visual information and focus on cognitive demands. For example, in a study by Kucewicz and colleagues (2018), participants blinked more often (21 versus 8 blinks per minute) and longer (120 versus 100 ms) during an idea generation task (internally focused) compared to a reading task (externally focused). Both measures provide complementary indices of information processing, as blinks appear to be especially sensitive to the onset/offset of stimulus-related information processing, whereas pupil dilation seems most sensitive to sustained information processing (Siegle, Ichikawa, & Steinhauer, 2008).

Only about 5 degree of the visual field we see in detail. Therefore, a visual scene needs to be scanned to build a coherent image from pieces. Saccades are rapid, short, ballistic movements that bring relevant information to the high-resolution fovea. However, saccadic eye movements are also involved in processes that do not subserve vision, such as working memory (Sahan, Dijck, & Fias, 2022), mental time travel (Hartmann et al., 2014), arithmetic (Salvaggio, et al., 2022), and long term memory retrieval (Ehrlichman et *al*., 2007).

In fact, among non-visual cognition, NEMs rate is higher for tasks that require long term memory (LTM) search (Ehrlichman et al., 2007; Micic et *al.*, 2010), compared to tasks requiring maintenance, sequential memory, and manipulation of information in short term memory.

In visual long term memory tasks, people make non-visual saccades in the direction of the remembered spatial location of previously presented visual stimuli and this has a facilitatory effect in episodic (Johansson, et *al.*, 2022) and scenic (Damiano, & Walther, 2019) memory recognition. For instance, Scholz, Mehlhorn, and Krems (2016) asked participants to remember a word that was associated with a visual stimulus on one quartile of a grid cell on the computer screen. Participants reliably looked at the previous location of the associated visual stimulus in a blank grid. Together, the literature suggests a functional role of eye movements in memory by reinstating the encoding context. However, people also make saccades while answering questions without any visual components. For example, Ehrlichman and colleagues (2007) compared tasks that required verbal LTM search (semantic, episodic, and autobiographical memory) with verbal tasks that did not require search in LTM (tasks requiring maintenance, sequential memory, and manipulation of information in short-term memory); the former elicited high NEMs rate (mean = 1.08), while the latter relatively low NEMs rate (mean = 0.52). The authors concluded that eye movements accompany memory processes, especially those requiring maintenance and search through long term memory. Building on their results, Micic, Ehrlichman, and Chen (2010) compared high-retrieval tasks (phonemic fluency) with low-retrieval tasks (adapted auditory n-back task) while manipulating gaze conditions (fixed gaze and free gaze). The authors found that NEMs rate in the free gaze condition was greater for the high retrieval tasks (mean = 1.08) than for low retrieval tasks (mean = 0.28). In the fixed gaze conditions, participants were able to reduce but not fully suppress eye movements, especially in the fluency tasks. Nevertheless, although the NEMs rate differed between conditions, the groups' performance was identical, suggesting that: 1. LTM retrieval is a critical trigger of saccadic generation in non-visual cognitive tasks, and 2. spontaneous saccadic activity accompanying high retrieval LTM tasks does not play a functional role in memory retrieval.

Although there is a clear link between eye movements and memory retrieval, this phenomenon is not yet well understood. Hence, to better understand how NEMs occur, we need to look at oculomotor and memory systems and how they interact, which will be the scope of the next sections.

1.2 The Oculomotor System

The oculomotor system is a complex, highly interconnected network, spread through different brain regions (such as multiple areas of cortex, brainstem, superior colliculus (SCs), basal ganglia, and cerebellum). Some eye movements are generated in the brainstem, but some are controlled by the cerebral hemispheres.

Frontal areas are responsible for the generation of both intentional saccades, blinks, and the maintenance of fixation (Coiner et *al.*, 2019). Specifically, Frontal Eye Field (FEF) is involved in saccades, and particularly in the generation of all voluntary (internally triggered) saccades, slow pursuit eye movements along with Medial Temporal Complex (MT), and the maintenance of fixation; this area is also activated during eye blinks (Coiner et *al.*, 2019). Supplementary Eye Field (SEF) relates to all areas involved in eye motor control; it is crucial in predictive eye movements and is involved in the motor preparation of successive saccades or saccade(s) combined with body movements (Pierrot-Deseillingny, 2002), although it is more active during increasingly cognitively demanding tasks (Coiner et al., 2019). Still within frontal lobe, DLPFC executive components of the oculomotor network are involved in eye motor control (Pierrot-Deseillingny, et *al.*, 2002), playing a crucial role in saccadic inhibition, decision processes, short-term spatial memory, as well as facilitating both predictive and anticipated saccades (Pierrot-Deseilligny, et *al.*, 2004; Pouget, 2015). Frontal cortex is also involved in the allocation of both top-down and bottom-up attention, namely FEF, as its connections with frontal areas are responsible for the encoding of the target (of the saccade) and saccade execution, whereas parietal connections are concerned with representations of the visual stimuli, and it is responsible for the encoding of the visual target and saccade execution (Schall, 2009).

Parietal areas are responsible for the control of both voluntary and reflexive (stimulus- driven) saccades and attention shifts. Parietal Eye Field (PEF) is responsible for the control of reflexive saccades and is likely involved in representing attentional priorities in multiple reference frames in navigation together with SEF (Coiner et *al.*, 2019), in spatial integration to create egocentric reference frames and exogenous attention, in conjunction with other regions of PPC. PEF is also modulated by head position, as a result of its role in sensorimotor integration (Pierrot-Deseilligny et al., 2004). It projects both to the FEF (mostly involved in visual processing) and to the Superior Colliculus (related with executing saccades; Pouget, 2015).

Below (Figure 1) is a depiction of the main cortical areas involved in saccadic control and related cognitive processes.

Figure 1.

Main cortical areas involved in the eye movement network.
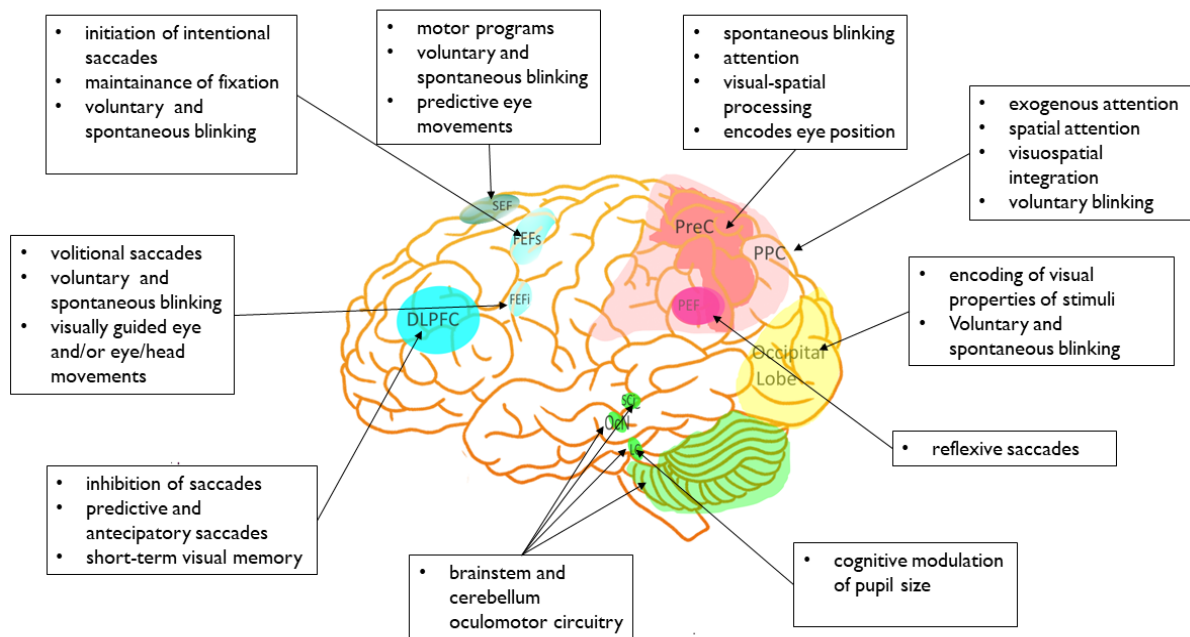
FEF is involved in the generation of intentional saccades, slow pursuit eye movements along with MT; maintenance of fixation; and contributes to the allocation of both top-down and bottom-up attention; is also activated during eye blinks. SEF relates to all areas involved in eye motor control; it is involved in the motor preparation of successive saccades or saccade(s) combined with body movements; DLPFC is responsible for the executive control of eye movements. PEF is responsible for the control of reflexive saccades, is involved in representing attentional priorities in multiple reference frames in navigation together with SEF, and in spatial integration. PEF is also modulated by head position, because of its role in sensorimotor integration.

DLPFC Dorsolateral Prefrontal Cortex, FEFi inferior Frontal Eye Field, FEF superior Frontal Eye Field, LC Locus Coeruleus, MT MiddleTemporal Complex, OcN Oculomotor Nucleus, PEF Parietal Eye Field, PPC Posterior Parietal Cortex, PreC Precuneus, SC Superior Colliculus, SEF Supplementary Eye Field.

Note. This is an oversimplification, with illustrative purposes of the areas relevant to this study. The brain image was retrieved from an open source website and the figure was created based on the works of Coiner and colleagues (2019); Pierrot-Deseilligny and colleagues (2004); and Pouget (2015).

1.3 Looking & Memory

Declarative memory is our ability to store and recollect events and facts that may persist over the course of a lifetime. It is acquired through our senses and so, the reciprocal

link between eye movements and memory comes as no surprise (see Ryan et *al*., 2020 for a review): as the visual input that forms our representations is formed by eye movements that scan the world, these representations are later stored and used to guide behavior in similar circumstances. Therefore, not only does where we look influence the formation and retrieval of memories, but information retrieved from memory guides our ongoing viewing (Hannula et *al*., 2010; Meister and Buffalo, 2016).

Neuropsychological studies show that looking is sensitive to medial temporal lobe (MTL) deterioration, as in the elderly and in amnesia. Older age comes with alterations in the hippocampus and in the MTL, and these are in turn accompanied by oculomotor alterations as well, reflected both in memory and in perception (Ryan et al., 2021). For instance, aging is associated with a decrease in visual exploration and with a decline in activation of hippocampus when faced with novelty, when compared to younger adults (Liu et al., 2018).

Findings from neuroimaging studies further support the relationship between the two systems. In macaques, single units of MTL regions are modulated by saccades (Ringo et al, 1994; Sobotka, Nowicka, & Ringo, 1997) and the activity of grid cells in the entorhinal complex (see below) has been shown to code for eye position/ the direction of a saccade (Killian et *al.,* 2015). In humans, neural activity in the hippocampus increases proportionally with the number of fixations when one is faced with novelty (Liu et al. 2017), and in turn, hippocampal activity predicts expression of memory which is reflected in subsequent eye patterns (Hannula et al., 2009). Furthermore, in a functional magnetic resonance imaging (fMRI) study, restricting visual exploration in a visual memory task is accompanied by functional differences both during encoding and subsequent recognition. (Liu, Rosenbaum, & Ryan, 2020).

1.4. Navigating Memory – searching through Cognitive Maps

This dynamic exchange between eye movements and memory does not occur in a vacuum. Looking back at 500 million years ago, the hippocampus homologue – the telencephalon – allowed early vertebrates the capability of storing memories – of foraging fields and haven, their spatial layout, and the order and timing in which obstacles should be encountered during a journey (Murray, Wise, & Graham, 2018), that is, a cognitive map (O'keefe, & Nadel, 1978).This provided animals evolutionary advantages, as such maps allowed animals to navigate outside their immediate sensory range, relying heavily in visual and auditory systems. In fact, recent studies suggest that the navigational organization of

space allows organizing non-spatial concepts, such as memory (Robin, Buchsbaum, & Moscovitch, 2018), odors (Bao, 2019), words (Viganò et al., 2021), abstract conceptual reasoning (Constantinescu, O'Reilly, & Behrens, 2016), and multidimensional feature space (Theves, Fernandez, & Doeller, 2019; 2020).

1.4.1 The Navigation System

Human navigation abilities rely on two intertwined mechanisms for the representation of the spatial environment. One mechanism allows allocentric navigation – place cells in the hippocampus, responsible for spatial relationships between landmarks independent of the subject's perspective and grid cells in the entorhinal cortex, responsible for spatial relationships between landmarks from the subject's position along with other cells in the parahippocampal complex (head cells, border cells, and speed cells) – that encodes locations relative to reference points external to the person (Moser & Moser, 2015). The other mechanism drives egocentric navigation: posterior parietal cortex (PPC) and the frontoparietal pathway perform transformations between sensory and motor systems (Whitlock, et al., 2008). This integration of signals from multiple reference frames is an integral part of PPC, combining visual with other sensory inputs into coordinates intelligible to the motor system. Specifically, PPC seems to be involved in computing the end goals of limb position relative to an eye-centered reference frame in visual search when the response is a motor command (Muggleton, et *al*., 2011), reflecting PPC's role in interpreting sensory signals for action.

In sum, we need an egocentric (e.g., body-centered) reference frame to coordinate goal-directed body movements and an allocentric (e.g., world-centered) reference frame to navigate from one location to another. Moreover, the more enduring world-centered representations combine with the more precise but fleeting egocentric representations to guide our behavior (Burgess, 2006) into malleable reference frames, with continuous transformation between the two frames of reference mediated by the retrosplenial cortex and PPC (Alexander, & Nitz, 2015; Byrne, Becker, & Burgess, 2007).

1.4.2 Navigating Memory or Memorable Navigations?

Given the closeness between the systems, Buzsáki and Moser (2013) proposed a model of phylogenetic continuity, according to which declarative memory systems arose from the navigational system. Under the assumption that semantic knowledge is acquired

progressively as similar episodes are encoded repeatedly by the self-referenced episodic memory system, the authors draw a parallel between allocentric navigation and semantic memory, and between egocentric navigation and episodic memory. As in navigation, grid cells provide the hippocampus with a metric, which in turn allow the relational sequential organization of space and consequent flexibility of behavior (facing new journeys and learning with old experiences) (Fortin, Agster, & Eichenbaum, 2002), as seen in non-spatial domains (Bao, et al., 2019; Constantinescu, O'Reilly, & Behrens, 2016; Robin, et al., 2018; Theves, et al., 2019; 2020; Viganò et al., 2021). Episodic memory, in turn, is felt and recollected as a continuous, coherent event, and as such, these personal experiences depend on the ability to create a timeline that organizes the details and temporal successions (Dere et al., 2006; Weger & Pratt, 2008) as if in an imaginary line extending backward and forward across future and past. This spatial distance of non-spatial domains (such as time, numerical knowledge, verticality, and ordered domains) is encoded from a view-point dependent perspective, which seems to be represented in egocentric low-dimensional schemas (Bottini & Doeller, 2018). For instance, in a study by Committeri and colleagues (2020) participants with better egocentric navigational abilities (i.e., path integration) performed better on an item recognition task, suggesting a relationship between egocentric capabilities and episodic memory. Further analysis revealed that the latter were predicted by the performance of the former and no correlation was found between egocentric abilities and semantic memory. Building on their results, Fragueiro and colleagues (2021) tested whether the interaction between egocentric and episodic memory skills could be found in physical, mental, and categorical domains, while controlling for short term memory potential confounds. The authors found a significant positive correlation between the scores in the egocentric navigation and the episodic memory tasks. It was also found a significant positive correlation between the episodic and the semantic memory scores, and between the egocentric navigation and the semantic memory performances. However, the correlation between egocentric navigation and semantic memory was not significant after controlling for episodic memory and short term memory performance, and it turned out that the relationship between egocentric navigation and semantic memory was mediated by episodic memory. Hence, the findings support that the egocentric abilities positively correlates and predicts the episodic memory performance, and that this relationship is independent of short term memory abilities.

1.4.3 Taking a Closer Look – The practicality of low-dimensional reference frames.

However, Viganò and colleagues (2021), showed that conceptual navigation also elicits absolute direction (low-dimensional schemas). In an fMRI study, participants learned to name 9 novel audiovisual objects, distinguishable for their size and for their sound, with 9 novel words. Participants trained three different tasks, an association task (match objects to their correct name), a naming task (the name of each object), and a semantic comparison task (compare the meaning of the words according to their underlying features). On the last day, participants compared pairs of words according to one of their defining features. Instead of a grid-like representation, the authors found absolute direction between stimuli in a comparative task, that is, individual directions were represented separately how the two concepts differ along their definitional dimensions together. This low-level representation was supported by a network of regions in frontoparietal and ventral occipital cortices. The authors suggest that this directional coding might be interpreted as a representation of the relation between the items of a conceptual space, which might be an efficient complementary mechanism for conceptual navigation besides the grid-like (allocentric/ map-like) representations.

Holding information in low-dimension schemas might be one of the solutions for navigating multidimensional information in a workable reference frame. That is, semantic representations, spanning through multiple domains, are organized in such highly complex and abstract conceptual geometries that forming patterns and organizing information might become impractical in a particular context. Consider, for instance, a ball. There are multiple dimensions one can think of – shape, weight, diameter, size, bounciness, surface, graspability (tennis vs football vs bowling), hardness (?), utility, etc. However, if I ask you the similarity between a ball and the sun, you must put aside all "irrelevant" dimensions and work with only the ones of interest (for instance, are round), in this case, where they converge. That is when egocentric, low-dimensional, representations become relevant, as they allow organizing and searching data by clustering together objects with similar properties for a given problem (Bottini & Doeller, 2018). Hence, low dimensional representations by sacrificing coding efficiency for robustness are useful for transfer of knowledge to different contexts, facilitating generalization and establishing relations between otherwise untouchable domains (Summerfield, Luyckx, & Sheahan, 2019).

1.4.4 Thinking Eyes – Searching Through Memory?

Ehrlichman and colleagues (2007) suggested that searching for information in LTM may be analogous to searching for information in the visual environment because higher cognitive functions may engage processes like those used by phylogenetically older systems of bottom up attention/perception. By analogy, people make saccades when they scan for information in long term memory and fixate more when locating a stimulus of interest, when scanning ceases and they focus on that information. Hence, they draw the parallel where the maintenance process is associated with visual fixation and the process of bringing in new information is associated with saccadic eye movements. The authors suggest that the ability to search for information in long-term memory may have evolved from the circuitry used for searching for information in the visual environment, while the ability to maintain information in the buffer may have come from the neural circuitry used for focusing on relevant visual stimuli. Nonetheless, whereas the phylogenetic continuity model focuses solely on the relationship between memory and navigation systems, this model makes the actual link between memory and eye movements.

As previously shown, we organize knowledge in navigational coordinates, mobilizing both allocentric (map-like; elevated complexity; high-dimensional schemas) and egocentric reference frames (along a continuum; low complexity; low dimensional schemas) to organize and navigate through information, according to the problem imposed. The link between navigation and oculomotor systems is clear, as one heavily relies on vision to search for information in the visual environment, a process carried by eye movements, to create a map of the environment (more enduring, allocentric representations), and construct view-point maps (precise but transient egocentric representations) that allow for self-motion in space and immediate actions. Briefly, visual information is routed to the superior colliculus (SC), where saccades are computed based on the salience (bottom-up) and relevance (top-down) of relevant information. A reflexive (bottom-up) saccade is triggered by the PEF, information is transmitted from the PEF to the FEF for active (top-down) fixation and from the intraparietal areas to the DLPFC for short term spatial memorization, which is involved in executive processes governing ocular motor behavior by inhibiting unwanted reflexive saccades (controlled by the PEF) or facilitating the triggering of anticipatory saccades (by the FEF) (Pierrot-Deseilligny et *al.*, 2004).These signals inevitably carry information about the relation of objects in the scene from an egocentric perspective, which allows inferior parietal lobe (IPL) to form representations of scene structure independent of its contents,

and thus potentially supporting relational generalization between similar scenes (Summerfield, Luyckx, & Sheahan, 2019). The contents of the egocentric frame are then maintained in working memory through reciprocal fronto-parietal connections (Dhindsa et *al.*, 2014) and object/landmark locations within PPC are continuously updated through reciprocal connections with the MTL (Whitlock et *al.,* 2008). Inferior parietal lobe (IPL) in particular, contains neurons with eye-centered (Andersen, Essick, & Siegel,1985), object-centered (Chafee, Averbeck, & Crowe, 2007), and world-centered (Snyder, et al., 1998) reference frames. These pathways between PPC and MTL could be used for spatial transformations between egocentric and allocentric systems. IPL also mediates abstract cognitive capabilities, such as mental time travel (Abraham, Schubotz, & von Cramon, 2008), social and symbolic relationships (Klostermann, Kane, & Shimamura, 2008; Parkinson, Liu, & Wheatley, 2014), working memory (Pilacinski, Höller-Wallscheid, & Lindner, 2020), and motor planning (Whitlock, 2017), posing, therefore, the PPC as a candidate to integrate the three systems.

If, in fact, we organize our knowledge according to navigational computations, and if the processes of search through long-term memory and maintenance in the episodic buffer were built on ancient systems that evolved from visual perception, as Ehrlichman and colleagues (2007) propose, then the NEMs that occur during internal processing may have no function and can be thought of as a byproduct of the evolutionary co-interaction of the three systems mobilized in lower-level cognition. In this case, we could expect one of two possibilities: we can expect saccadic eye movements to be an effect of overflow in the PPC during memory search/processing in working memory or to reflect the involvement of PPC in the construction of egocentric reference frames to manipulate information more flexibly.

1..5 To think or to look, is there even a difference? – Searching for the neural dynamics underlying eye moments in visual and non-visual saccades

As previously seen, two cortical areas have a crucial role in the generation of eye movements, PEF and FEF. PEF is the interface of sensory and motor processing. This area processes spatial information in many frames of reference (eye, head, and body centered) and is involved in coding spatial memory for saccades. FEF, in turn, is involved in the generation of voluntary saccades (see section 1.2). Studies have shown that both areas are involved in pro-saccade and anti-saccade generation (Bells, et *al.*, 2020; Connolly et al., 2002; Munoz, & Everling, 2004). The pro- and anti-saccade task is a simple paradigm that allows to

dissociate the stimulus component (visually driven) from the motor goal of the saccade. The rationale behind this task is that saccades toward (pro-saccade) and away from (anti-saccade) the target have the same stimulus component but an opposite goal component. The anti-saccade paradigm also tests saccade inhibition, because before performing a correct intentional anti-saccade in the opposite direction of a brief peripheral visual target, the subject has first to inhibit a reflexive saccade to the target. Hence, the first part of execution of an anti-saccade is under the control of the DLPF, whereas the second part, that is, the triggering of the intentionally anti-saccade (away from the target), depends on FEF control.

Synchronized brain activity gives rise to rhythmic activity that can be recorded using electroencephalography (EEG), which allows measurements with great temporal resolution. Synchronized brain activity may provide a mechanism to achieve large-scale communication and integration of cognitive processes across distant populations of neurons, allowing coherent cognition and behavior (Ward, 2003). From these, we can explore the spectral power (as a proxy of synchronization) of different frequency bands within or between tasks, and within the same or between different populations of neurons. Gamma band (> 30 Hz) would mediate the active maintenance of working memory (Jensen et al., 2007), by promoting and binding sensory information, and is also thought to play a decisive role in the activation and maintenance of neural representations (activated items from LTM; Herman et *al.*, 2004). Alpha band (8–14 Hz) would facilitate attention and memory processes – specifically, alpha synchronization would reflect a regulatory mechanism inhibiting task irrelevant areas and facilitating neural processes in task relevant networks whereas alpha band desynchronization has been related to increased processing or excitability of the respective areas (Köster & Gruber, 2022; Medendorp et al., 2007). Beta band (15- 40 Hz) has been proposed to be associated with motor control; endogenous, top-down attention, and communication between distal regions (Engel and Fries, 2010; Khanna and Carmena, 2014).

Focusing on the memory period in a delayed-saccade task (pro/anti-saccades) and using the high temporal resolution of magnetoencephalography (MEG), Medendorp and colleagues (2007) analyzed the temporal dynamics of sensorimotor processing during saccade planning. The authors found parietooccipital power suppression in the alpha band and power enhancements in the gamma band in the hemisphere contralateral to the stimulus. Van Der Werf, and colleagues (2008), exploring the same paradigm, found the

emergence of sustained direction selective high-frequency gamma activity over PPC during planning of forthcoming saccades. More specifically, by contrasting the spectral topographies for left versus right pro-saccades, they found significant sustained parietal gamma activity contralateral, compared to ipsilateral, to target location, and by comparing these results to the outcome of the anti-saccade task, the authors were able to distinguish two gamma-broad components, an early broadband component (40-85 Hz) modulated by stimulus location, and a second gamma band (85-105 Hz), which would appear later (~500 ms after stimulus presentation), selective to the direction of the forthcoming saccade. On the other side, the alpha band showed a general decrease in power during both pro- and anti-saccades, which the authors suggested would reflect ongoing sustained stimulus representation and a late build-up of the goal representation for the execution of the saccade. Similarly in frontal areas, Lachaux et al. (2006) have shown increased gamma-band power during both pro and anti- saccades in FEF. On a tangential complementary vein, Bells, and colleagues (2020) conducted an ERP study, also using MEG, with a pro/anti- saccade paradigm, focusing on the inhibitory mechanisms involved in the regulation of anti-saccades. The authors found the temporal sequence relative to stimulus of neural activity on correct anti-saccades, as it follows: contralateral PEF, followed by ipsilateral PEF, and then by ipsilateral FEF. Interestingly, they also observed greater frontal brain activity on anti-, compared to pro-saccade trials, as in the former neurons triggering automatic pro-saccades must be inhibited, or else direction errors occur.

1.4.6 The current study

Why do we move our eyes when we think? There is a clear link between eye movements and memory, as where we look influences our memory and our memory influences where we look. It was recently proposed that we use the navigational computations to organize non-spatial domains, among them, declarative memory. PPC plays an integrative part in egocentric navigation, memory, and eye-movements, and could be the intermediate between the three systems. Moreover, studies focus either on the link between eye movements and memory or on the link between memory and navigation systems. To the best of our knowledge, this is the first study on the power dynamics of oculomotor programming of non-visual eye movements in LTM search. We hypothesize that our "thinking eyes" are an epiphenomenon caused by PPC, reflecting the involvement of PPC in memory search.

For that, we studied NEMs in verbal long term memory retrieval, and how mental search through the verbal long term memory system is translated in NEMs. We employed behavioral and electrophysiological data to study NEMs in three dimensions: performance, NEMs rate, and spectral power. We conducted two experiments, a behavioral one, and built on the results and limitations of the former, a second experiment, using both eye-tracking and electroencephalography (EEG).
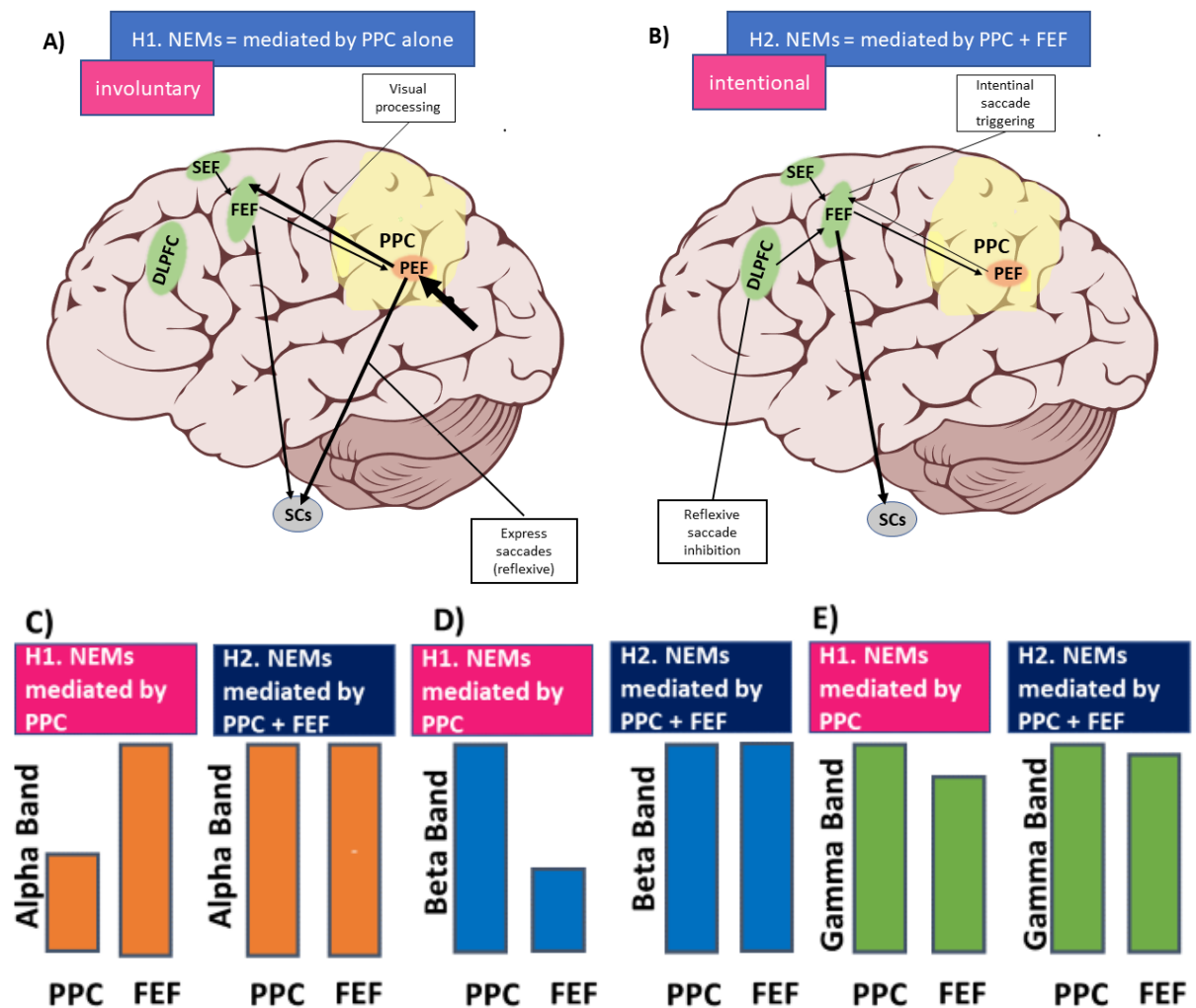
The first study aimed to see if the structure of search through the memory system (structured or not structured) would be reflected in differences in the rate of eye movements for the retrieval of verbal information from LTM. More precisely, it questioned if eye movements would vary according to the type of search in LTM and level of abstractness. In structured search, participants had to refer to the similarities between two elements whilst in the not-structured search, participants had to describe or define one element (see attachment 1). The questions were grouped in four blocks, with increasingly growing abstractness between blocks. We hypothesize that restricting search requirements likewise restricts eye movements – that is, open questions elicit more eye movements than structured questions, given that the former require more search in LTM. Eye movements were analyzed following type of question (open or structured) and block (reflecting increased abstractness). Additionally, eye movements were manipulated as the dependent variables and type of question and block as independent variables.

The aim of the second study was to assess the neural dynamics of NEMs during verbal long term memory retrieval. For such, we combined EEG and implemented the experimental task from the first experiment and a simple pro- followed by an anti-saccade task, in which participants had two small circles interlayered by a fixation cross and they were instructed to either look toward the blinking circle (pro) or avert the gaze, looking to the other circle (anti). We also asked whether restricting gaze during memory retrieval would impair performance. To the best of our knowledge, there is no study on the spectral dynamics of non-visual eye movements. Therefore, we aim to compare our thinking task with a pro/anti-saccade task. If NEMs are mediated by the same neural circuitry as reflexive saccades, we expect to find a similar activation to pro-saccades programming, as these are (**A**). Neuronally, this should translate into power enhancements in the gamma band and suppression of the alpha band in PPC programming of saccades. It is more challenging to predict what will happen in frontal areas, as there are no studies (with EEG/MEG) on the spectral power in FEF with similar paradigms as used here. However, we can speculate that

we will find a weaker markers activity (i.e., power) in frontal compared to parietal regions. On the other side, if NEMs are internally triggered, like voluntary saccades we would expect no differences between PPC and FEF (**B**) (see Figure 2.). We predicted that if NEMs are triggered by PPC alone (**A**), we would see higher synchronization of beta (**D**) and gamma (**E**) bands and higher desynchronization of alpha bands (**C**) in PPC, compared to PM. On the other hand, if saccadic eye movements are triggered by PPC and PM (**B**), then we would expect no substantial differences between frontal and parietal regions (see below).

Figure 2.

NEMs Hypotheses

2. Methods

2.1. Experiment 1

The first experiment is a behavioral study that aimed to see if the structure of search through the memory system (structured or open questions) would be reflected in NEMs for the retrieval of verbal information from LTM. More precisely, it questioned if eye movements frequency would vary according to the type of search in LTM and level of abstractness. We made two key predictions. First, open questions elicit more NEMs than structured questions, as constraint is associated with reduced search through the memory system (Ehrlichman, et al., 2007). Second, we predicted that greater levels of abstraction produce more NEMs and longer trials, as participants require more time to answer. For that, we utilized questions from WMS-III (Wechsler, 1997; Portuguese Version Cegoc, 2008), namely 20 questions from Similarities subtest, 10 questions from Information, and 10 questions from Comprehension (see methods). We used eye-tracking to record eye data that were then analyzed following the type of question (open or structured) and block (reflecting increased abstractness).

2.1.1 Subjects

Forty-five participants (13 males) took part in this experiment, naive to the experimental hypothesis and received no compensation for their participation. Thirty-three subjects had to be excluded from the sample due to poor data quality – loss of eye position during the experiment in more than 30% of the trials and/or equipment failure (irregular data sampling that could not be corrected for through interpolation). This was detected only during data preprocessing. All twelve subjects in the final sample (7 males; age M=29.73 years) were right-handed, had normal or corrected-to-normal vision and provided oral consent prior to participation. Participants were recruited from the University of Psychology and Educational Sciences of Coimbra and the surrounding Coimbra population. All experimental procedures were performed according to the Declaration of Helsinki.

2.1.2 Stimuli

Stimuli used in this experiment consisted of 40 questions retrieved from Information, Comprehension and Similarities subtests from Wechsler Adult Intelligence Scale (WAIS-III; Wechsler, 1997; Portuguese Version Cegoc, 2008). Half of the questions were from

Similarities (structured questions), 10 from Information (open questions) and the other 10 from Comprehension (open questions). Answers were scored as correct/incorrect according to WAIS-III criteria. All questions were presented via recorded audio files so that no visual processing was required and to ensure a standardization across participants. The open questions required comparing and finding the commonalities between two concepts while the structured questions involved defining or answering to single concepts. These questions involve not only LTM search and retrieval, but also verbal conceptualization and degree of abstract reasoning, as well as both word and acquired knowledge (Vocabulary); categorical thinking and logical abstractive (Similarities); together with cause-effect-relationships, social intelligence, and culture-loaded knowledge (Comprehension).

The 40 questions were divided in 4 blocks, each with 10 trials, randomized within blocks (see appendix 1). The stimuli were assigned so there would be a progressively increased level of abstraction from block to block (for example, what is a thermometer [1st block] vs. why do we pay taxes [4th block], or the similarity between a dog and a lion [1st block] vs. the similarity between a friend and a foe [4th block]).

2.1.3 Task

Participants were instructed to answer the best they could, and to think thoroughly when answering (to save "I do not know" to the last resource, unless they really did not know the answer).

Additionally, participants were instructed to fixate on a white central dot while listening to the questions and to look freely within the gray oval on the screen while answering, with 2 milliseconds inter trial interval. Participants received feedback of their performance at the end of each block, to stimulate their motivation. One of the researchers was responsible for moving on to the next block, as so, at the end of each, participants were given the chance to do a small break if they needed to (Figure 3).

Figure 3

Experimental task
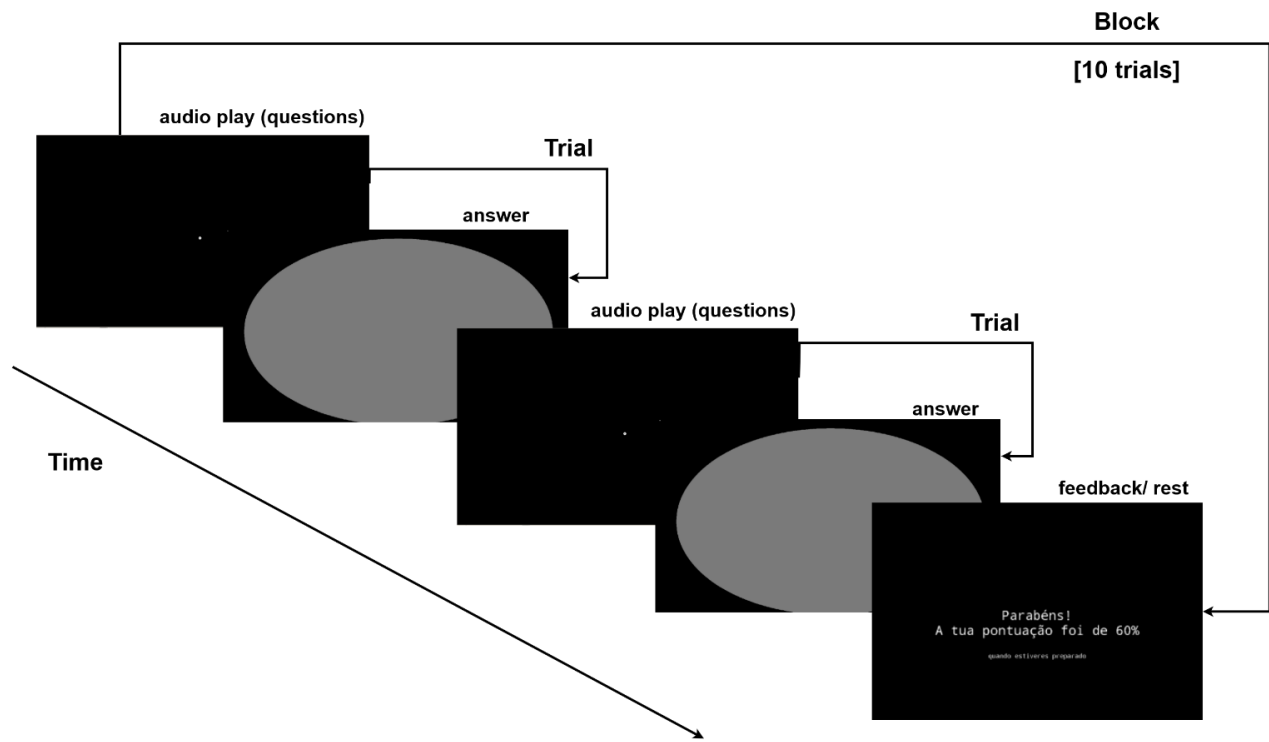
2.1.4 Apparatus

All experiments were performed using a Tobii TX300 eye tracker connected to an experimental computer running Opensesame v.3.2.8, with 1920 × 1080 pix. resolution and sampling rate of 300 Hz. We used a chinrest to stabilize the subjects' head position at 65 cm visual distance from the screen.

2.1.5 Analyses

2.1.5.1 NEMs Analyses. Eye movements were analyzed in the period between the end of question and the end of the answer. All analyses were performed in Matlab 2022a (MathWorks) based on raw eye data obtained from Tobii SDK.

Eye data were low pass filtered at 0.3 radians*pi/sample using a zero-phase filter with stopband attenuation of 60 dB applied to eye x and y position to remove noise. The data was interpolated to 300 Hz to remove duplicate data points or correct for missing data points. Then, the x and y eye positions were overwritten with the filtered data.

Saccades were detected using an eye-velocity-based algorithm. Eye velocities were calculated for x and y coordinates together and two thresholds were applied, one for detecting all saccades (50 deg/s), and another one to detect big saccades (100 deg/s), estimated according to saccadic amplitude/velocity ratio.

Eye blinks were detected based on the loss of eye position over ten continuous samples, and 30 samples before and 30 samples after the blink were removed to eliminate parts where the pupil was partially occluded (eyelid closure/pupil size change could corrupt the data and potentially be detected as a saccade or pupil size change).

Pupil constriction/dilation was calculated after smoothing the pupil data with a Gaussian kernel applied over 10 continuous samples.

Eye movement frequency was computed by dividing the number of eye movements by the number of seconds from the end of the question to the end of the answer.

2.1.5.1 Statistical Analyses. NEMs (saccadic and blink frequency, pupil dilation) and trial duration were analyzed using a 2 x 4 repeated measures ANOVA with type of question (open/structured) and block (1st, 2nd, 3rd, 4th) as factors. The alpha threshold for statistical significance was 0.05 and paired t-tests were run for post-hoc comparisons.

3. Results

To see if type of LTM search and abstractness (increasingly across block) had an effect on NEMs frequency and trial duration, we performed a 2 x 4 repeated measures ANOVA, with type of question (open/structured) and block (1st 2nd 3rd 4th) as factors, and NEMs type and trial duration (i. e., saccadic frequency, blink frequency, pupil size, and trial duration) as dependent variables.

The analysis revealed a main effect of type of question in blink rates ($F_{(1, 15)}$ = 4.327, p = 0.043, $\omega 2$ = 0.009), with significantly less blink rates in open compared to structured questions (M = - 0.056, SE = 0.025; t (1) = -2.211, p = 0.043). This effect was also found in trial duration ($F_{(1, 15)}$ = 9.548, p = 0.022, $\omega 2$ = 0.009), with longer trials in open comparatively to structured questions (M = 1554, SE = 503. t (1) = 3.090, p = 0.007).

A main effect of block was found in saccadic rates ($F_{(2, 42)}$ = 9.441, p <.001, $\omega 2$ = 0.137), with higher saccadic frequency rate in the first block, comparatively to the

second (M = 0.387, SE = 0.089; t(6)= 4.353 , p < 0.001); third (M = 0.387, SE = 0.089; t(5)= 4.353 , p < 0.001); and fourth (M = 0.385, SE = 0.089; t(5)= 4.330 , p < 0.001) blocks. Similarly, block effect was also found in blink rates (F (3, 45) = 4.327, p = .009, $\omega 2$ = 0.180), with significantly higher rates in the first block relatively to second (M = 0.275, SE = 0.097; t (5) = 2.839, p = 0.027); third (M = 0.294, SE = 0.027; t (5) = -2.211, p = 0.025); and fourth (M = 3.025, SE = 0.025; t (5) =2.950 , p = 0.025) blocks. This effect was also observed in trial duration (F (3, 45) = 7.610, p < 0.001, $\omega 2$ = 0.140), with significantly shorter trials in the first compared to the fourth blocks (M = - 5706, SE = 1566; t (5) = -3.643, p = 0.003); as well as in the second block, comparatively to third (M = - 4112, SE = 1566; t (5) = -2.265, p = 0.047), and fourth (M = -6717, SE = 1566; t (5) = -4.288, p < 0.01) blocks, but not between the third and the fourth blocks (M = - 2605, SE = 1566; t (5) = - 1.663, p < 0.206).

An interaction effect between type of question and block was found in trial duration (F (1, 9) = 5.289, p = 0.003, $\omega 2$ = 0.023). Post-hoc t-test revealed differences on open questions length between the first and fourth blocks (M = - 5429, SE = 1679; t (27) = - 3.232, p = 0.036), and between the second and the third (M = - 5718, SE = 1679; t (27) = - 3.232, p = 0.024) and fourth (M = - 6119, SE = 1679; t (27) = - 3.643, p = 0.014) blocks. On structured questions, both first and second blocks were significantly shorter than the fourth block (M = - 5983, SE = 1679; t (27) = - 3.562, p = 0.016; and M = - 7315, SE = 1679; t (27) = - 4.355, p = 0.001, respectively), while no statistically significant difference was found between the fourth and the third block (M = - 4809, SE = 1679; t (27) = - 3.643, p = 0.087).

There was no statistically significant effect found regarding pupil dilation.

We didn't find statistically significant differences between incorrect vs. incorrect answers in saccadic (t (15) = 0.317, p = 0.716) or blink (t (15) = 0.920, p = 0.372) rates.

Table 1. below presents a synthesis of mean NEMs and trial duration for open and structured questions across blocks.

Table 1.

Mean non-visual eye movements (NEMs) rate for open and structured questions across blocks.

NEMs Rate	1st Block		2nd Block		3rd Block		4th Block		Correct Answers	Incorrect answers
	Open	Struct.	Open	Struct.	Open	Struct.	Open	Struct.		
Saccades	1.220 (0.694)	1.279 (0.510)	0.877 (0.376)	0.849 (0.422)	0.851 (0.422)	0.875 (0.345)	0.894 (0.387)	0.835 (0.276)	0.852 (0.401)	0.807 (0.398)
Blinks	0.642 (0.468)	0.791 (0.758)	0.431 (0.203)	0.453 (0.285)	0.412 (0.233)	0.435 (0.179)	0.415 (0.285)	0.446 (0.214)	0.477 (0.304)	0.429 (0.207)
Pupil	5.132 (3.267)	4.859 (1.702)	4.356 (0.712)	4.392 (0.462)	4.449 (0.521)	4.417 (0.570)	4.043 (0.779)	4.329 (0.858)		
Trial (ms)	8859 (9254)	8290 (7322)	8169 (3289)	6235 (890)	13887 (6749)	9464 (4222)	14288 (7060)	14273 (7359)		

4. Discussion

The type of search through LTM has an impact on blink rates, as open questions produce less blinks compared to structured ones; and in trial duration, with open questions producing longer trials. Moreover, "abstractness" (increasing through blocks) also affects NEMs, with higher saccadic and blink rates in the first block comparatively to the remaining ones. This effect was also observed in trial duration, with significantly shorter trials in the first compared to the fourth blocks; as well as in the second block, comparatively to third and fourth blocks.

Although non-significant, NEMs rate slightly decreased along blocks, in line with some previous evidence, as less imageable concepts lead to looking more at blank locations (Kumcu, & Thompson, 2020). Our results further show that throughout a concrete to abstract continuum, which results in less imageable concepts and also requires deeper search in LTM, people take more time to answer (to search through their knowledge), although it is not accompanied by more NEMs. Interestingly, we see a trend of less NEMs across blocks, with less saccadic frequency, less blinking frequency, and smaller pupil size,

which is a behavior typical of WM engagement (Luke, Darowski, & Gale, 2018), with longer saccades and longer fixations, which we will discuss more deeply in the General Discussion.

It is vital to note that Experiment 1 had some issues that might hinder the results. To begin with, our final sample size is small, underpowering our results. Another problem was the restricted field of view of the eye-tracker, limited to its screen area, which resulted in losses of eye position for saccades larger than 10 degrees. This was treated as missing-trials, due to loss of eye position. A different issue was the lack of control over the response characteristics (per example, in the similarity between a table and a chair: both are made of wood or have four legs compared with both are furniture that usually are coupled together), as well as type of incorrect answers ("I don't know" compared with an incorrect). Therefore, we tried to compensate for these issues in Experiment 2, by using an eye-tracker embedded in a virtual reality headset (bigger effective field of view), and by controlling the response characteristics (abstract, concrete, or functional). Our aim is twofold: to replicate our first experiment controlling its limitations and, with EEG, to understand if saccades associated with LTM search are triggered by the same mechanisms as saccades subserving vision.

5. Methods

5.1 Experiment 2

This experiment aimed to compare the spectral power of gamma and beta band in the motor programming of saccadic eye movements subserving vision and verbal LTM search. We recorded EEG while participants were performing the tasks. Participants were randomly divided into fixed or free gaze groups in the first task [40 Question Task]. In the second task, in the perceptual task they had to look towards (pro) or against (anti) a blinking dot [Perceptual Pro/Anti Saccade Task], or towards or away from where the memorized target dot was before [Memory Pro/Anti Saccade Task]. These saccadic tasks were meant to control for perceptual vs. non-perceptual (i.e., memory-guided) saccadic-related EEG activity.

5.1.1 Subjects

Fifty-seven participants (age: 18 – 57, mean 28, 30 (8.87); 31 males) recruited from the Coimbra population took part in this experiment, 5 were left-handed. As, to the best of our knowledge, there are no known handedness effects on eye movements, they were not excluded from our sample. All participants had normal or corrected-to-normal vision, no history of neurologic or psychiatric disorders and provided written informed consent prior to participation.

All experimental procedures were performed according to the Declaration of Helsinki.

5.1.1.1 256-Channels Wet Cap. Eighteen participants (9 males) took part in the experiment with 256 channels wet cap. Five participants had to be excluded, two due to loss of triggers from the eye-tracker computer to the EEG, and three due to very noisy data (loss of ≥50% of channels and/or less than ≥50% of trials). The final sample comprised twelve participants (5 males; age M=30,69 years, SD=11,16).

5.1.1.2 64-Channels Dry Cap. Thirty-nine participants (22 males) took part in the experiment with a 64 channel dry cap. Three participants had to be excluded due to loss of triggers from the eye-tracker computer to the EEG, and seven due to very noisy data (loss of ≥50% of channels and/or less than ≥50% of trials). The final sample comprised twenty-six participants (17 males; age M=27,27, SD=7,28).

5.2.2 Stimuli

Two tasks were employed: the 40 Questions from Experiment 1, and a pro- and anti-saccade task.

40 Questions Task. This task was previously described (see Experiment 1). The open questions required comparing and finding the commonalities between two concepts while the structured questions involved defining or answering to single concepts.

Perceptual Pro- and Anti-Saccade Task. In the pro-saccade task, the participants were instructed to make a saccade towards the target in the periphery, whereas in the anti-

saccade task, subjects are required to make a saccadic eye movement away from a target, rather than towards it.

The task consisted of two blocks of 50 trials each, lasting 4 min in total. The color of the dot indicated the block condition (green = pro, red = anti) and target location (left/right) was randomized with equal frequency throughout each block (25 right / 25 left). Each trial began with the appearance of a fixation cross in the center of a dark gray screen and two bright dots (20 cm diameter) 20° visual angle from the fixation cross for 1000 milliseconds. One of the dot flashes for 750 milliseconds. Then, for 750 milliseconds, both the fixation cross and the dots remained unaltered (as in the beginning), after which the fixation cross disappeared for 750 milliseconds. This is when participants must saccade: on pro trials, participants were instructed to look at the respective dot once the fixation cross disappeared; on anti-trials, participants were instructed to look toward the other dot (i.e., to the one that did not blink) as soon as the fixation cross disappeared.

Memory Pro- and Anti-Saccade Task. It was similar to the previous task, but instead of looking towards the target, participants would have to look to the position where the target used to be, in a blank, dark gray screen. The first block was the pro-saccade task (green dots) whilst the second block was the anti-saccade task (red dots) (Figure 4).

Figure 4

Pro and Anti Saccade Tasks
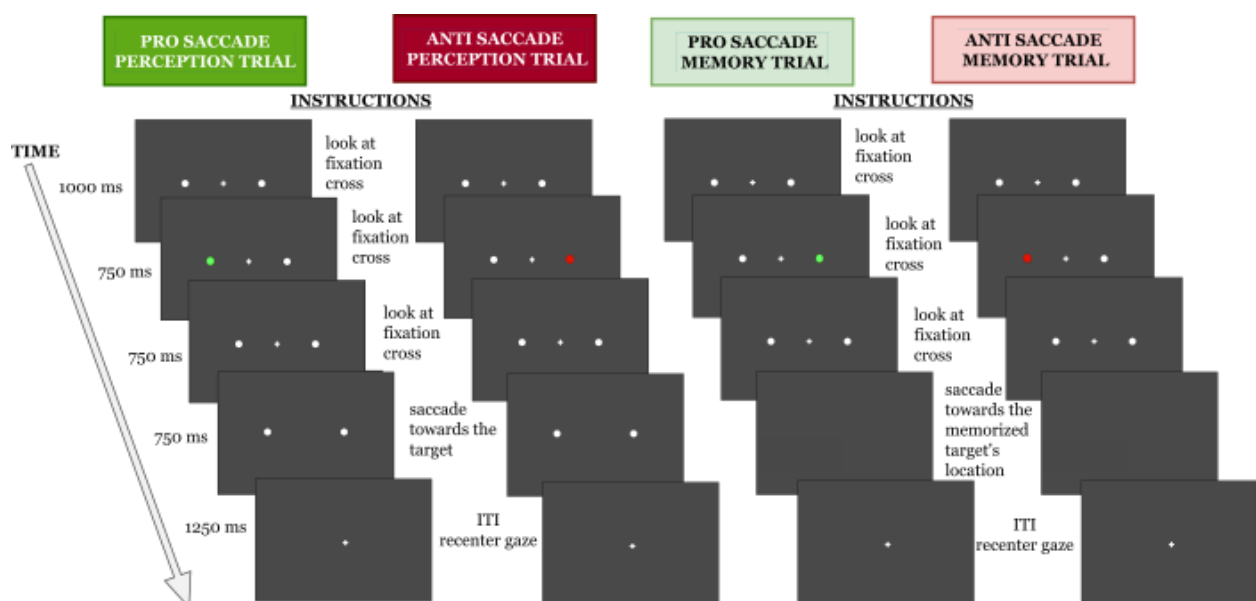
ITI inter trial interval

5.2.3 Pilot Study for Experimental Design

Due to the substantial novelty of our tasks, we conducted a procedure testing through pilot studies collected before the main experiment in independent samples of subjects. Initially, given the EEG's sensibility to artifacts such as motion and speech, participants were instructed to think thoroughly in the answer as if they were answering out-loud and press a button once they were finished. They were supposed to press the right-hand if they knew the answer or a button in the left-hand if they did not know. At the end of each block, participants were asked to answer verbatim as they thought. However, we noticed they were thinking while answering the question later. Therefore, to not bias the results, we opted for the tradeoff between more artifacts for more accuracy. Regarding the Pro- and Anti-saccades task, trials' duration was adjusted based on feedback of pilots.

5.3 Procedure

For the 40 Questions Task, participants were randomly assigned to either fixed gaze or free gaze conditions. In the fixed gaze condition, participants were instructed to keep their eyes in a central fixation cross while answering the questions. Participants in the free gaze condition were told that the fixation cross served as a reference point, as they were embedded in a virtual environment, and had no other relevance for them (in the pilots we ran, when participants were not instructed regarding fixation cross, they assumed they should stare at it). They were instructed to answer the most complete they could, and to think thoroughly when answering (to save "I do not know" to the last resource, unless they really did not know the answer). Participants were informed that if they required to, they could do a small break between trials.

5.4. EEG Recording and Processing

EEG was acquired either with a 64-channel or a 256-channel system (ANT Neuro, Enschede, Netherlands). Electrodes were positioned according to an equidistant montage using an elasticated cap. With the 64-channel system, two electrodes placed on the left and right mastoids serve as online ground and reference electrodes respectively. Electrode impedances were kept below 25 kΩ. With the 256-channel system, electrodes CPz and another electrode placed on the left mastoid served as online reference and ground.

The analyses were conducted using EEGLAB (Delorme & Makeig, 2004), which is an open-source Matlab package for EEG analysis. Data was filtered with a notch filter of 50Hz ±1.5 Hz to remove contamination from electrical noise, followed by a low-pass filter of 1 Hz. Bad channels with more than four high-frequency noise standard deviations were rejected. Careful visual exploration followed, and noisy channels that survived the previous step were also deleted. Then data was re-referenced to the average reference and bad channels were interpolated based on all neighboring channels.

5.5 Analyses

5.5.1 Power Spectral Analyses. For the spectral analysis of the 40 Questions Task, the EEG continuous recording was segmented epochs of 1000 ms timed-locked to the end of the audio file and prior to the moment participants started speaking. This time window was selected to capture the "thinking period". Capturing the entire response period was not of interest here because of potential contamination by movement artifacts associated with articulation. For that reason, shorter trials were discarded.

For the spectral analysis of Pro- and Anti- Saccade Task, the EEG was divided into epochs of 1500 ms time-locked to the interval from beginning of the third to the end of the fourth moments of the task (see Figure 3), that is, when participants must hold a saccade and later saccade towards the target. Regions of interest (ROIs) were defined by visual proxy of electrode disposition over parietal regions of interest (see appendix 2).

5.5.2 Statistical Analyses. Statistical analyses were performed using Jasp (Version 0.17; JASP Team, 2023) We conducted two repeated measures ANOVAs on the average spectral power in each band. For the Control Task, we considered ROIs (frontal and parietal electrodes) and task (perception pro; perception anti; memory pro; memory anti) as factors, and cap (256 wet/ 64 dry) as between subjects factor; in the Thinking Task, we used ROIs (frontal and parietal) as factor, and gaze (fixed/ free) and cap as between subjects factors. The alpha threshold for statistical significance was 0.05 and paired t-tests were run for post-hoc comparisons.

6. Results

To see if the motor programming of non-visual saccades differs from visual saccades, we compared a "thinking task" with a pro- and anti- saccade task, both visually and memory oriented. Firstly, to see whether there are differences within the control task conditions, we performed a 2 x 4 mixed-design ANOVA, on spectral power as the dependent variable, with frequency bands (alpha, beta, and gamma), ROIs (frontal/parietal) and task (Memory anti-saccade; Memory pro-saccade; Perception anti-saccade; Perception pro-saccade) as within-subjects factors; and cap (dry/wet) as a between-subjects factor. However, because we found statistical differences in the pro/anti saccade tasks, we cannot use it as a valid control task without testing assumptions exceeding the aims of this thesis. Therefore, we briefly address the results for the Pro- and Anti- saccade in appendix 3 while focusing on the 40 Questions task results here.

To test whether there are EEG differences within the 40 Questions task conditions, we performed a 2 x 4 repeated measures ANOVA, on spectral power (alpha, beta, and gamma) as dependent variable; with ROIs (frontal/parietal) and as within-subjects factors; spectral power (alpha, beta, and gamma) as dependent variable; and cap (wet/dry) as a between-subjects factor. The ANOVA revealed significant differences between power bands ($F_{(2, 68)} = 600.313$ $p < 0.001$, $\eta_p^2 = 0.946$), with higher alpha synchronization compared with both beta and gamma (M = 5.668, SE = 0.505, $t(3) = 11.232$, $p < 0.001$, and M = 17.159, SE = 0.505; $t(3) = 34.003$, $p < 0.001$, respectively), and higher beta synchronization, in relation to gamma band (M = 11.491, SE = 0.505; $t(3) = 22.772$, $p < 0.001$). No significant differences were found neither between caps ($F_{(1, 34)} = 1.851$ $p = 0.183$, $\eta_p^2 = 0.052$) nor between gaze ($F_{(1, 34)} = 0.598$ $p = 0.445$, $\eta_p^2 = 0.017$; see Figure 5 below).

Figure 5

40 Questions Task Results
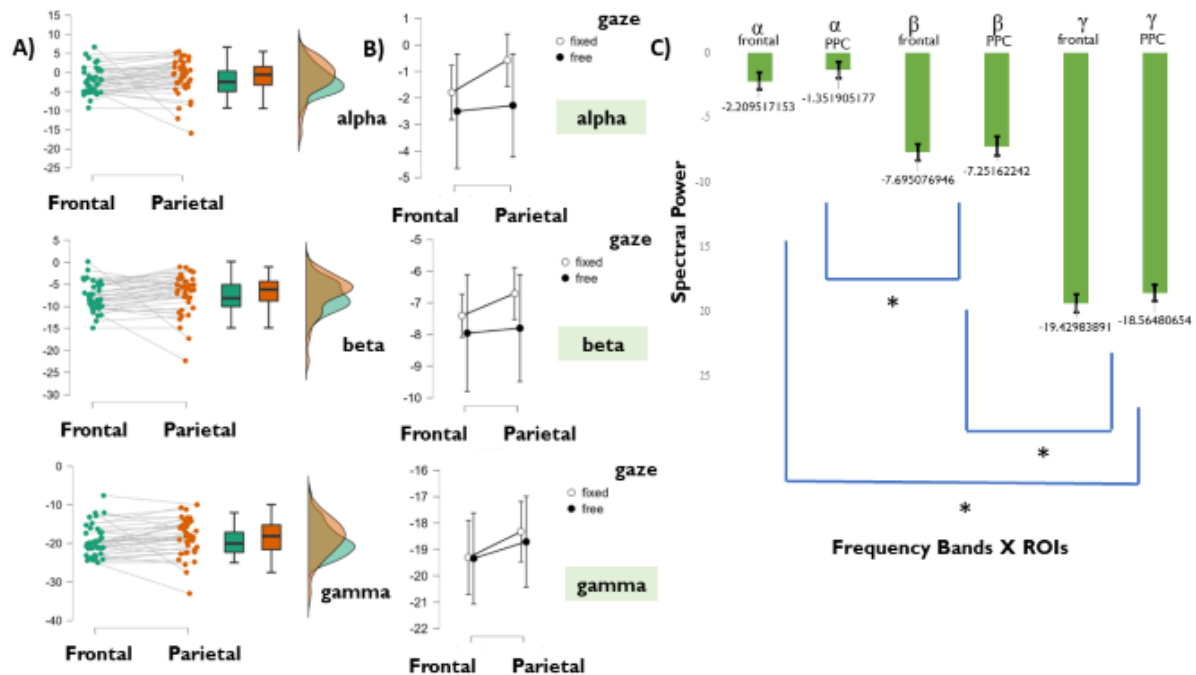
(A) Spectral power in alpha, beta, and gamma frequency bands in frontal (green) and posterior parietal (orange) ROIs. We see similar power of each band between regions, although posterior ROI shows greater variability. (B) Comparison of spectral power of each frequency band (alpha, beta, gamma, respectively) in frontal and parietal regions between gaze conditions (fixed/ free). There is no significant difference between conditions, although we see a trend of lower values in fixed compared to free gaze across all bands, more notably in parietal ROI. (C) There are differences between all frequency bands, but not between frontal and parietal ROIs.

7. Discussion

Our results on the 40 Questions Task revealed significant differences between power bands in both frontal and parietal oculomotor areas, but not between regions – in fact, we found similar average values of spectral power across frontal and parietal areas (see Figure 5). We found desynchronization across the three power bands, with highest gamma desynchronization, followed by beta and then by alpha values (see Figure 5). These results go against the literature (Medendorp, 2007; Van Der Werf et *al.*, 2008), as previous studies

reported alpha desynchronization and gamma synchronization in posterior oculomotor regions in the programming of saccades. We will discuss our findings in the next section.

In addition, we did not find significant results between gaze conditions, although we found higher desynchronization of the spectral power of alpha, beta, and gamma bands in fixed, in comparison to free gaze, especially in posterior regions (see Figure 4).

8. General Discussion

The goal of this thesis was to quest if the structure of search through the memory system (structured or open) would be reflected in differences in the rate of eye movements for the retrieval of verbal information from LTM and to explore the spectral power dynamics during verbal long term memory retrieval in areas responsible for generation of saccades. For that, we employed a LTM search task, that required participants to search through their memory system either in a structured or open manner. We also manipulated abstractness of the items.

In Experiment 1, we examined NEMs rate in the retrieval of LTM contents depending on both factors. We found that open questions elicit less blinks compared to structured ones and produce longer trials. This goes against our hypothesis, as we predicted open questions elicit more NEMs than structured. One explanation might be the need to maintain two items in WM and find similarities between elements is more demanding than retrieving already known information, as Similarities requires establishing connections that are not explicitly taught, nor as immediately accessible as "factual, encyclopedic" knowledge. The absence of differences in saccadic rate could, in turn, be due to no differences in the access to information in LTM. That is, saccades might reflect the search through memory system but not the manipulation of that information (a process carried by WM), when scanning ceases and they focus on that information, where the maintenance process is associated with visual fixation rather than saccadic eye movements (Ehrlichman et *al.*, 2007).

Our results support the evolutionary model proposed by Ehrlichman and colleagues (2007). The authors suggest that NEMs might be an epiphenomenon of evolution, where searching in LTM might have evolved from the circuitry responsible for searching in the visual environment, and focusing on and manipulating information in the WM buffer might have evolved from the network involved in focusing on relevant visual stimuli. This could justify the absence of significative differences in NEMs rate between correct and incorrect

answers, as saccades would reflect the process of search rather than the access to information in LTM. At first, our results might seem to be inconsistent with previous studies, where NEMs were shown to be associated with performance (for instance, Damiano & Walter, 2016; Johansson et *al.*, 2022; Scholz et *al.*, 2016). However, most studies on NEMs on memory retrieval focus on either visual, scenic, or spatial memory (Damiano & Walter, 2016; Johansson et *al.*, 2022; Kinjo et *al.*¸ 2020*;* Ladyka-Wojcik et *al.*, 2021; Wynn et *al.*, 2019), where NEMs show to reinstate the visual context of the stimuli, therefore impacting performance. On verbal LTM retrieval, although there is a consensus on the functional role of NEMs, the conclusions on its functionality are more inconsistent. For instance, whereas Ehrlichman and Micic (2012) and Kumcu and Thompson (2018) did not find evidence of a functional role of NEMs in verbal memory retrieval, other studies demonstrated that manipulating NEMs affects performance (Scholz et *al.*, 2014; 2016). We propose that NEMs strongly depend on the cognitive processes and therefore on task characteristics. This implies that the observed differences across studies must be interpreted in the context of the different cognitive processes involved in the different tasks. Hence, differences in experimental approaches and focus on different aspects of memory processes (e.g., encoding, retrieval, recognition, or recall, or both encoding and recall) of studies on the link between eye movements and memory retrieval hazard generalizations across studies. Therefore, we call for the need for systematic manipulations of NEMs and consistency of task designs. For instance, pupil dilation could be a sensitive measure of successful memory retrieval (Laeng et *al.*, 2007), as more constricted pupil is associated with correct recall of information (Kucewicz et *al.*, 2018) and increase in pupil diameter over time seems to be associated with items more difficult to recall (Jansen et *al.*, 2021). However, we cannot conclude on that, as our tracker had issues detecting/ differentiating pupil in dark eyes, hindering possible interpretations from our results in that dimension.

We also found significantly shorter trials in the first two blocks, compared to third and fourth blocks, supporting that throughout a concrete to abstract continuum, less imageable concepts require deeper search in LTM, as people take more time to answer (to search through their knowledge), although it is not accompanied by more NEMs. In fact, despite not significant, we see a trend of less NEMs across blocks, with less saccadic frequency, less blinking frequency, and smaller pupil size, which is a typical behavior of WM engagement (Luke, et *al.*, 2018).

Are these involuntary NEMs, more specifically saccades, triggered by PPC alone, as in reflexive saccades (as we propose as Hypothesis 1), or are they internally triggered, involving other cortical areas, such as FEF (as we propose as Hypothesis 2)? We tried to explore the spectral power dynamics of posterior and frontal oculomotor regions during the "thinking period", using the task from Experiment 1. Our results revealed differences between power bands in both frontal and parietal oculomotor areas but not within – in fact, we found similar average values of spectral power between frontal and parietal areas, which supports our second hypothesis. Nevertheless, these are not completely voluntary either, as even when instructed to, participants can reduce NEMs but not extinguish them (Liu, et *al.*, 2020; Micic et *al.*, 2010), and congenitally visual blind show NEMs (Kömpf & Piper, 1987). Then, what are they? Again, with the second hypothesis we propose that NEMs reflect parieto-frontal network of processing saccades and voluntary shift of attention.

8.1. Limitations and Future Directions

Nevertheless, our Experiment 2 also had some limitations. We analyzed epochs with fixed lengths (1 second), therefore impoverishing our conclusions, as 1. In the 40 questions task, we not only discarded trials faster than 1 second, but this restricted epoch length precluded finer-grained analysis, as we didn't explore differences across the whole "thinking period" – highly variable, both between and within participants – and 2. in order to compare the Control task with 40 Questions, we defined the epochs of the control task involving both saccade programming and execution (1.5 seconds) – we could control for this defining saccade-aligned events, with ~200 ms time window before saccades in both tasks, which would reflect more securely we were exploring saccadic programming without possible interferences from other processes. Speaking of which, gamma band activity is also known to reflect muscular artifacts, such as eye movement, that we did not control for. We did not control for correct/incorrect trials in the control task, which might have hindered our results, as we know that the motor programming of saccades shows a contralateral preference in both frontal and parietal oculomotor regions, and the execution of saccades in the anti-saccade task is different that in the pro-saccade task. Last, within the Control Task, recency time should have been longer, to account for possible after image effects and prevent directional errors.

As future directions, we want to scrutinize how gaze restriction impacted NEMs and performance, and explore saccade-align events, compensating for the limitations we

presented above. It would be interesting to explore if the results found are exclusive to semantic memory search, or if they are common to all types of memory search, by creating new paradigms that would engage different types of memory, such as episodic and associative memory. What about creative thinking and problem solving? Furthermore, additional control tasks, such as a verbal working memory and an attentional task could help us to better clarify and understand our model. It would be curious to compare with a simple egocentric task, using the VR headset, for instance, to further build possible bridges between conceptual and real world navigations.

8.2. Conclusions

In summary, our results from both experiments suggest that NEMs are a byproduct of attentional shifts that necessarily engage parieto-frontal saccadic planning network and that, when thinking, we scan the activated concept space just as if we were looking at the objects in front of our eyes. It seems that the term "the mind's eye" may be more literal than we suspect.

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Appendices

Appendix 1. 40 Questions Stimuli

Block 1

- ✪ In which country were the Olympic Games born? **[Information]**
- ✪ What are the similarities between an orange and a banana? **[Similarities]**
- ✪ At which temperature does water boil in normal conditions? **[Information]**
- ✪ What are the similarities between a fork and a spoon? **[Similarities]**
- ✪ In which direction does the sun set? **[Information]**
- ✪ What is a thermometer? **[Information]**
- ✪ What are the similarities between a dog and a lion? **[Similarities]**
- ✪ In which continent is the desert of Sahara? **[Information]**
- ✪ What are the similarities between yellow and green? **[Similarities]**
- ✪ What are the similarities between a coat and a shirt? **[Similarities]**

Block 2

- ✪ Refer one of the constitutive powers of a democracy. **[Comprehension]**
- ✪ What is the main theme of the book of Genesis? **[Information]**
- ✪ What is the capital of Sweden? **[Information]**
- ✪ What are the similarities between the eye and the ear? **[Similarities]**
- ✪ What are the similarities between joy and sadness? **[Similarities]**
- ✪ What are the similarities between a car and a boar? **[Similarities]**
- ✪ What are the similarities between a piano and a drum? **[Similarities]**
- ✪ To which scientist is the "theory of relativity" associated? **[Information]**
- ✪ Who was Mahatma Gandhi? **[Information]**
- ✪ What are the similarities between a table and a chair? **[Similarities]**

Block 3

- ✪ Refer some reasons that justify the importance of the study of History.
  [Comprehension]
- ✪ For what reason do deaf people have difficulty in learning to speak? **[Comprehension]**
- ✪ What are the similarities between Democracy and Dictatorship? **[Similarities]**
- ✪ What are the similarities between a fly and a tree? **[Similarities]**
- ✪ What are the similarities between an egg and a seed? **[Similarities]**

✿ What are the similarities between a poem and a statue? **[Similarities]**

✿ Why are defendants considered innocent until proven guilty? **[Comprehension]**

✿ Why do we pay taxes? **[Comprehension]**

✿ What are the similarities between fog and steam? **[Similarities]**

Block 4

✿ What are the similarities between work and game? **[Similarities]**

✿ What are the similarities between praise and punishment? **[Similarities]**

✿ Why is the freedom of press important in a democracy? **[Comprehension]**

✿ Why do we need medical prescriptions to buy remedies? **[Comprehension]**

✿ Why do we wash our clothes? **[Comprehension]**

✿ What are the similarities between a friend and a foe? **[Similarities]**

✿ Refer some reasons why we need to cook some foods. **[Comprehension]**

✿ For what reason some people prefer to rob a bank rather than a friend?

[Comprehension]

✿ What are the similarities between a coat and a suit? **[Similarities]**

✿ What are the similarities between hibernation and migration? **[Similarities]**

Appendix 2. ROIs in both 256 wet and 64 dry caps

64 channels dry cap electrodes ROIs (A)

FEF : 3L (left) and 3R (right);

PPC: 6L 7L 3LA 4LB 5LB (left) and 6R 7R 3RA 4RB 5RB (right);

Figure 6.

64 channels dry cap selected electrodes.
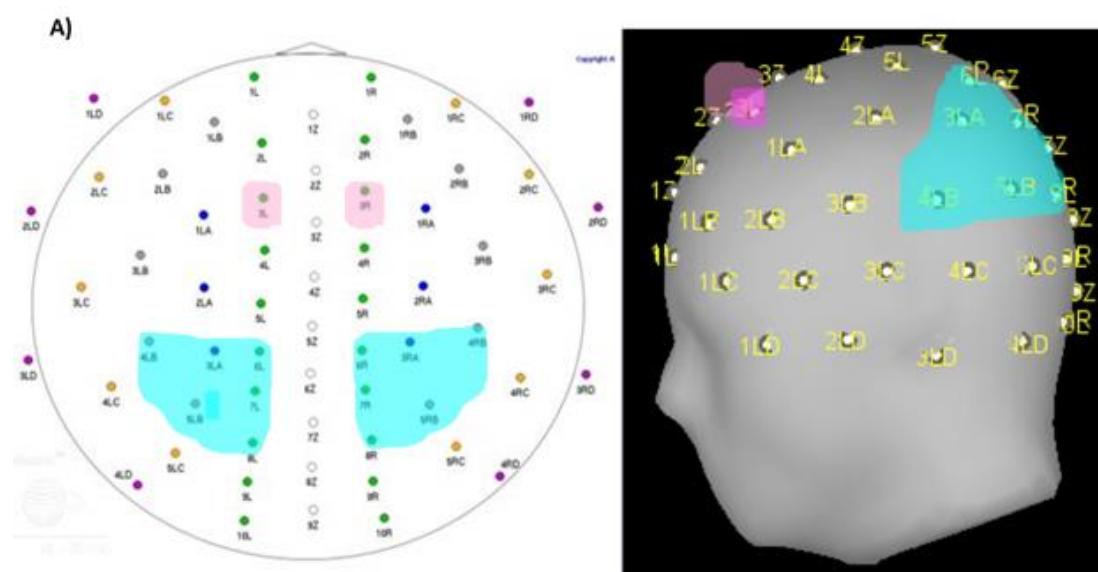
256 channels wet cap electrodes ROIs (B)

FEF : L6Z L7Z L6L and Z6L (left), and R6Z R7Z R6R and Z6R (right);

PPC: Z11L – Z14L; L11Z – L14Z; L11L-L14L; L5A L6A, L5B L6B L7C L7D L6D L7D L8D L8C (left), and Z11R – Z14R; R11Z – R14Z; R11R – R14R; R5A, R6A, R5B R6B R7C R7D R6D R7D R8D R8C (right).

Figure 7.

256 channels wet cap selected electrodes.
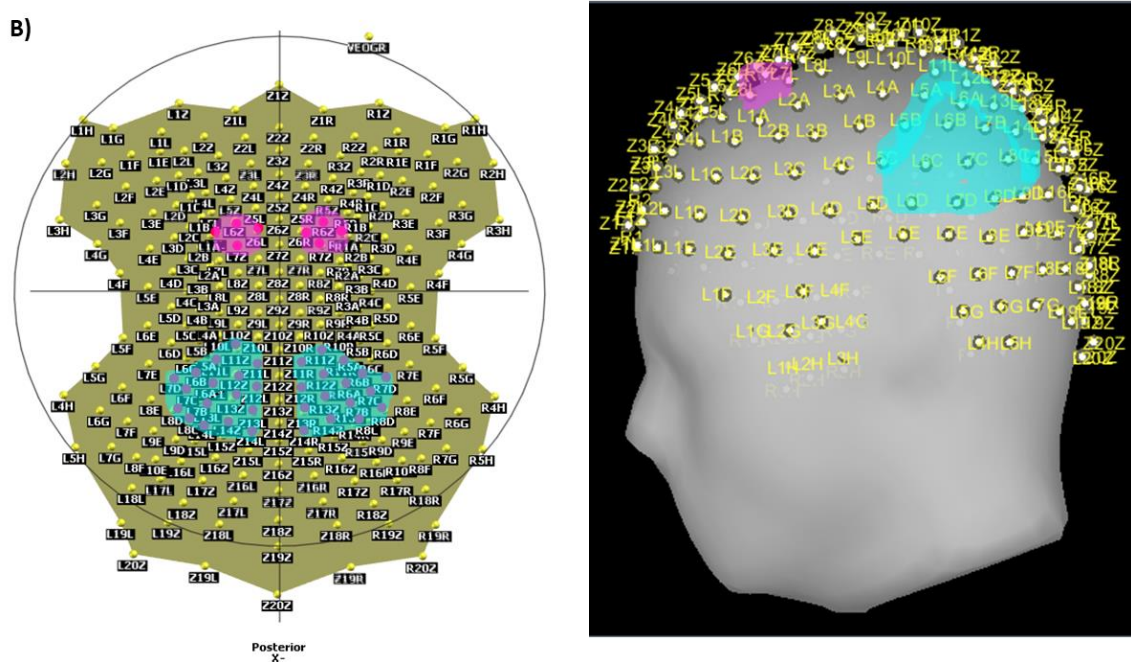
Appendix 3. Results Within The Control Task - Perceptual and Memory Pro and Anti-saccade Task

The analysis revealed a main effect of task ($F_{(3, 108)}$ = 14.827, $p < 0.001$, η_p^2 = 0.976) and differences between power bands ($F_{(2, 15.827)}$ = 1494.70, $p < 0.001$, η_p^2 = 0.292), an interaction of power band and task ($F_{(6, 216)}$ = 3.689, $p = 0.002$, $\eta_p^2 = 0.092$) and between ROIs and task ($F_{(6, 216)}$ = 16.239, $p = 0.003$, $\eta_p^2 = 0.086$). We did not find significant differences between cap types ($F_{(1, 36)}$ = 1.682, $p = 0.203$, $\eta_p^2 = 0.045$).

Post-hoc t tests revealed differences between all power bands (α *Vs.* β : M = 6.246, SE = 0.383; t(3)= 4.353 , $p < 0.001$; α *Vs* .γ : M = 18.643, SE = 0.414; t(3)= 44.985 , $p < 0.001$; β *Vs.* γ : M = 12.397, SE = 0.208; t(3)= 59.588 , $p < 0.001$). Within Control Task, Memory anti-saccade task significantly differed from Perceptual pro-saccade M = 2.877, SE = 0.509; t(6)= 5.650 , $p < 0.001$), but not from Memory pro-saccade (M = 0.831, SE = 0.455; t(6)= 1.826 , $p = 0.228$); Memory pro-saccade also differed from Perceptual pro-saccade (M = 2.046, SE = 0.455; t(6)= 5.650 , $p < 0.001$); and Perceptual pro-differed from perceptual anti-saccade (M = 2.261, SE = 0.536; t(6)= 4.216 , $p < 0.001$). On the interaction between spectral power and task, comparing each spectral power with itself within tasks, we find the same pattern as before, with higher alpha, beta, and gamma synchronization in Memory anti-saccades, comparatively with Perceptual Pro-saccades (M = 2.416, SE = 0.208, t(66)= 4.652, $p < 0.001$; M = 2.478, SE = 0.626, t(66)= 3.956, $p = 0.005$; M = 3.736, SE = 0.712; t(66)= 5.249, $p < 0.001$, respectively); in Memory pro-saccades, comparatively to Perception pro-saccades (M = 1.744, SE = 0.529; t(66)= 3.298 , $p = 0.026$; M = 2.264, SE = 0.606; t(66)= 3.736 , $p = 0.009$; M = 2.130, SE = 0.613, t(66)= 3.473 , $p = 0.018$, respectively); and higher gamma synchronization in Perceptual anti, comparatively to perceptual pro-saccades (M = 12.397, SE = 0.208; t(3)= 59.588 , $p < 0.001$) (see Table 2. below).

Table 2.

Post Hoc Comparisons - power band $*$ task

		Mean Difference	SE	t	p
alpha, Mem. anti	alpha, M. p	0.672	0.590	1.138	1.000
	alpha, P. a	1.156	0.533	2.170	0.257
	alpha, P. p	2.416	0.519	4.652	< .001 ***
beta, Mem. anti	beta, M. p	0.215	0.407	0.527	1.000
	beta, P. a	0.947	0.583	1.623	0.680
	beta, P. p	2.478	0.626	3.956	0.005 **

Table 2.

Post Hoc Comparisons - power band ✻ task

		Mean Difference	SE	t	*p*
gamma, Mem. anti	gamma, M. p	1.606	0.596	2.694	0.096
	gamma, P. a	-0.255	0.901	-0.283	1.000
	gamma, P. p	3.736	0.712	5.249	< .001***
alpha, Mem. pro	alpha, P. a	0.485	0.451	1.074	1.000
	alpha, P. p	1.744	0.529	3.298	0.026*
beta, Mem. pro	beta, P. a	0.732	0.467	1.568	0.680
	beta, P. p	2.264	0.606	3.736	0.009**
gamma, Mem. pro	gamma, P. a	-1.861	0.765	-2.432	0.161
	gamma, P. p	2.130	0.613	3.473	0.018*
alpha, Percp. anti	alpha, P. p	1.259	0.451	2.793	0.083
beta, Percp. anti	beta, P. p	1.532	0.518	2.958	0.060
gamma, Percp. anti	gamma, P. p	3.991	1.035	3.856	0.007**

 * p < .05, ** p < .01, *** p < .001

On the interaction between frequency band and task in our ROIs, comparing each spectral power with itself within tasks, we find the same pattern as before, with higher alpha, beta, and gamma synchronization in Memory anti-saccades, comparatively with Perceptual Pro-saccades (M = 2.416, SE = 0.208, t(66)= 4.652, *p* < 0.001 ; M = 2.478, SE = 0.626, t(66)= 3.956, *p* = 0.005 ; M = 3.736, SE = 0.712; t(66)= 5.249, *p* < 0.001, respectively); in Memory pro- saccades, comparatively to Perception pro-saccades (M = 1.744, SE = 0.529; t(66)= 3.298 , *p* = 0.026 ; M = 2.264, SE = 0.606; t(66)= 3.736 , *p* = 0.009 ; M = 2.130, SE = 0.613, t(66)= 3.473 , *p* = 0.018, respectively); and higher gamma synchronization in Perceptual anti, comparatively to perceptual pro-saccades (M = 12.397, SE = 0.208; t(3)= 59.588 , *p* < 0.001;) (see Table 3. below).

Table 3.

Post Hoc Comparisons - power band ✳ rois ✳ task

		Mean Difference	SE	t	p	
alpha, frontal, Mem. anti	alpha, ppc, M. a	-1.935	0.959	-2.018	1.000	
	alpha, frontal, M. p	0.135	0.291	0.465	1.000	
	alpha, ppc, M. p	-0.727	1.339	-0.543	1.000	
	alpha, ppc, P. a	-0.307	1.194	-0.257	1.000	
	alpha, frontal, P. p	1.002	0.458	2.185	1.000	
	alpha, ppc, P. p	1.894	1.118	1.694	1.000	
beta, frontal, Mem. anti	beta, ppc, M. a	-1.411	0.421	-3.348	0.127	
	beta, frontal, M. p	-0.917	0.415	-2.206	1.000	
	beta, ppc, M. p	-0.065	0.658	-0.099	1.000	
	beta, frontal, P. a	0.999	0.556	1.798	1.000	
	beta, ppc, P. a	-0.517	0.595	-0.869	1.000	
	beta, frontal, P. p	1.559	0.434	3.595	0.070	
	beta, ppc, P. p	1.986	0.842	2.358	1.000	
gamma, frontal, Mem. anti	gamma, ppc, M. a	-1.332	0.451	-2.955	0.307	
	gamma, frontal, M. p	1.880	0.557	3.373	0.122	
	gamma, ppc, M. p	-3.338×10^{-4}	0.720	-4.635×10^{-4}	1.000	
	gamma, frontal, P. a	-1.129	1.059	-1.066	1.000	
	gamma, ppc, P. a	-0.713	1.054	-0.677	1.000	
	gamma, frontal, P. p	2.734	0.667	4.098	0.018	*
	gamma, ppc, P. p	3.407	0.876	3.888	0.032	*
alpha, ppc, Mem. anti	alpha, frontal, M. p	2.071	0.966	2.143	1.000	
	alpha, ppc, M. p	1.208	1.100	1.098	1.000	
	alpha, frontal, P. a	2.619	0.790	3.317	0.136	
	alpha, ppc, P. a	1.629	0.962	1.693	1.000	
	alpha, frontal, P. p	2.937	0.762	3.855	0.034	*
	alpha, ppc, P. p	3.829	0.926	4.135	0.016	*
beta, ppc, M. a	beta, frontal, M. p	0.494	0.372	1.329	1.000	
	beta, ppc, M. p	1.346	0.990	1.360	1.000	
	beta, frontal, P. a	2.410	0.713	3.380	0.121	
	beta, ppc, P. a	0.894	0.822	1.087	1.000	
	beta, frontal, P. p	2.970	0.568	5.233	< .001	***
	beta, ppc, P. p	3.397	0.948	3.584	0.072	
gamma, ppc, M. a	gamma, frontal, M. p	3.213	0.623	5.161	< .001	***
	gamma, ppc, M. p	1.332	0.877	1.518	1.000	
	gamma, frontal, P. a	0.204	0.910	0.224	1.000	

Post Hoc Comparisons - power band ✳ rois ✳ task

		Mean Difference	SE	t	p	
	gamma, ppc, P. a	0.620	1.133	0.547	1.000	
	gamma, frontal, P. p	4.066	0.648	6.276	< .001	***
	gamma, ppc, P. p	4.739	0.931	5.091	< .001	***
alpha, frontal, Mem. pro	alpha, ppc, M. p	-0.863	1.307	-0.660	1.000	
	alpha, frontal, P. a	0.549	0.329	1.666	1.000	
	alpha, ppc, P. a	-0.442	1.153	-0.383	1.000	
	alpha, frontal, P. p	0.866	0.368	2.353	1.000	
	alpha, ppc, P. p	1.759	1.084	1.623	1.000	
beta, frontal, M. p	beta, ppc, M. p	0.851	0.940	0.905	1.000	
	beta, frontal, P. a	1.916	0.623	3.074	0.233	
	beta, ppc, P. a	0.400	0.753	0.531	1.000	
	beta, frontal, P. p	2.476	0.489	5.068	0.001	**
	beta, ppc, P. p	2.903	0.904	3.212	0.172	
gamma, frontal, M. p	gamma, ppc, M. p	-1.881	0.602	-3.125	0.207	
	gamma, ppc, M. p	-1.881	0.602	-3.125	0.207	
	gamma, frontal, P. a	-3.009	0.920	-3.270	0.152	
	gamma, ppc, P. a	-2.593	0.868	-2.986	0.288	
	gamma, frontal, P. p	0.853	0.546	1.564	1.000	
	gamma, ppc, P. p	1.526	0.786	1.943	1.000	
alpha, ppc, M. p	alpha, frontal, P. a	1.412	1.191	1.185	1.000	
	alpha, ppc, P. a	0.421	0.849	0.496	1.000	
	alpha, frontal, P. p	1.729	1.144	1.511	1.000	
	alpha, ppc, P. p	2.621	1.052	2.491	0.945	
beta, ppc, M. p	beta, frontal, P. a	1.065	0.762	1.397	1.000	
	beta, ppc, P. a	-0.452	0.727	-0.621	1.000	
	beta, frontal, P. p	1.625	0.757	2.146	1.000	
	beta, ppc, P. p	2.052	1.047	1.960	1.000	
gamma, ppc, M. p	gamma, frontal, P. a	-1.129	1.079	-1.046	1.000	
	gamma, ppc, P. a	-0.713	0.915	-0.779	1.000	
	gamma, frontal, P. p	2.734	0.747	3.658	0.060	
	gamma, ppc, P. p	3.407	0.814	4.187	0.014	*
alpha, frontal, P. a	alpha, ppc, P. a	-0.991	1.027	-0.965	1.000	
	alpha, frontal, P. p	0.318	0.202	1.574	1.000	
	alpha, ppc, P. p	1.210	0.963	1.257	1.000	
beta, frontal, P. a	beta, ppc, P. a	-1.516	0.556	-2.728	0.538	
	beta, frontal, P. p	0.560	0.445	1.258	1.000	
	beta, ppc, P. p	0.987	0.761	1.296	1.000	
gamma, frontal, P. a	gamma, ppc, P. a	0.416	0.948	0.439	1.000	
	gamma, frontal, P. p	3.862	0.974	3.966	0.026	*
	gamma, ppc, P. p	4.535	1.299	3.492	0.091	

Post Hoc Comparisons - power band ✳ rois ✳ task

		Mean Difference	SE	t	p
alpha, ppc, P. a	alpha, frontal, P. p	1.308	1.002	1.305	1.000
	alpha, ppc, P. p	2.201	0.892	2.468	0.978
beta, ppc, P. a	beta, frontal, P. p	2.076	0.658	3.157	0.193
	beta, ppc, P. p	2.503	0.736	3.401	0.116
gamma, ppc, P. a	gamma, frontal, P. p	3.446	1.065	3.236	0.164
	gamma, ppc, P. p	4.119	1.297	3.176	0.187

$* p < .05, ** p < .01, *** p < .001$

*Note.* P-value adjusted for comparing a family of 276

Figure 8.

Control Task Results
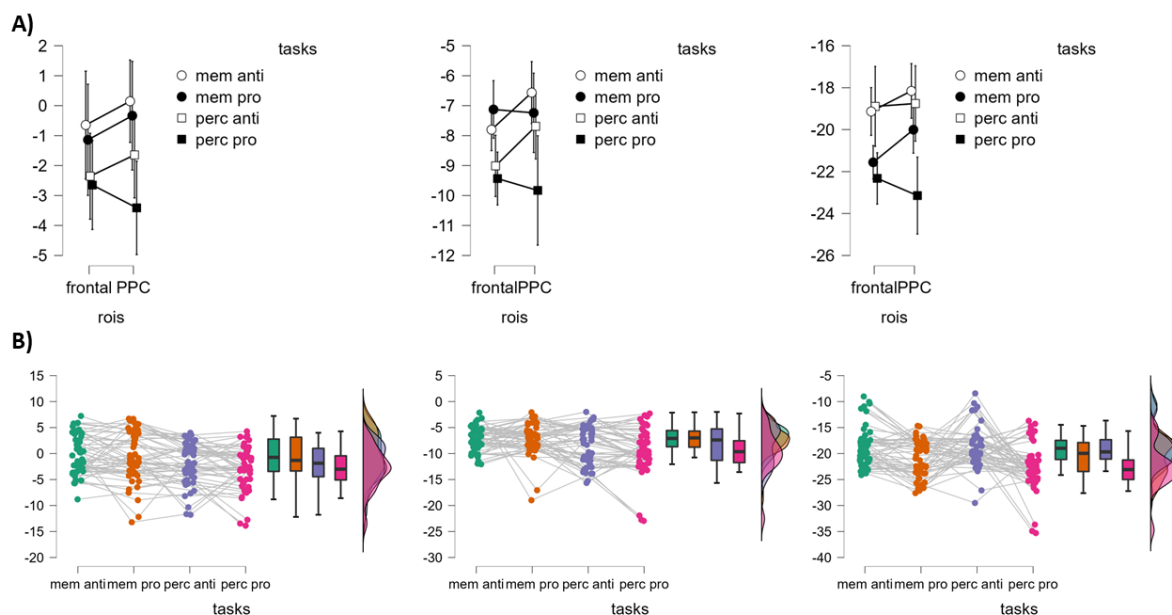
(A) Spectral power in frontal and posterior parietal ROIs. We see similar power of each band between regions, although posterior ROI shows greater variability. (B) Comparison of spectral power of each frequency band (alpha, beta, gamma, respectively) in memory anti-saccade (green), memory pro-saccaade (orange); perception anti-saccade (purple); and perception pro-saccade (pink).

Appendix 4. 256 channels Wet Vs. 64 channels Dry Caps in Control task (A B) and in 4o Questions Task (C D)

We did not find any significant differences between caps in either the control task nor in the 40 questions task, as reported elsewhere. In fact, we found very similar results with wet and dry cap. See the figure below for a visual comparison:
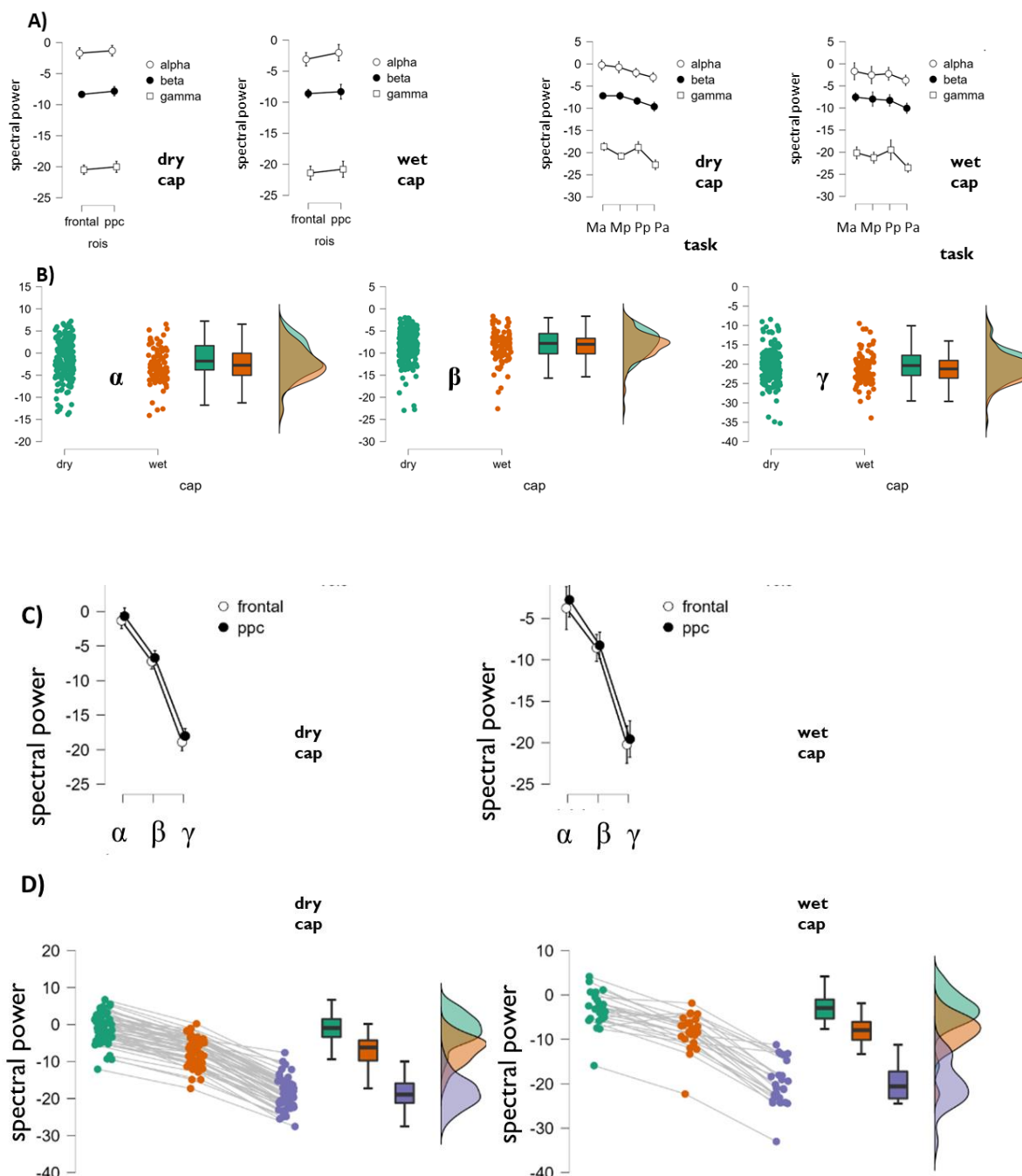
(A) Control Task. We see similar power of each band between ROIs (**A left**) and similar power in alpha, beta, and gamma frequency bands in the four subtasks (**A right**). **(B)**

Control Task. Comparison of spectral power of alpha, beta, and gamma frequency bands with dry (green) and wet (orange) caps. **(C) 40 Questions Task.** spectral power of alpha, beta, and gamma frequency bands in frontal and posterior parietal ROIs in dry (**C left**) and wet (**C right**) caps; **(D) 40 Questions Task.** Spectral power of alpha, beta, and gamma bands with dry and wet caps.