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Department: Department of Neuroscience (DNS) and Padova Neuroscience Center (PNC)

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A deeper look into visual cognition: low dimensionality in visual exploration dynamics and visual memory retrieval

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Coordinator: *Prof. Antonino Vallesi*

Supervisor: *Prof. Maurizio Corbetta*

Co-Supervisor: *Prof. Giorgia Cona*

Ph.D. student: *Miriam Celli*

Publications

Chapter 3 reports the work from the following publication:

Zangrossi, A., Cona, G., Celli, M., Zorzi, M., & Corbetta, M. (2021). Visual exploration dynamics are low-dimensional and driven by intrinsic factors. Communications Biology, 4(1), 1–14.

Chapter 4 reports the work from the following publication:

Celli, M., Mazzonetto, I., Zangrossi, A., Bertoldo, A., Cona, G., & Corbetta, M. (2022). One-year-later spontaneous EEG features predict visual exploratory human phenotypes. Communications Biology, 5(1).

Chapter 1: General Introduction

The general aim of this project is to characterize the relationship between spontaneous eye movement patterns and spontaneous brain activity.

This is rooted in two main hypotheses: 1) apparently complex and variable behaviours are in part driven by low dimensional intrinsic dynamics; 2) these intrinsic behavioural dynamics match intrinsic neural data (i.e., resting-state).

We focus here on eye movement behaviour (i.e., free visual exploration). Visual exploration is an apparently complex behaviour, thought to be controlled by sensory inputs (e.g., Itti et al., 1998a) and top-down goals (e.g., Einhäuser & Koch, 2008) – hence by a quite high-dimensional environment. However, we show that they are partly driven by intrinsic low-dimensional dynamics (Zangrossi et al., 2021). Here, low dimensional means that many kinds of eye movements to a large number of different pictures 1) can be summarized by relatively few features; 2) these features are common across many subjects.

The second hypothesis is that these intrinsic behavioural dynamics reflect intrinsic neural data (i.e., resting state). According to recent resting-state theories, the brain may work as a generative model. As recently discussed by Pezzulo et al. (Pezzulo et al., 2021b), during active tasks generative models may provide top-down sensory and motor prediction, while when stimuli are weak or absent (i.e., rest) top-down dynamics may optimize generative models for future interactions. Generative models (e.g., deep Boltzmann Machines) compress information sequentially, by encoding simpler to more complex summary representations (e.g., time- and space-invariant) at increasingly higher hierarchical levels and can reuse them across different tasks. Accordingly, several findings suggest that stimuli or movements in the cortex are not coded individually (e.g., Chang & Tsao, 2017). A reason why this compression strategy is efficient is that behavioural patterns may be low dimensional too (e.g., Avella et al., 2003a; Cona et al., 2019b;

Pappalardo, Simini, Rinzivillo, Pedreschi, & Giannotti, 2015; Zangrossi et al., 2021). Moreover, this low dimensionality of neural (and behavioural) patterns has been shown also at rest (e.g., spontaneous activity in the mouse cortex replays principal components of face movements in Stringer et al., 2019).

Therefore, we argue that spontaneous activity may encode endogenous information and behavioural states. So, if the brain comes with self-organized dynamics that constrain how it acts on the world, patterns of brain activity recorded in a data-driven manner can be used to model stimuli or behaviours. In other words, there should be a match between intrinsic behavioural dynamics and intrinsic neural data.

This thesis is divided into three main sections. First, we discuss the theoretical basis of this approach by reviewing the existing literature on the low dimensionality of behaviour (Chapter 2). In the second and third sections (Chapters 3-4-5) we present three experimental studies. In the second section (Chapters 3 and 4) we characterize visual exploration phenotypes and their neural correlates in healthy controls in two separate studies; while in the third section (Chapter 5) we analyze visual memory retrieval: a behavioural correlate of visual exploration.

Low dimensionality in behaviour

In **Celli et al.** *(in preparation) we discuss the theoretical basis for our approach to behavioural data. Brain research has massively changed in the last thirty years with the development of new technologies and analysis, such as functional brain imaging, optical imaging and optogenetics, connectomics, etc. In contrast, behavioural science has been moving more slowly. The emphasis has remained strong on the characterization of specific processes or mental operations through carefully designed behavioral paradigms requiring nearly always a stimulus and response presented and recorded on a computer. In the last twenty years, the perspective has moved strongly from a purely* *cognitive one to one taking into account the influence of the body and social functions on cognition (embodied cognition, social neuroscience). Recently it has been advocated (Box-Steffensmeier et al., 2022) that cognitive studies shall focus more on ecological paradigms and move away from key presses recording more complex signals like eye movements or sensors. In addition, most cognitive studies have typically focused on relatively small groups of subjects (typically multiple groups of 10-20 subjects per experiment) running several closely controlled tasks looking for main effects of one condition over another, or for the interaction between two or more conditions. The individual subject variance in these experiments is typically treated as a variable of no interest that gets in the way of finding interesting differences between conditions. Common effects across conditions are also removed statistically looking for differences between conditions. A separate influential body of research has focused on individual differences across subjects and/or cognitive functions measured with traditional neuropsychological tasks or batteries. A prime example of this research is that on the g factor, a common factor that explains across hundreds of subjects nearly 50% of the variability across cognitive tasks (E. J. Austin et al., 2002; Floyd et al., 2009). Hence the extant cognitive literature contains a real tension between small-group studies that emphasize the specificity of processes or mental operations averaging out common processes across subjects and large-scale studies that show strong commonalities of cognitive functions across subjects. In Chapter 2 I will review behavioral studies that show that data reduction in low dimensional components commonly occurs in cognitive data and also when measured with high-resolution signals like eye movements or sensors during behavioral paradigms. And, that this strategy may allow for a computational sound way of encoding high dimensional sensory input and motor responses.*

Characterization of Visual Exploration Phenotypes and their neural correlates in healthy controls

In this study, we focus on free visual exploration, an extremely variable phenomenon. As noted above, *eye movements were historically considered as driven exclusively by external stimuli or task goals. Here, we propose that they are low dimensional and partly driven by intrinsic dynamics.*

In **Zangrossi et al.** *(Zangrossi et al., 2021), we analyze a large eye-tracking dataset (n=120) recorded while people were performing a free visual exploration task. We show that visual exploration is low dimensional (i.e., 3 PCs explain 60% of the variance), and viewers can be classified into one of two viewing styles (Static viewers, characterized by longer fixations; and Dynamic viewers, characterized by shorter fixations), which are identifiable also in absence of a stimulus (i.e., blank screen). In* **Celli et al.** *(Celli et al., 2022), we show that spontaneous neural activity recorded one year later predicts these visual exploration phenotypes. Static viewers have higher alpha and lower high-frequency power, a slower alpha peak (IAF), and strong long-range temporal correlations (i.e., LRTCs, meaning that the temporal structure of the signal is strongly self-similar). The opposite hold for Dynamic Viewers. These results suggest that the timing of oscillations (IAF, LRTCs) and inhibition (alpha power) may correlate with a mechanism for controlling the duration of fixation and eye movement shifts. Studies currently being carried out involve the simultaneous recording of EEG and eye movements to obtain a more direct correlation between behavioral and neural features.*

Behavioural correlates of Visual Exploration Phenotypes: the case of visual memory

Visual exploration is surely not a stand-alone process: it is linked to many aspects of cognition (e.g., attention, memory). In the second part of the thesis, we focus on visual memory. Previous works have suggested a relationship between eye movements during the exploration of a visual scene and the subsequent memory of that scene. However, to our knowledge, such relationship has never been examined topographically. In **Celli et al.** *(in preparation), we quantify the contribution of eye movement exploration patterns (i.e., gazemaps) in remembering the visual objects of a scene, and the impact of endogenous subject-related vs. Image-specific variables on recollection. We show that endogenous information (i.e., gaze fixation topography) is the preferential source of information for* *memory (i.e., has a higher overlap with memory maps), as compared to image-specific variables (i.e., saliency and semantics). We show that this unbalance between endogenous and image-specific variables varies across subjects with one cluster relying more than the other on saliency information.*

Chapter 2: Is behaviour low dimensional?

Introduction

How do we think about behaviour and shall we change the way we study it?

Traditional cognitive theories view complex behaviours emerging from the interaction of simple operations that are strung together as a stimulus is transformed into a decision and finally a motor response. The goal of most cognitive studies in the last fifty years has been then to identify what are the elementary operations of the mind and have used lesions to dissociate these operations. Hence the emerging view is not dissimilar from the Fodorian perspective even though it is now well established that these operations closely interact in space and time for mediating behavioral routines.

Brain research has undergone massive changes in the last thirty years thanks to the emergence of new technologies (brain imaging, optical imaging, optogenetics, viral manipulations, connectomics) that have moved the field from a neuron-centered modular view to a more integrated network-centered view of brain function.

However, the study of behaviour through experimental designs, statistical methods, and interpretation continues to stick to a fairly modular, yet more interactive, view of behaviour. In contrast, we believe that in this new era of big data, there is the opportunity to examine if this traditional perspective of behavior still holds. For instance, given the relative easiness to collect large data sets one may begin to test whether the traditional cognitive functions (attention, memory, emotion, etc.) still make sense or whether new ontologies of cognition shall be envisioned. Another important opportunity is to evaluate cognitive performance vis-a-vis individual variability. Current methods and statistics crush individual variability as a variable of no interest. However, there is growing evidence for strong similarities both across cognitive domains and subjects, which suggests a potential low dimensionality of cognitive architectures at the population level. A potential low dimensionality of behavior may need to be evaluated in relation to the dimensionality *of neural activity which is the ultimate mechanism underlying behavior. All these questions are novel and largely unexplored in cognition today. A recent editorial for the 10 years of Nature Human Behavior (Box-Steffensmeier et al., 2022) emphasizes the need for moving cognitive science from reaction times to better and more in-depth signals (eye movements, sensors, etc.), from small to big groups of subjects to properly address individual variability, and from laboratory to ecologically based paradigms.*

In the following sections, we will present first the distinction between a modular localization approach to brain function to a more integrated network. Then I will discuss some issues with current cognitive studies. Finally, I will consider several studies in different domains that seem to indicate a low dimensionality of cognition, and what are the implications of this perspective.

Low dimensionality structure of complex data

What do we mean by "low dimensionality"? The basic idea is to search for hidden relationships between apparently independent variables. One way to capture these relationships (i.e., synergies) is to look for latent factors or components (e.g., from PCA, factor analysis etc.) which can be described as a set of linear combinations of variables, each one explaining a certain amount of variance. A low dimensional structure can emerge from complex data when the variance across a set of N variables can be described by a set of k components (i.e., where k is way lower than N). Such structure is potentially identifiable both inside and across cognitive domains, if synergies exist among apparently independent variables. Conversely, if data is not correlated (i.e., noise), a low dimensional structure is not found (Figure 1). Among the techniques that can be used to identify latent components, Principal Component Analysis (PCA) is one of the most used. In brief, this technique extracts linear combinations of variables explaining a progressively small amount of variance (i.e., the first PC explains more variance than the second, and so on). This is true only if synergies (i.e., correlations) are detectable within the set of variables under investigation. This means that the use of dimensionality reduction techniques (as PCA) on a set of uncorrelated variables would not suggest a low dimensional structure, since there are no relations among data. Indeed, if a PCA is computed on noise, the solution will suggest a number of components equal to the number of variables in the original set.

To sum up, the use of dimensionality reduction strategies allows for capturing latent factors that can summarize interindividual variability within a complex set of variables using a few components, if such variability is structured and not if it is merely noise.

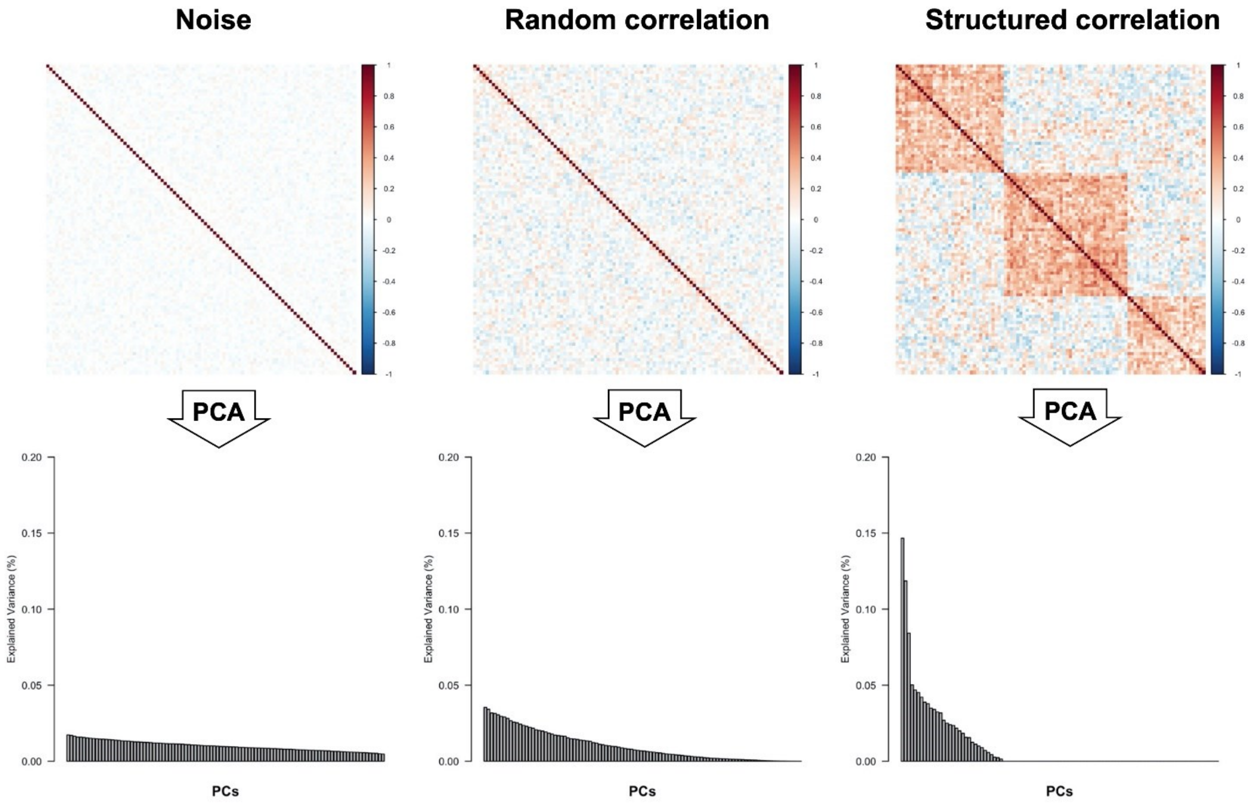

Figure 1| Correlation matrices (upper panels) from simulated data with different levels of correlations (noise, random and structured correlations), along with barplots (lower panels) showing the variance explained by different PCs.

1. On the modular study of behaviour

Behaviour is the output of the brain; thus, it is not surprising that brain and cognitive sciences have been historically linked. Franz Joseph Gall was among the first scientists to explain cognitive *functions with brain variables (Gall, 1818). He claimed that distinct mental abilities had distinct brain locations, as evinced from the bumps and the geometry of the skull. His work had a huge impact on the following literature, starting the localizationalist view that prevailed in the last century. A prominent example is Broca's work on language (Broca, 1861). The main thrust of localizationism was to search for a one-to-one mapping between the brain and behaviour, with each location in the brain responsible for a specific cognitive function. In 1983 Jerry Fodor wrote "The Modular Mind" (Fodor, 1983), where he postulated that stimuli are elaborated by a system of mental modules, distinct and separated vertically, each one with its specific function. In Fodor's view, cognitive processes rely upon discrete cognitive units. Cognitive processes are mediated by segregated neuronal populations contained in specialized modules that carry out computations in isolation from the rest of the system.*

However, the localizationist approach was opposed early on by a more holistic and integrated view of brain function. In 1906 Pierre Marie reported (Marie, 1906) on cases of non-fluent aphasia without any lesions in Broca's area and patients with damage in Broca's area without any speech deficits. Nowadays it is clear that localizationism fails to explain several phenomena: e.g., the impairment resulting from pure damage of white matter tracts (Philippi et al., 2009), frontal syndromes following non-frontal lesions (Duffau, 2012), the preservation of executive functions and above-average metacognitive abilities after bilateral prefrontal resection (Lemaitre et al., 2018). Moreover, the development and evolution in the last thirty years of brain imaging methods, and brain research in general, has clearly shown different regions of the brain work jointly even for simple behavior, and are synchronized even for single cognitive operations. Starting in 2000 decade, neuroscientists have begun to focus on brain connectivity and networks (e.g., Sporns et al., 2005). Network analyses of the brain at different scales and in different species have revealed non-random topologies and network communities linked by highly connected nodes (i.e., hubs).

An additional criticism of localizationism was the implicit assumption that brain regions mediated single functions within specific domains; however, more recent data clearly show that when considering single brain regions, it's very hard to find one that participates in one cognitive function alone. More commonly the same region participates in different functions (one-to-many). At the same time, many regions participate to perform the same operation (many-to-one). A distinguished example is the case of the hippocampus (e.g., Buzsáki & Moser, 2013). For instance, memory consolidation and navigation in space are apparently different processes. Theories on the hippocampus had been historically divided between these two main functional hypotheses: memory consolidation and navigation in space. The first hypothesis began with the observation of patient H.M. (Scoviille & Milner, 1957), a patient who suffered from amnesia after the surgical resection of the hippocampus and associated structures. The latter hypothesis began with the discovery of place cells in rats (i.e., cells that increase their spiking activity in response to the spatial position of the animal as in O'Keefe & Dostrovsky, 1971). Several attempts had been made in the following years to reconcile these apparently different functions (see Buzsáki & Moser, 2013). Hence most scientists today believe that the hippocampus does not serve a single function in the strictly modular view of cognition and that the separation of episodic memory and spatial navigation as distinct cognitive functions may be arbitrary.

These dramatic changes in the way we study the brain have not yet triggered corresponding changes in the way cognition is studied.

Most behavioral studies are still focused on the identification of specific processes; most studies use artificial computer-based paradigms based on sensory input and speeded or not speeded responses; experimental designs and statistics in psychology are traditionally designed to isolate experimental conditions underlying specific processes, notwithstanding much larger main effects across subjects. However, they usually rely on the assumption that interindividual variability is noise and thus it is unpredictable. In contrast, a way to test the opposite hypothesis (i.e., interindividual variability is *predictable to some degree) is to apply techniques that extract latent factors. Finally, possibly the strongest limitation as stated by Buzsáki (2019): "the most serious nonsense [..] is trying to find "boxes" (or processes, we add) in the brain for human-invented terms and concepts". This is a real epistemological risk that goes back to William James' categories of behavior (perception, memory, thinking, attention, etc.). Tons of experiments have been run to test hypotheses based on concepts and processes defined qualitatively based on introspection that were in turn products of prior experiments on slightly different concepts and categories.*

How do we move the field forward?

2. Why we should change the way we think of behaviour

One major development in cognitive studies has been the so-called big data revolution. It is possible today to collect with relative ease a vast amount of behavioral data that can be interrogated with sophisticated statistical methods in search of hidden patterns (see Gomez-Marin et al., 2014).

Advances in technology now allow researchers to 1) collect data at spatial and temporal scales inaccessible to the human perceptual system (e.g., high-speed videos); 2) collect and store large amounts of data easily; 3) use sensors based on wireless systems, even controlled by small devices such as smartphones; 4) interface easily large amounts of behavioral data with other body or brain signals (e.g. blood pressure, temperature, EEG, EMG). These technological advances open new scenarios for a modern behavioral science by: (1) allowing for more ecological paradigms in real-life conditions; 2) moving from segmented (trial-to-trial) to continuous behaviours; 3) switching or integrating stimulus-response paradigms with studies of spontaneous behaviour; 4) enriching datasets at the individual level by deep phenotypization of multiple signals, but also allowing for *the study of hundreds to thousands of individuals to characterize variability at the population level.*

Highly constrained laboratory paradigms are very helpful to separate different features of a stimulus or response and to abate trial-to-trial noise, however, they have also important drawbacks. The paradigm is based on the researcher's assumptions about the underlying cognitive architecture, which in turn calls for the so-called "fallacy of the misplaced concreteness" (e.g., Thompson, 1997). This notion refers to the act of mistaking the abstract (e.g., a hypothetical construct) for the concrete (i.e., reality). Another limitation is brought up by the second point: the arbitrary nature of the segmentation of behaviour. With big data, we can begin considering behaviour as a continuous variable. In addition, large amounts of data will allow to model noise present in behavior more accurately, especially under noisier spontaneous or ecological conditions. Finally, large amounts of data will allow the enrichment of datasets not only at the individual level but also in terms of the number of individuals. This is crucial since it would allow us to finally embrace and characterize inter-individual variability beyond population-mean effects.

This latter consequence is particularly important in our view. In fact, in population-mean-based approaches, the implicit assumption is that every individual behaves in the same way, while individual differences are unpredictable variability or noise.

However, apparently complex behaviours may be split into simpler components. This has been elegantly explained with color vision (e.g., Pang et al., 2016). As humans, we can perceive an impressively wide range of colours. However, our retina is equipped with only three kinds of colour sensors (L, M, and S cone types). Our colour perception is indeed a three-dimensional representation of the original infinite-dimensional spectrogram, in which all the colours we perceive are a combination of these three perceivable wavelengths.

Moreover, the unexplainable variability in behaviour, when massively collected and analyzed may also reveal different paths towards the same goals: strategies. Strategies, or styles, have a long *history in cognitive science. In the 1950s a massive interest in cognitive styles exploded; the search was for a psychological dimension representing consistencies in an individual's cognitive functioning (Ausburn & Ausburn, 1978). For instance, Witkin and Ash (Witkin & Asch, 1948) reported two different strategies (i.e., field-dependent and field-independent) in perception of the orientation of a rod in the Rod-and-Frame Test. However, this approach had two main problems: first, the claim that opposite poles of style dimension are equally valuable usually wasn't true; second, the paradigm was essentially to expose subjects to a task with two or more possible ways to solve it, but this, in turn, created a lot of punctual and disconnected cognitive style dimensions. While basic cognitive research lost interest in cognitive styles, studies exploded in applied psychology (e.g., organizational psychology in Kirton, 1976; for a comprehensive review see Kozhevnikov, 2007). However, recently, aided with advances both in technology and knowledge, an increasing number of studies is going back to styles; although in a new way (e.g., Vidal & Lacquaniti, 2021a).*

Finally, there are already several cues that different behaviours covary. A distinguished example is the G factor, first introduced by psychologist Charles Spearman a hundred years ago (Spearman, 1961a). This factor is sometimes referred to as "general intelligence" or "general mental ability". Its existence is motivated by the consistent observation of universal positive correlations between different cognitive tasks. This means that across a very different range of cognitive tasks, those who perform better in one task are more likely to perform better in all the others. Initially extracted with factor or principal component analysis, the G factor represents the structure of individual differences across a population. The G factor is remarkably stable across different batteries (Thorndike, 1987), and it seems to reflect individual differences in information processing per se. It is correlated with various physical correlates (e.g., heritability in Reed, 1988), averaged evoked potential (Schafer, 1985) suggesting that the G factor may be a product of evolution (Jensen, 1993).

3. Low dimensionality inside domains

Even if we are used to think about cognitive functions as separate boxes, simpler structures do emerge even inside these domains. In this paragraph, we will give some examples of low dimensionality inside domains. We will range from motor functions (in which it is possible to compute the number of available degrees of freedom) and end with emotions (in which counting the available degrees of freedom is not possible).

3.1 Motor

Across a number of species (e.g., Avella et al., 2003b; Chiovetto et al., 2010; Takei et al., 2017), the motor system must solve the so-called control problem. The combination of temporal and spatial configurations of muscle and kinematics typically results in a high number of available degrees of freedom. However, the actual dimensionality of movements is typically way lower than the available degrees of freedom. A good way to model motor behaviour is by exploiting linear dimensionality reduction strategies: few components are generally enough to recover most of the variability of the original data. These techniques allow to identify stable relations within the variables of interest that allow to explain interindividual variability using a small set of components.

Motor synergies (or primitives) are a long-standing model in motor studies. They are a valuable and comprehensive model to describe motor behaviour, spanning from small movements in animals (Avella et al., 2003a) to whole-body movements in humans (Chiovetto et al., 2010).

The kinematics of human hand movements have approximately 20 available degrees of freedom, while the effective dimensionality can be reduced to only two linear combinations (while keeping more than 50% of the variance in the original data) (Ingram et al., 2008). These kinematic motor synergies have been also shown to be represented in cortical areas devoted to hand motor control, *outperforming other existing models of hand posture control (see Leo et al., 2016). Hand motor synergies had been demonstrated also for motor neuron activity, with four synergies accounting for 70% of the variance, along with four functionally similar synergies in muscles (Tanzarella et al., 2021). For a comprehensive review see Santello et al., 2016.*

In human facial expressions, traditionally modeled with the 44 Action Units of the Facial Action Coding System (FACS in Ekman & Friesen, 1978), 2 spatiotemporal primitives are sufficient for the reconstruction of the original expressions (Chiovetto et al., 2018). Moreover, a low dimensional coding has been demonstrated not only for production but also for facial expression recognition (Calder et al., 2001). If we move to human arm movements, there is a very large set of possibilities both in terms of paths and time (i.e., the time at which each point of the path is reached). However, the data shows that the final resulting movements are a set of trajectories of low dimensionality relative to the 100-dimensional set of possibilities (Sanger, 2000). This also holds for several other human movements (e.g., lip motion during speech in Ramsay et al., 2017, typing in Soechting & Flanders, 1997, and, trunk bending in Alexandrov et al., 1998). This dimensionality reduction strategy still works when moving to more complex whole-body movements, such as equilibrium tasks (Degani & Latash, 2008), locomotion (Ivanenko et al., 2004), and even dual tasks such as arm reaching during locomotion (Chiovetto & Giese, 2013).

As reviewed by Vidal and Laquaniti (Vidal & Lacquaniti, 2021b), considerable interest in styles and strategies is currently growing in motor studies. For instance, Maselli and colleagues (Maselli et al., 2019) recently showed four main strategies in throwing (motor styles), which were highly consistent across individuals (i.e., most participants were stable in their throwing strategy across two different sessions). Another example is a study from Hilt and colleagues (Hilt et al., 2016), in which they explained individual motor styles in a whole-body reaching task by using a continuum between ankle and knee strategies.

The control problem should affect also the visuomotor system that needs to decide paths and timing of eye movements in space. First attempts to determine the effective dimensionality of eye movements seem to go in the same direction as motor synergies. In Poynter et al. (2013a), a factor analysis on a set of 6 eye movement features revealed they load on a single factor. In Zangrossi et al. (2021), a 58-dimensional set of eye movement features during free viewing can be reduced to 3 PCs while keeping more than 60% of the variance of the original data. Moreover, across the large eye-tracking dataset (n=120) analyzed, subjects could be classified into one of two styles: Static Viewers (characterized by longer fixations and higher similarity to a power law distribution) and Dynamic Viewers (characterized by shorter fixations and lower similarity to a power law distribution).

3.2 Language

For language here we mean the dynamics of speech production. Therefore, we focus on the form rather than the content of language. Muscle movements during speech production follow the motor synergy schema: the actual dimensionality is lower than the available degrees of freedom (Gracco, 1994; Ramsay et al., 2017). Muscles operate in concert (i.e., covariation of different muscles can be summarized by the same number of principal components as required to summarize the variation of any single muscle in Ramsay et al., 2017). Another level of analysis of speech dynamics is the study of speech fluctuations. Several theories have been trying to model this phenomenon. Apparently very complex, speech fluctuations had been described in time as the result of two interacting sources (source-filter theory in Titze & Martin, 1998) or as low dimensional chaos (Luque et al., 2015a). The pattern of energy releases during speech is power law distributed, as well as interevent statistics (i.e., silences in Luque et al., 2015b). Interestingly, these results hold across different languages and different number of speakers, pointing towards a universal pattern. Inter-word intervals (IWIs) are also not random: they are characterized by a low dimensional chaotic attractor *and a minimum of 4 variables (i.e., dimensions) are thought to underlie the system (Todder et al., 2001).*

Finally, speech perception has been shown to rely on a 2-dimensional perceptual space in which axes roughly correspond to the larynx (pitch) and supra-laryngeal vocal tract (formants). These two components also mirror the two components of source and filter in speech production (see source-filter theory in Titze & Martin, 1998).

3.3 Attention

Attention has been traditionally studied by using very different paradigms (e.g., visual search, change blindness), which determined a fragmentation of the attention literature. Several attempts had been made to unify the many attentional theories: e.g., the feature integration theory (Treisman & Gelade, 1980) and the theory of visual attention (Bundesen, 1990). However, it remained largely unclear how the different tasks relate to each other. For this reason, in 2012 Huang and colleagues (Huang et al., 2012) recorded 9 visual attention tasks from a large cohort of subjects (i.e., more than 200) to search for a possible common attentional factor across tasks. The results of this study show that a single factor across all the tasks explains 35% of the variance. This means that 1) there is a general attentional factor, which is common across all the different attentional tasks; 2) much of the variance of the tasks is indeed unique to the tasks themselves (since the general attentional factor explains just 35% of the variance). It is, however, unclear how much these results are due to the g factor (Spearman, 1961b) since there is a positive correlation (even if moderate) between general intelligence and general attentional factor. Moreover, recently Yoo and colleagues (2022) proposed a brain-based general measure of attention. In this study, the authors show that several brain regions (located in salience, subcortical and frontoparietal networks) predict accurately general attentional performance across different tasks, which was distinguished from task-specific prediction.

3.4 Emotions

Different strategies had been taken in time to classify and structure emotions. The principal attempt had been to find a set of basic emotions (e.g., 7 basic emotions in Ekman & Friesen, 1986). Another strategy was to apply factorial analysis or multidimensional scaling on different items linked to emotions (words, facial expressions, vocal expressions, etc.). This latter strategy often highlights two dimensions, which could be generally interpreted as valence and arousal. This is the case for four different theories that can be read as pointing to the same axes: Russell's arousal/pleasure axes (Russell & Barrett, 1999), Watson and Tellegen's high positive/negative affect (Watson & Tellegen, 1985), Larsen & Diener's activation/pleasantness axes (Larsen & Diener, 1992) and Thayer's energy/tension axes (Thayer, 1989).

Recently, emotional experiences have been shown to be represented in right temporo-parietal cortex following three orthogonal and spatially overlapping gradients (encoding polarity, intensity and complexity in Lettieri et al., 2019).

However, recently it has been argued against this low dimensional representation (Cowen et al., 2019).

4. Low dimensionality across domains

Outside of the existing cognitive "boxes" (attention, memory, etc.), there are already some cues that the brain, and relatedly behaviour, implement a dimensionality reduction.

We will review three main arguments: 1) the observation of correlation across different tests; 2) the observation of patterns of symptoms in brain diseases; 3) the observation of reduced representations of the environment.

Regarding the first point, the observation of correlation across different tests is deeply rooted in psychology. As discussed above, the most distinguished example is Spearman's G factor (Spearman, 1961b). This factor cuts across different tasks: historically, it was the first suggestion that there may be something else other than the traditional cognitive functions. Another example is the work from Michelini and colleagues (Michelini et al., 2019), in which a large dataset of 9- and 10- years old children, as well as their parents (i.e., the ABCD dataset Casey et al., 2018) was analyzed to delineate the hierarchies of dimensions. In children, a general psychopathology factor (i.e., p factor) emerged at the apex of the hierarchy, while five additional factors emerged below (i.e., internalizing, somatoform, detachment, neurodevelopmental, and externalizing). Interestingly, five similar factors were found also in children's parents.

Second, deficits due to brain diseases usually appear in patterns across the population. For instance, stroke is by definition focal brain damage. According to the traditional localizationist view, focal lesions tend to cause predominantly "pure syndromes" based on the injured area (e.g., (Broca, 1861). However, when analyzing a large cohort of patients (Corbetta et al., 2015), a few clusters of behavioural deficits spanning multiple functions account for the majority of the variability of neurological deficits. This low dimensionality of neurological impairment at the population level has been replicated using a different neuropsychological battery (Bisogno et al., 2021), and it has been shown to be independent of lesion location, volume, and subcortical vs. cortical lesion location.

Finally, we conclude with the general observation that the brain generates reduced representations of the environment. We propose that representations may be a way in which the brain implements low dimensionality to increase the readability of the environment. Due to the complexity of the environment, we are called to solve the categorization problem: the grouping of (a potentially infinite number of) stimuli into discrete concepts. From the computational point of view, there is recent and increasing evidence that compressed models are convenient to predict behavioural data *(e.g., Battleday et al., 2020; Hebart et al., 2020a) as well as large portions of variance in brain responses (e.g., Bonner & Epstein, 2021). Computational models built on large sets of images have proven to be efficiently predictive of human similarity judgments performed by large cohorts of participants (Battleday et al., 2020; Hebart et al., 2020a). For instance, in Hebart et al. (Hebart et al., 2020b) similarity scores on triplets extracted from 1854 images (~1.06 billion combinations) can be predicted by using 49 dimensions and even 9-15 dimensions to retain 95-99% of the performance of the full model. Not only this strategy works in predicting behavioural scores, but also in predicting brain responses. Such compressed models (e.g., object2vec compression, representing statistical co-occurrence of objects in Bonner & Epstein (2021) had been proven to be useful in explaining large portions of variance in brain activity. Recent accounts (Konkle & Alvarez, 2022) based on simulations propose that the visual system has really a domain-general learning function: it maps unlabelled input into useful representation formats.*

Conclusions

In this Chapter, we review the hypothesis of low dimensionality in behaviour, pointing out some examples suggesting low dimensionality inside and across cognitive functions. Since we are in the era of big data, it is now possible to collect large amounts of data and focus on interindividual variability. The idea that inter-individual variability is noisy and unpredictable has led to strategies to cancel it out rather than analysing it. However, it has been shown that inter-individual variability is predictable to some degree and structured across subjects. We conclude that this field is worth exploring, in order to rule out possible hidden structures in the data.

Chapter 3: Visual exploration dynamics are low-dimensional and driven by intrinsic factors

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Visual exploration dynamics are low-dimensional and driven by intrinsic factors

*Andrea Zangrossi[1,2,3], Giorgia Cona[2,4], Miriam Celli[2,3], Marco Zorzi[4,5], Maurizio Corbetta[1,2,3]**

[1] Department of Neuroscience, University of Padova, Padova, Italy; [2] Padova Neuroscience Center (PNC), University of Padova, Padova, Italy; [3] Venetian Institute of Molecular Medicine, VIMM, Padova, Italy; [4] Department of General Psychology, University of Padova, Padova, Italy; [5] IRCCS San Camillo Hospital, Venice, Italy;

Abstract

When looking at visual images, the eyes move to the most salient and behaviorally relevant objects. Saliency and semantic information significantly explain where people look. Less is known about the spatiotemporal properties of eye movements (i.e., how people look). We show that three latent variables explain 60% of eye movement dynamics of more than a hundred observers looking at hundreds of different natural images. The first component explaining 30% of variability loads on fixation duration, and it does not relate to image saliency or semantics; it approximates a power-law distribution of gaze steps, an intrinsic dynamic measure, and identifies observers with two viewing styles: static and dynamic. Notably, these viewing styles were also identified when observers look at a blank screen. These results support the importance of endogenous processes such as intrinsic dynamics to explain eye movement spatiotemporal properties.

Introduction

The exploration of visual scenes through eye movements is a complex behaviour mediated by the sequential and recursive interactions of multiple cognitive processes. For many years it was thought that eye movements were predominantly guided by stimulus-driven factors such as the sensory distinctiveness of different objects in the visual field. A highly influential model by Itti and colleagues (Itti et al., 1998a) proposed a neural network that selects attended locations in a single topographical saliency map formed by multiscale low-level features of different objects. Indeed, the pattern of eye movements while viewing complex scenes is in part predicted by the saliency of the visual images (e.g., videos (Carmi & Itti, 2006) or pictures (Elazary & Itti, 2008). A cognitive model for the control of visual attention during search is also based on the parallel analysis of visual features (Wolfe, 1994).

However, since the seminal studies of Yarbus (1967), it has been known that the patterns of eye movements depend not only on low-level features, but also on the behavioral relevance of stimuli in the visual scene, e.g. people, faces, etc., as well as the goals of the observer. Therefore, current theories, and computational models, propose that visual exploration is guided both by sensory and cognitive signals (Elazary & Itti, 2008; Itti, 2005; Torralba et al., 2006b). However, even the best *models of fixation location to static natural images account for about 30% of the potential information present in an image (Kümmerer et al., 2015b). In general, these models see the brain as a sensory-motor analyser whose activity is mainly driven by the analysis and transformation of sensory stimuli into motor decisions.*

Understanding naturalistic eye movement behaviour is not limited only to the topographical aspects of visual exploration, but also to its spatiotemporal dynamics. Most studies to date have focused on the spatial pattern of fixations during natural visual exploration (Carmi & Itti, 2006; Elazary & Itti, 2008; Itti, 2005; Itti et al., 1998b; Kümmerer et al., 2015b; Torralba et al., 2006b; Wolfe, 1994; Yarbus, 1967). The spatiotemporal pattern of fixation selection is of increasing interest to the field, but much less studied. One study found that eye movement parameters (e.g. fixation duration, saccade amplitude) were correlated across different laboratory tasks (e.g. sustained fixation vs. search vs. Stroop paradigm), and that the majority of variability across subjects could be summarized with a single factor putatively related to visual attention (Poynter et al., 2013c). Other studies found important individual variability, but also high consistency of spatiotemporal patterns across tasks (e.g., visual search vs. fixation (Andrews & Coppola, 1999b; Boot et al., 2009; Castelhano & Henderson, 2008; Rayner et al., 2007) or different versions of the same picture (Privitera & Stark, 2000).

These results suggest that eye movement spatiotemporal patterns may reflect an intrinsic or endogenous signature relatively independent of visual input or goal (Andrews & Coppola, 1999b). These patterns have been related to individual cognitive styles (Bargary et al., 2017b), personality traits (Hoppe et al., 2018), and genetic influence (Kennedy et al., 2017b).

Here we aimed to quantify the role of stimulus-driven vs. endogenous (intrinsic) parameters by examining eye movement spatiotemporal features in a large group of healthy participants while *they viewed a large set of real-world scenes vs. when they viewed a blank screen, i.e., without any visual stimulus.*

First, we were interested in testing whether the variability of eye movement (e.g., amplitude, velocity), fixation (e.g., duration, rate), and pupil parameters across many subjects, and across many visual scenes, was explained with a relatively high or low number of dimensions. High dimensionality would indicate that different subjects look differently, or that different image features yield different eye movement patterns or both. A low dimensional solution, instead, would indicate that eye movement/fixation patterns across subjects can be explained with a few components relatively independent of stimulus content.

Secondly, we asked whether eye movement spatiotemporal features during visual exploration were modulated by sensory or semantic content – stimulus-driven information – or by a power-law-like distribution of gaze steps (Stephen & Mirman, 2010) – a measure of intrinsic dynamics. Power law relations are ubiquitously found in nature and predict many complex phenomena such as earthquakes (Christensen et al., 2002), volcanic eruptions (Papale, 2018), stock market (Gabaix, 2016), and foraging behavior of many species (D. Austin et al., 2004; Ramos-Fernández et al., 2004). Power-law behavior in biological systems is thought to reflect the intrinsic constraints of the system, e.g. anatomical connections or neural dynamics in the case of the brain (Bullmore & Sporns, 2009; He, 2014; Plenz & Thiagarajan, 2007a; Tomasi et al., 2017). Power-law scaling relations have been also found in eye movement patterns during visual search (Stephen & Mirman, 2010).

Finally, to further tease apart sensory driven vs. endogenous factors, we measured spatiotemporal eye movement parameters in the absence of visual stimuli, i.e., when looking at a blank screen, and compare them to parameters found during visual exploration. A large parameter difference in the *two conditions would be consistent with the importance of sensory-driven factors; in contrast, their similarity would be more consistent with intrinsic factors controlling eye movement patterns. This study highlights a low dimensionality of eye movements spatiotemporal dynamics and a role of intrinsic factors (i.e., similarity between eye movements while watching scenes vs. blank screen, and power-law distribution of eye-movements). These results suggest that visual exploration dynamics are partially independent from the visual content.*

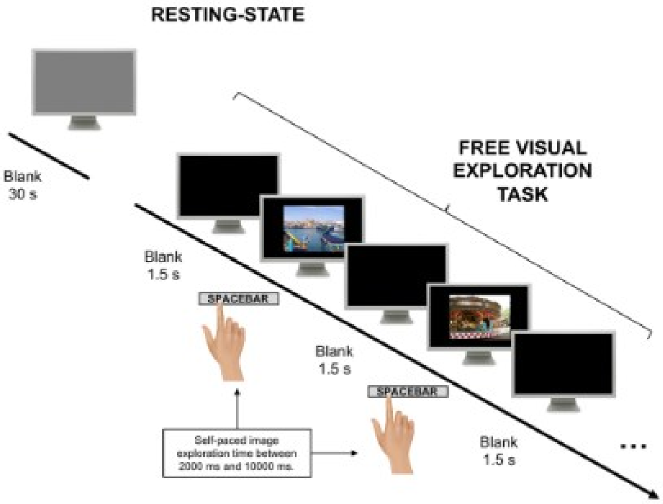

Figure 1. Experimental paradigm*. The experiment begins with a blank screen viewing condition in which participants were asked to look at a grey screen for 30 seconds. Next, participants were presented with a set of static images representing a variety of different scenes (e.g., indoor, outdoor scenes with or without humans or natural vs. man-made). Subjects were asked to explore with their eyes the picture and press a bar when ready to explore the next picture. They were also told that they will be asked some questions at the end of the experiment.*

Results

Healthy participants (n=120) were recruited at the University of Padova, with n=114 satisfying inclusion criteria (Supplementary Table 1 for demographic information). All participants had normal or corrected-to-normal (i.e., glasses, N=54) vision. Participants (aged 19-34 years) were *tested in a single experimental session lasting approximately two hours during which their eye-movements were tracked while watching a blank screen or freely exploring a set of 185 real-world scenes. These scenes were selected from a larger set of 36,500 pictures99 (Supplementary Figure 1 for the flowchart used for selection) to be representative of the following categories: indoor vs. outdoor, which in turn were divided into natural vs. man-made. The content of the pictures had no emotional valence and half of them contained human figures (Supplementary Figure 2 shows exemplars of each category). Participants were asked to look at each picture carefully, as they were told that they would be asked some questions later on, and, when ready, to advance to the next picture by pressing the spacebar on the computer keyboard (Figure 1). After the free viewing phase, they were asked to recall and describe a subset of images which were repeated five times.*

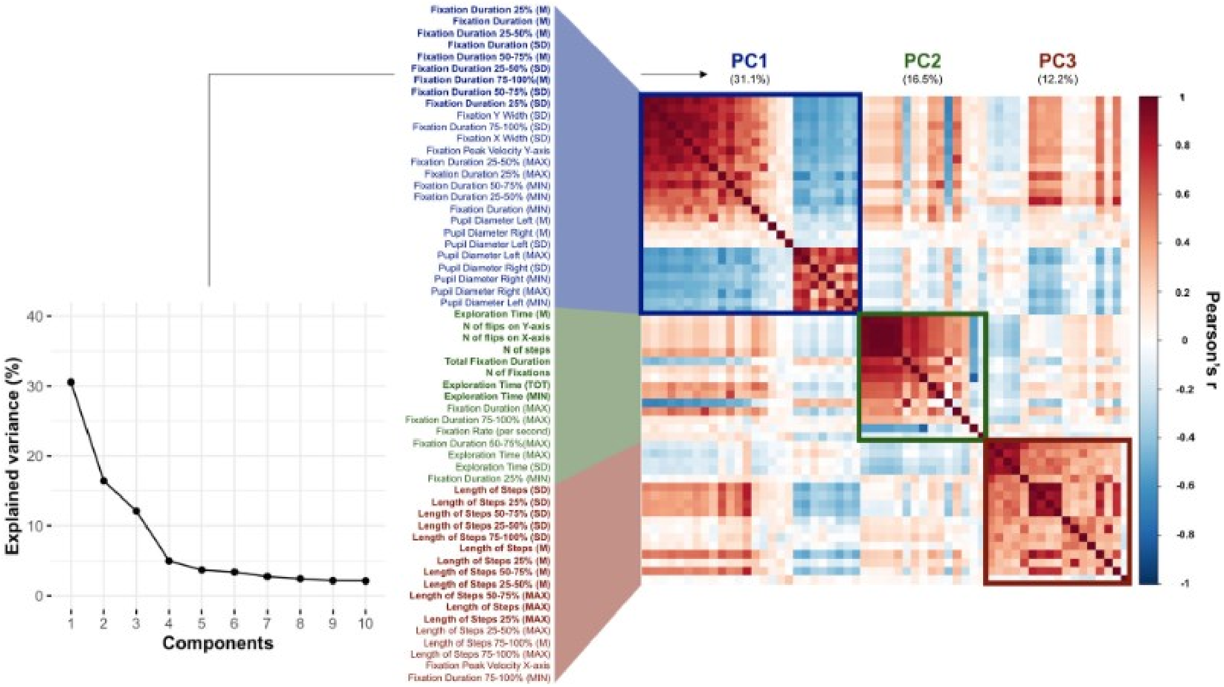

Figure 2. Correlation matrix of spatiotemporal features and principal components (PCs). *The line plot shows the variance explained by different PCs. The matrix shows the correlation (Pearson's r) between features, which are ordered according to their loadings in the first three PCs. The color of Y axis labels indicates the PC with the highest loading for the corresponding feature, and features written in bold are those with loadings > 0.2.*

The average number of freely recalled details was 59.97 (SD=20.5; range: 22-141; 2.6% false memories) across all the five images.

A large set of eye movement features (i.e., 58) were extracted including: fixation duration and number, gaze step length and number of direction flips, pupil diameter, velocity, exploration time, etc. (Supplementary Table 2). A battery of behavioural tests and questionnaires was then administered to evaluate working memory, visuospatial memory, impulsivity, anxiety, and personality traits (Supplementary Table 1 for a list of the measures). All volunteers received 10€ for their participation.

Low dimensionality in eye movement dynamics

The first question we addressed is whether eye movement dynamical features during visual exploration are 'different' or 'similar' across individual observers and many different images. We examined the pattern of correlation across eye movement features, images, and subjects by running a principal component analysis (PCA) on the scaled and mean-centred full set of features extracted from the gaze data acquired during the exploration of images. A three-components solution accounted for 59% of total variance (Figure 2 and Supplementary Table 3). The first component (30.5%) mainly loaded on fixation duration, the second (16.4%) on gaze step direction and exploration time, and the third (12.1%) on gaze step length, where gaze steps are defined as gaze shifts between consecutive timepoints (see Methods section for further details). Pupil diameter inversely correlated with fixation duration, in line with previous literature showing that pupils tend to contract during prolonged fixations (Choe et al., 2016), and suggesting the existence of a common mechanism that regulates both pupillary response and fixation disengagement through the *activity of the superior colliculus, as demonstrated in primates' brain (Joshi et al., 2016; Wang & Munoz, 2021).*

We then performed a k-means cluster analysis splitting the sample in two clusters. The k=2 clustering solution emerged as the most reliable after comparing the similarity between k-means and hierarchical clustering solutions obtained with different distance measures and values of k (Supplementary Figure 3 for details). Figure 3a shows the distribution of observers along the first three principal component (PC) scores. The best separation (ROC analysis accuracy = 99.9%, 95% C.I. [95.83-100] with cut-off value of 0.69, AUC=99.9%) was obtained along the PC1 score (Figure 3b). Participants with high PC1 scores were nicknamed "Static Viewers", because they showed a

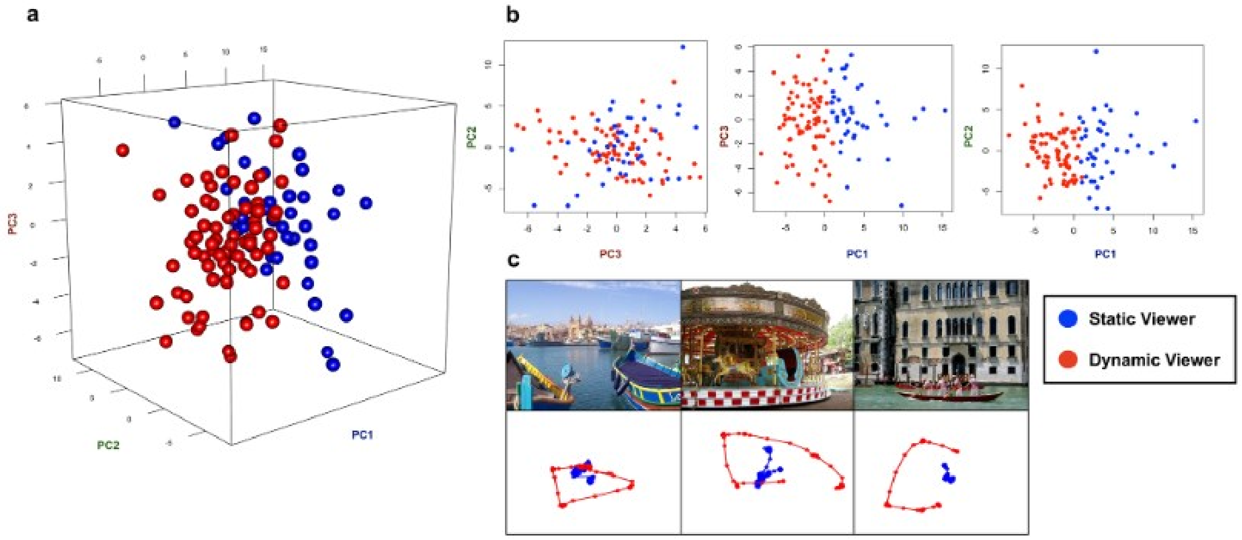

Figure 3. Relation between clusters and principal components. a. *Clusters' projection in the three-dimensional space defined by the first three principal components.* **b.** *Two-dimensional relation between PC scores. The values of PC1 are those best describing the two clusters;* **c.** *Examples of Static and Dynamic eye-movements pattern (each dot represents gaze position sampled at a timepoint). Static viewers are represented in blue and Dynamic viewers in red.*

lower fixation rate but longer fixations. Participants with low PC1 scores were nicknamed "Dynamic Viewers", because they showed more frequent but shorter fixations (Figure 3c).

In general, static viewers explored images for a longer time and showed on average higher amplitude and more numerous gaze steps, more gaze flips, smaller pupil diameter, as well as a distribution of gaze steps more similar to a power law. Moreover, they looked less at regions in the image with high semantic and saliency information (see Methods section for details on the extraction of semantic and saliency information). Dynamic viewers showed an opposite pattern of features, with a higher fixation rate, more fixations, higher pupil diameter, and a distribution of gaze steps less similar to a power law. Figure 4 shows a characterization of the viewing styles in terms of individual features and their relative effect size (Cohen d).

The robustness of this solution was tested by splitting the images in odd and even, computing a PCA in each subset, and correlating the corresponding PC1 scores. We found a high degree of similarity (for all images vs. odd; all images vs. even; and even vs. odd images, all r values>0.97, Supplementary Figure 4). Furthermore, each participant cluster label remained substantially the same when the cluster analysis was run on even (92.1%, i.e., 105/114) or odd (97.4%, i.e., 111/114) images.

To check that the component scores (PC1-3) were a good model of the original observations, we used PC1, PC2 and PC3 scores to reconstruct the original features matrix and compared the similarity of the resulting reconstruction (Supplementary Figure 5A). As expected, the most accurate reconstruction was obtained using PC1, compared to the other components. Next, we reconstructed individual patterns of features for exemplar Dynamic and Static viewers. The PC1-reconstructed patterns showed the highest similarity with the original ones, measured with the

Pearson's correlation coefficient (Supplementary Figure 5 B; Static viewer r=.86; Dynamic viewer r=.77).

Next, we examined if PC1 scores were modulated across different image-categories. We first computed the set of features for each image category (i.e., indoor, outdoor natural, outdoor manmade, scenes with humans, scenes without humans), separately. Then, we computed individual PC1 scores from category-specific features by applying PC1 loadings calculated on all images. This procedure allows to obtain comparable individual scores within the same components space. PC1 scores obtained from all images were very similar to those obtained from different category-specific features (all Pearson's r=.97; Figure 5). Inspection of the PC1 scores at the individual subject level

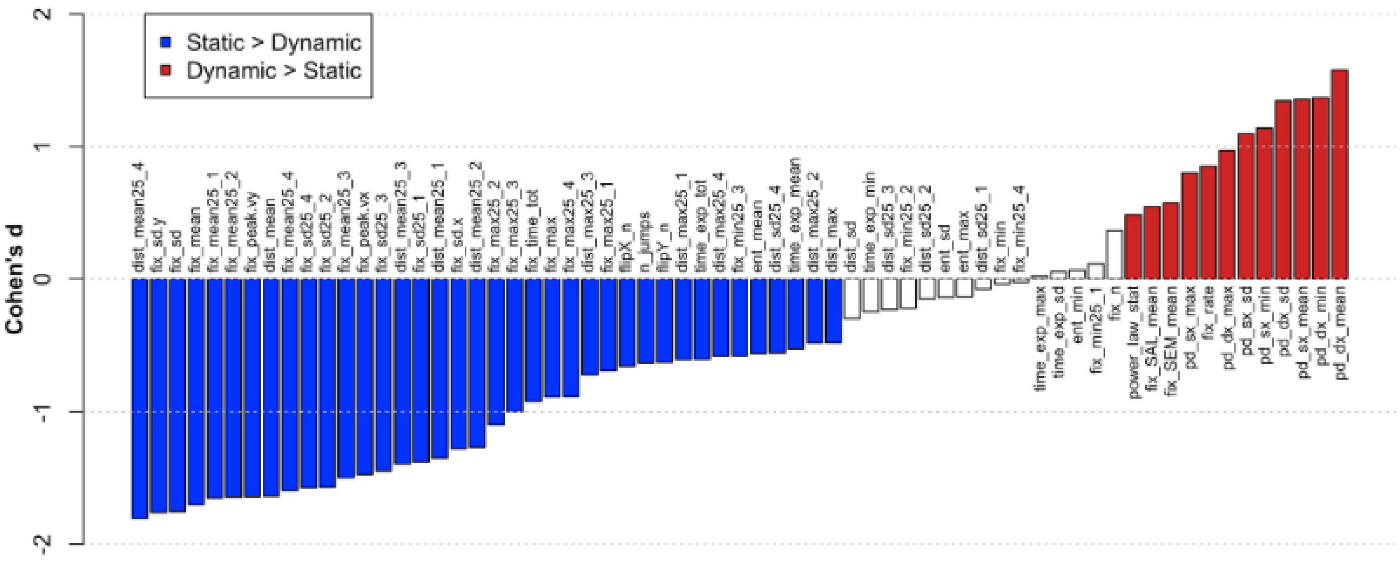

Figure 4. Characterization of the static vs. dynamic viewing styles. *A series of t-test was run comparing Static (N=42) and Dynamic (N=72) Viewers across all features. Supplementary Table 2 shows a description of features' labels. In order for the different metrics to be comparable, an effect-size measure (i.e., Cohen's d) has been computed (Y-axis). Significant results surviving False Discovery Rate (FDR) correction for multiple comparisons are represented by coloured bars and the corresponding features are coloured accordingly. Red bars indicate significantly higher value for Dynamic viewers compared to Static viewers in the corresponding feature, while blue bars reveal the opposite pattern (i.e., Static viewers higher than Dynamic). White bars indicate t-tests not reaching significance after FDR correction.*

shows that subjects with high/low PC scores overall maintained high/low PC scores for each different image category.

Overall, these findings support a low dimensionality of eye movement dynamic features across many subjects and types of visual scene, and the idea that eye movement dynamic features are relatively independent of image content.

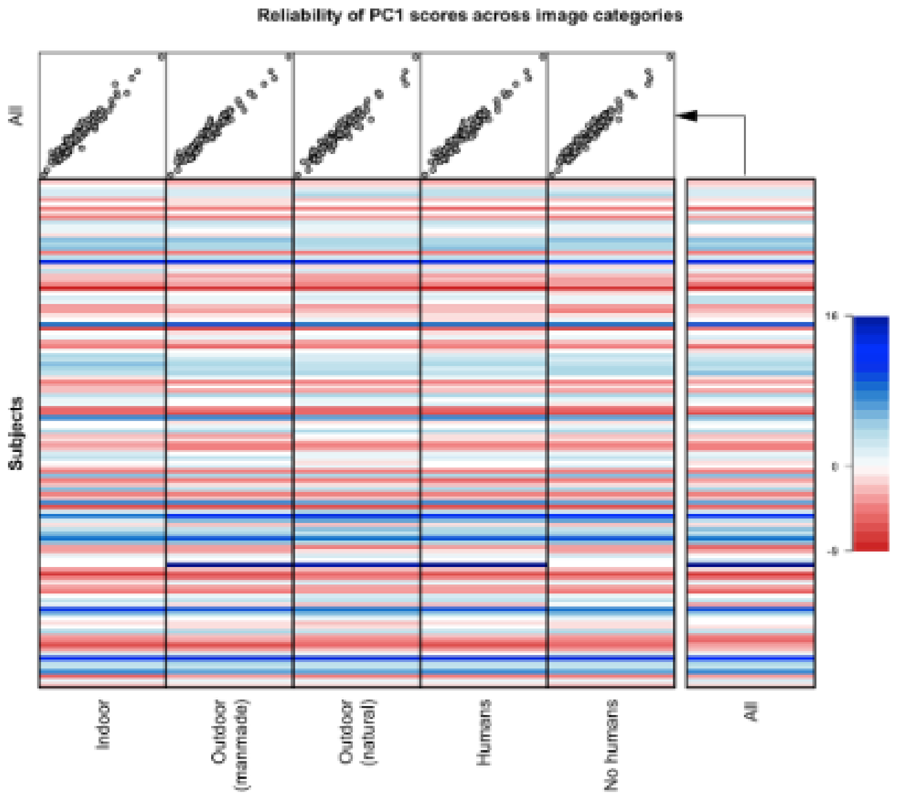

Figure 5. Reliability of the first Principal Component (PC1) across image categories. *The full set of features used for the Principal Component Analysis (PCA) in the main analysis was extracted separately for each image category (i.e., indoor, outdoor natural, outdoor manmade, scenes with humans, scenes without humans). Next, we computed category specific individual PC1 scores in the component space of the main PCA by applying PC1 loadings (calculated on all images) on features computed from each category. This procedure compares PC1 scores obtained on all images vs. specific image category and on all images. The upper five scatterplots represent the correlation between PC1 scores extracted from each specific image category (x axis) and from all images (y axis). The similarity is very high (all Pearson's r=.97). The matrix shows the PC1 scores for each subject across different image categories. Note high variability across subjects and similarity across image categories.*

Relative influence of sensory, semantic, and endogenous variables on eye movement dynamics

Once established that eye movement dynamics across many subjects and visual images can be summarized with a low number of components, we examined more directly if eye movement across subjects were predicted by stimulus-driven or intrinsic factors. We used PC1 scores as dependent variable in a linear regression model that included for each subject and across images: (1) the mean of local sensory saliency values across fixations (SAL), computed as an estimate of the overlap between fixation positions and the local values of the salience-based map derived for each scene from the Itti and Koch model1; (2) the mean of local semantic values (SEM), computed similarly on semantic maps for each scene derived from a convolutional neural network trained on 10,000,000 images(Zhou et al., 2018a) (see Methods sections for further details, and Supplementary Figure 6 for a graphical representation of the procedure used to compute SAL and SEM variables); (3) the complexity of visual exploration topography quantified with Shannon Entropy (ShEn), a measure of visual search strategy(Katsini et al., 2017; Shiferaw et al., 2019); (4) the Kolmogorov-Smirnov distance (KSD) between the individual distribution of gaze steps and a power-law distribution. Since power laws in a neural system suggest the existence of intrinsic system constraints(Plenz & Thiagarajan, 2007a), we used this measure to study the intrinsic component of eye movements dynamics, as previously suggested(Rhodes et al., 2014; Wallot & Kelty-Stephen, 2014).

Four nested linear regression models were built and compared by means of Likelihood Ratio Test (LRT) to determine whether adding a predictor significantly improved model fit. All models included PC1 scores as dependent variable and different set of predictors. Specifically, M1 included only SAL; M2 included SAL and SEM, M3 included SAL, SEM and ShEn, and M4 included SAL, SEM, ShEn, and KSD. The LRT showed that M4 was significantly the best model (F[1, 109]=14.49, p<.001; see Supplementary Table 4 upper part for details) and led to an increase in *explained variance of about 10% (i.e.,* R^2_{M1}*=.083,* R^2_{M2}*=.087,* R^2_{M3}*=.099,* R^2_{M4}*=.198; all values indicate adjusted* R^2*). This model (i.e., including all predictors; model F[4, 109]=7.59, p<.001) showed a significant effect of KSD (t=-3.79, p<.001; Figure 6a and Supplementary Figure 7) and a trend to significance for ShEn (t=1.76, p=.081). In contrast, SEM and SAL were not significant even though the set of pictures was highly variable in terms of semantic and saliency content (Supplementary Figure 6). See Spatiotemporal features model in Supplementary Table 5 for further details. These results suggest that the model best explaining a significant fraction of PC1 scores (~20% variance explained) is the one containing KSD, and that SAL and SEM do not significantly contribute to explain spatiotemporal patters of eye movements during free viewing of static natural images.*

Control analyses on PC1-PC3

The M4 model was validated in a split-half design in which 57/114 participants were randomly selected to fit the model parameters while the remaining 57 were used only for testing (i.e., prediction of PC1 scores). This procedure was repeated 1,000 times and the Pearson's r coefficient was collected for each iteration to test the correlation between actual and predicted PC1 scores. All correlations were positive (97.4% of them were significant), with a mean Pearson's r value of .42 (SD=.078; Figure 6b).

Next, to rule out the possibility that the results were biased by the eye-tracker's relatively low spatial resolution (~0.2°, 120Hz acquisition rate), we checked the similarity of eye-movements patters to power-laws, as computed through the KSD, using different thresholds of gaze-step length (0.2°-8.1°). Specifically, we removed gaze-steps smaller than each threshold, recomputed the KSD calculation, and the linear regression model predicting PC1 values. This analysis showed that the contribution of KSD was stable across multiple thresholds (0.2°, 0.4°, 0.8°, 1.6°, 3.2°, 4.0°, 4.9°)

eliminating the possibility that this effect was driven by small eye-movements not detected by the eye-tracker (Supplementary Figure 8).

In control analyses, we ran the same model on PC2 (loading on gaze steps direction flips and exploration time) and PC3 (loading on gaze steps length). The full model (SAL, SEM, ShEn, KSD)

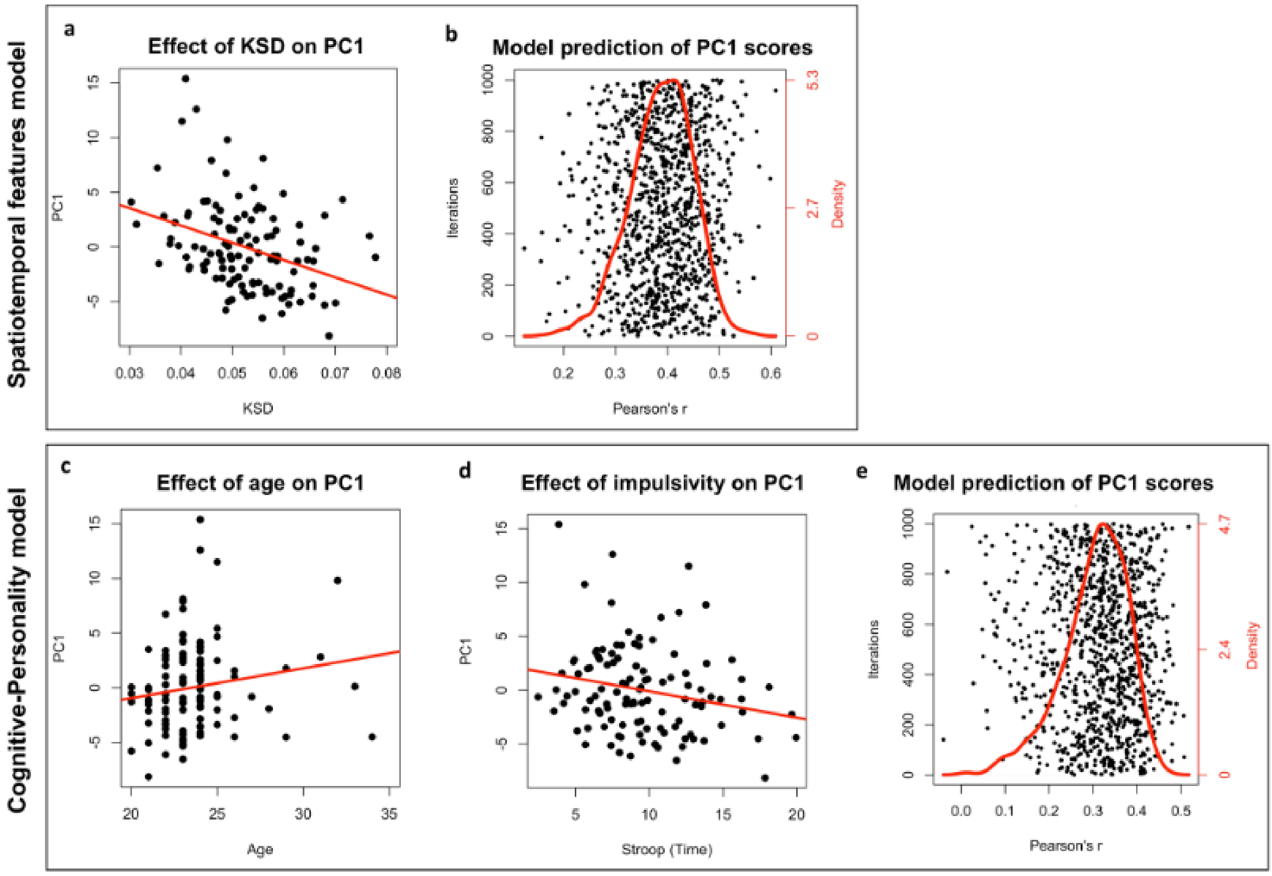

Figure 6. Significant results of regression models and prediction performance. ***a.*** *Significant relation between KSD and PC1 scores in visual exploration model;* ***b.*** *Pearson's correlation values between actual and model-predicted PC1 scores obtained over 1,000 iterations of split-half validation procedure. At each iteration the sample (N=114) was randomly split in 2 halves, one was used as training set to fit the regression model and the other one (i.e., test set) was used to assess the model prediction of PC1 scores for unseen data. The red line indicates the frequency distribution of the correlation values in the scatter plot. The peak of the red line indicates the mean r value =.42. Significant effects of Age (**c**) and Stroop test (**d**) on PC1 scores in the Cognitive-Personality model;* ***e.*** *Pearson's correlation values between actual and model-predicted PC1 scores as described before (see **b**). The peak of the red*

indicated that KSD was predictive of PC2 (t=-2.96 p=0.004), while SEM was predictive of PC3 (t=-2.45 p=0.02). Again, we did not find a significant contribution of the SAL variable.

This analysis shows that the pattern of eye movement dynamic features during visual exploration of scenes is explained by a few components (~60% variance across images and subjects). These components can be used to separate two styles of viewing (>90% accuracy of classification) that are not predicted by sensory salience. On the other hand, the visual exploration style was significantly predicted (~20% variance) by intrinsic dynamics captured by the similarity of the eye gaze steps length distribution to a power law.

Relative influence of sensory, semantic, and endogenous variables on fixations distribution

Given most of the literature and available models focus on the spatial pattern of fixations(Carmi & Itti, 2006; Elazary & Itti, 2008; Itti, 2005; Itti et al., 1998b; Kümmerer et al., 2015b; Torralba et al., 2006b; Wolfe, 1994; Yarbus, 1967), we investigated whether intrinsic factors (distance between the distribution of gaze step length and a power law as measured by KSD) significantly contributed to the spatial distribution of fixations. However, since KSD is usually computed across all eye movements (fixation) in an image, we developed a method to estimate KSD from the distribution of gaze steps in different locations of an image. Map of regional KSD values were then compared to corresponding Fixation Density maps (FDMs), saliency, and semantic maps (See Methods section and Supplementary Figure 9 for details). A mixed-effects model approach was chosen since it allows to simultaneously take into consideration not only factors under experimental control (i.e., fixed effects), but also the so-called random effects (e.g., repeated measures). In our case, we built three mixed-effects models (MM) including a random intercept for both images and subjects, and the following fixed effects: saliency (MM1), saliency and semantic (MM2), saliency, semantic and KSD (MM3). ShEn was not included due to its high correlation with FDM. The different models *were compared by means of a LRT. Specifically, we tested if the addition of KSD to a model including saliency and semantic information explained the topographical distribution of fixations more accurately. The model comparison was run across subjects and also within each subject independently. In the latter case MMs were built with random intercept only for images.*

The model including saliency, semantic and KSD (MM3) was the best model ($\chi^2[1]=681.12$, $p<.001$; Supplementary table 4 lower part). This was confirmed at the individual level with MM3 being the best model in >70% of subjects. The winning model showed strong significant effects of SAL ($t=167.16$, $p<.001$), SEM ($t=123.32$, $p<.001$), and KSD ($t=-26.11$, $p<.001$; Figure 6a and Supplementary Figure 7). See Fixation topography model in Supplementary Table 5 for further details.

These results confirm the role of saliency and semantic information in explaining the topography of fixations (i.e., FDMs), and suggest a significant contribution of KSD, despite the proportion of explained variance did not increase significantly (i.e., $R^2_{MM1}=.151$, $R^2_{MM2}=.195$, $R^2_{MM3}=.196$).

Eye movement dynamics during blank screen viewing

Given the significant influence of intrinsic eye movement dynamics on visual exploration, we asked whether the pattern of eye movements could be used to accurately classify participants during visual exploration of a blank screen (herein blank screen viewing). A positive result would strongly support the idea that intrinsic factors independent of visual analysis are important in controlling eye movement patterns. To test this hypothesis, we applied the same pipeline of analysis, i.e., features extraction and PCA to 30-sec of blank screen viewing data prior to the presentation of the first image. It should be emphasized that subjects had not seen any of the images prior to the blank screen viewing observation period. Fourteen participants were removed from this analysis because they maintained steady fixation at the centre of the screen. The blank screen viewing data *analysis was thus conducted on a sample of N=100 subjects. The results did not change when all subjects were included.*

The PCA on blank screen viewing data (Supplementary Table 3 and Supplementary Figure 10) showed also a low dimensionality with 3 components explaining ~50% of variance (23.4%, 19% and 8.4%, respectively). Not surprisingly, the order of components during blank screen viewing was not the same as during visual exploration. Fixation features that loaded on PC1 during visual exploration moved to a weak PC3 during blank screen viewing (7 out 11 features, loading >=0.2). Conversely, PC1 in blank screen viewing loaded on the maximum length and variability of gaze steps, as well as on the number of flips on the Y axis, features that were mainly related to PC2 and PC3 during visual exploration (6 out of 7 features, loading >=0.2). This was also confirmed quantitatively by running a linear regression model with PC1 during blank screen viewing as dependent variable, and PC1-3 of image viewing (as well as their interactions) as predictors. This model showed that PC3 during image-viewing significantly predicted PC1 during blank screen viewing (t=2.98, p=.004).

Next, we used blank screen viewing eye movement features to predict individual subject labels (Static vs. Dynamic viewers) using a multivariate Random Forest algorithm in a cross-classification design. That is, the algorithm was trained on features extracted in the blank screen viewing condition and tested on cluster labels extracted during the image-viewing task. The model showed an accuracy of 79% (p<.001; 95% C.I. [71.3-87.0]) in predicting cluster labels from features extracted from blank screen viewing (Figure 7a; features importance is shown in Supplementary Figure 11). We also checked the stability of viewing styles between image-viewing and blank screen viewing conditions and we found that the individual viewing style was maintained in 68% of cases (Supplementary Figure 12). Inspection of the between-subjects correlation matrix of eye movement features during visual exploration and blank screen viewing shows that individuals tend to correlate significantly more with members of the same cluster (within) than with members of the other *cluster (between; Figure 7b and 7c; all Bonferroni-corrected t-test ps<.001). Moreover, mean correlation among subjects within the Static cluster was significantly stronger than among subjects within the Dynamic cluster, both in image-viewing (t[1451.1]=8.76, p<.001) and blank screen*

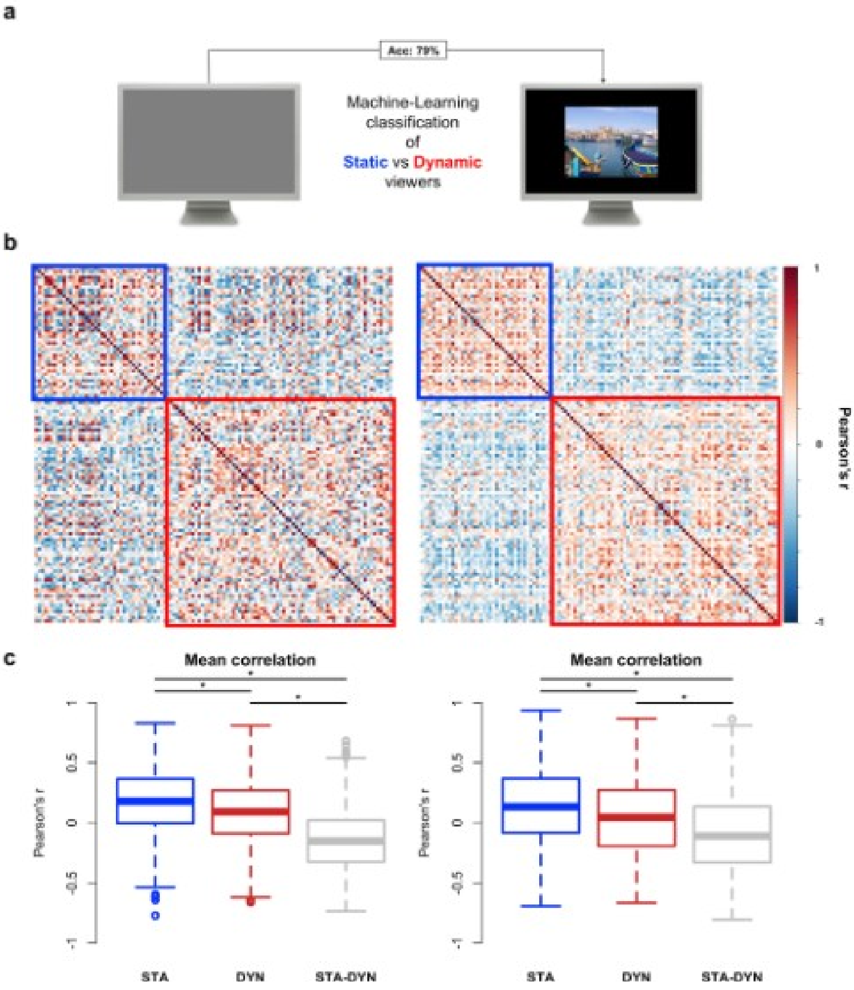

Figure 7. Subjects similarity in image-viewing and blank screen viewing. ***a.*** *Blank screen viewing eye movement features were extracted and used to predict individual subject labels (Static vs. Dynamic) by means of a random forest classifier. The algorithm was trained on features extracted from the blank screen viewing condition and tested on cluster labels extracted while participants were exploring visual scenes, in a cross-classification design. The model showed 79% accuracy in cluster classification from blank screen viewing features.* ***b.*** *For each pair of subjects a Pearson's r is computed between the vectors of z-scored features extracted from the image-viewing task (right) and the blank screen viewing condition (left). The numbers on X and Y axes indicate subject IDs. The color of each cell indicates the Pearson's correlation value, while the colored squares indicate the cluster (i.e., the visual exploration style; Blue = Static Viewers; Red = Dynamic Viewers).* ***c.*** *Bar plots showing the comparison between the mean correlation within each group (static= STA, N=42; dynamic= DYN, N=72) and between groups (STA-DYN). Error bars show 95% Confidence Interval. STA = within-group correlation in Static viewers; DYN=within-group correlation in Dynamic viewers; STA-DYN: between-groups correlation. *=Bonferroni-corrected significant*

viewing (t[1422.9]=6.59, p<.001). Importantly, the structure of the between-subjects similarity in visual exploration (Figure 7b left matrix) significantly correlated with that in blank screen viewing (Figure 7b right matrix; Pearson's r=.37, p<.001). These findings show that the visual exploration style found during free viewing of natural scenes is identifiable even in absence of visual stimuli.

Eye movement dynamics correlate with cognition and personality

The final analysis investigated whether eye movement spatiotemporal features (as indexed by PC1 scores) were related to individual characteristics, namely demographic information (i.e. age, sex, education), cognitive scores (i.e., inhibition, visuospatial and verbal memory) and personality traits (i.e. Big Five scores).

Indeed, an emerging body of research suggests a link between eye movements and personality traits (Baranes et al., 2015; Hoppe et al., 2018; Isaacowitz, 2005; Rauthmann et al., 2012; Risko & Kingstone, 2011), with Openness related to longer fixations108.

The full regression model (see Cognitive-Personality model in Supplementary Table 5) included all test scores listed in Supplementary Table 1 as predictors, with the exception of depression and anxiety scores (DASS) and visuospatial constructional abilities scores (copy of the Rey-Osterrieth Complex Figure; ROCF). The DASS scores were not included in the model since they were employed only to exclude participants with high levels of anxiety, depression and/or stress, to avoid biased eye movement data. The copy of the ROCF was excluded because it shows ceiling effect in healthy participants and for our purposes it was administered only to test the delayed recall. The model was significant (F[16,81]=1.84, p=.03, adjusted-R^2=.12) with a significant effect of Age (t=2.66, p=.009; Figure 6c) and impulsivity (i.e., Stroop test score; t=-2.36, p=.021; Figure 6d), and trend significance for the NEO-FFI subscale Openness (t=1.93, p=.057). Specifically, dynamic viewers were younger (range of the whole sample: 19-34 years old), showed higher impulsivity (i.e., lower inhibition of automatic responses at Stroop test), and a non-significant *tendency for being less open. The model was validated using the split-half procedure described above with 1,000 iterations (Figure 6e).*

Discussion

In this study we measured eye movements in a large sample of healthy participants during visual exploration of many real-world scenes. We found that eye movement spatiotemporal parameters were strongly correlated across pictures and participants, with three components explaining roughly 60% of the variance of eye movement dynamics. This low dimensional structure of eye movement patterns, especially the duration and number of fixation (PC1) identified two viewing styles: static and dynamic. The inter-individual variability of PC1 scores was significantly predicted by the similarity of gaze step length distribution to a power-law, an intrinsic property of dynamical systems, but not by the saliency or semantic content of the visual scenes. In addition, static and dynamic viewers could be identified by the pattern of eye movement features while participants looked at a blank screen, and they differed in their cognitive profile.

Herein, we discuss two main results: the low dimensionality of eye movement spatiotemporal features during visual exploration, and the role of intrinsic dynamics vis-a-vis sensory salience and semantic information in guiding visual exploration style.

The low dimensionality of eye movements is not an entirely novel result. Poynter and colleagues (2013), in a study on n=40 subjects, found that eye movement parameters correlated across different laboratory tasks (e.g. sustained fixation, search, Stroop), and could be summarized with a single factor, putatively related to visual attention. Their factor loaded on the duration and frequency of fixations that is also an important component of our PC1. Using a larger set of features, we separated two clusters of observers, static and dynamic, who differed not only in terms of the rate or duration of fixation, but also pupil diameter, spontaneous viewing time, amplitude *and number of gaze steps, and number of gaze flips (Figure 4). The assignment to one cluster or the other was stable (>90% accuracy) across different sets of images.*

Static viewers showed less frequent but longer fixations, longer exploration time, larger and more numerous gaze steps, more gaze flips (i.e., change of gaze direction), smaller pupil diameter, as well as a distribution of gaze steps closer to a power law. Moreover, they spent less time on parts of the images that were rich in semantic and saliency information. Dynamic viewers showed the opposite pattern. Intuitively, static viewers better approximated a power law distribution because they showed more small amplitude and relative few long-range gaze steps, while dynamic viewers made a more balanced combination of short and long gaze steps.

The covariance of fixation duration and gaze step distribution is consistent with an interdependent control process (Wallot et al., 2015). At the neural level, fixation and saccadic activity are inter-related at multiple levels in the brain (frontal eye field, superior colliculus, brainstem in Krauzlis, 2005; Krauzlis et al., 2014, 2017). At the cortical level, different neural systems, the dorsal and ventral attention networks (Corbetta et al., 2008; Corbetta & Shulman, 2002), control focal processing vs. re-orienting to novel locations.

Visual processing occurs during fixations, hence a longer fixation time in static viewers may imply more-in-depth processing of fewer stimuli. Conversely, dynamic viewers may look more rapidly, and more superficially, to more items in a visual scene. This interpretation is also consistent with the observation that PC1 scores were related to impulsivity, i.e., the ability to inhibit an automatic response. Specifically, dynamic viewers tend to be more impulsive than static viewers. This is in line with previous literature linking impulsivity to voluntary control of fixation behavior (Munoz et al., 2003).

The presence of low dimensionality and individual styles in human cognition that define inter-individual variability is consistent with other recent findings. For instance, a recent study classified individuals along the Big-Five dimensions of personality based on patterns of eye movements in *real life (walking on campus in Hoppe et al., 2018). Similarly, studies of human mobility have revealed two distinct styles (Pappalardo et al., 2015) during walking from one location to another in a city: "Returners" who tend to walk back-and-forth nearly always taking the same trajectory, and "Explorers" who explore more frequently new locations in their route. The authors showed also a social bias in the mobility profile, with a tendency to engage more socially individuals with a similar mobility profile.*

In the field of reward, we have recently shown that the temporal discount functions in a large group of healthy subjects (n=1200) show a Pareto optimality distribution that defines three archetypes: people who always wait for larger rewards; people who always take immediately; and people who take immediately when the reward is large (Cona et al., 2019a). The existence of different styles may reflect trade-offs in cognitive or physical traits that have been selected during evolution to maximize specialized performance, similarly to what shown in other fields such as animal behavior (Gallagher et al., 2013) or biological circuits (Szekely et al., 2015).

Next, we asked: what controls the low dimensionality of eye movement patterns across subjects? We first quantified sensory salience using a classic saliency model1, while semantic information was quantified based on a deep learning neural network (Zhou et al., 2018a). The amount of saliency and semantic information within fixated locations were then used as predictors of PC1 scores, along with a measure of visual scanning topography (Shannon entropy of eye movements), and the distance of each individual eye movement distribution to a power law (Kolmogorov-Smirnov distance; See Methods section). The presence of power law dynamics in behavior (including eye movements), as well as in neural systems (Plenz & Thiagarajan, 2007a), is thought to reflect intrinsic dynamics (Rhodes et al., 2014; Wallot & Kelty-Stephen, 2014). Surprisingly, we found that saliency or semantic information did not predict significantly PC1 scores (nor PC2). It is important to note that this result is not due to averaging of saliency or semantic information across pictures, thus leaving only shared information. Rather, estimates of saliency and semantic *information were computed fixation by fixation (i.e., amount of saliency/semantic information collected by the observer in each fixation), therefore taking into account eye movement patterns in each picture separately.*

On the other hand, saliency and semantic maps significantly predicted the topography of fixations, as expected from previous literature. Taken together these results support and extend previous literature suggesting that saliency models accurately predict eye movements behavior during free-viewing in terms of fixation topography (Foulsham & Underwood, 2008; Koehler et al., 2014; Parkhurst et al., 2002). This is in line with the assumption that when an observer is not engaged in a specific task eye movements will be directed to regions of higher saliency (Foulsham & Underwood, 2008; Parkhurst et al., 2002).

However, saliency plays a lesser role in predicting the spatiotemporal properties of eye movements, i.e., their dynamics (as previously shown for scanpaths in Foulsham & Underwood, 2008). Here, several results pointed to the importance of endogenous factors. First, the components mainly describing spatiotemporal eye movements features that are independent of image content (e.g., image category). Secondly, the low influence of saliency and semantics in explaining PC1 variability. Thirdly, the similarity of the spatiotemporal latent variables during free viewing of static natural images and blank screens. In contrast, we find that the distance of the distribution of gaze shifts from a power law (KSD) predicts about 20% of the PC1 score variability across subjects. In addition, KSD also contributes albeit less strongly than saliency and semantic information to the topography of fixations.

Power laws are ubiquitous in the world, as well as in the brain where they are thought to reflect neurobiological constraints imposed by anatomical connectivity and neural dynamics. Power laws have been described in fMRI, EEG/MEG, local field potentials, and single unit activity(He et al., 2010; Linkenkaer-Hansen, Nikouline, Palva, et al., 2001; Shriki et al., 2013). Moreover, behavioral performance fluctuations also follow a power law, including eye movements (Wallot et al., 2015), *and tend to correlate with slow and fast neuronal activity. Interestingly, the power law exponents of behavior and neural activity are correlated across individuals both during task and rest (Palva, Zhigalov, Hirvonen, Korhonen, Linkenkaer-Hansen, et al., 2013b). Therefore, we posited that a similar link may occur between eye movement dynamics and neural dynamics, even spontaneously at rest (i.e., during blank screen viewing). This implies that resting dynamics have an influence on how we move the eyes during visual exploration, thus potentially revealing stable, biologically determined, traits of the observer (de Haas et al., 2019).*

This was confirmed in our recordings of eye movements to a blank screen. We found in this case three components that explained a similar amount of variance (~50%) with the most variance explained by gaze step amplitude (gaze step length PC1: 29% variance), and the least variance explained by fixation duration and frequency (PC3: 9% variance). Hence, the features defining the three components resembled those found during visual exploration, but their relative weight differed. During exploration, eye movement variability was mainly explained by fixation duration; during blank screen viewing, the variability of eye movement spatiotemporal features was mainly explained by the amplitude of gaze steps. This indicates that similar components are active in both situations, but that visual exploration gently moves the attractor space of eye movement parameters. This finding is in line with the similarity of brain activity topography at rest and during tasks (Cole et al., 2014; Smith et al., 2009), with the relative correlation within and between networks adjusted during different tasks (Betti et al., 2013; Cole et al., 2014; Spadone et al., 2015). This is consistent with the idea that spontaneous neural dynamics function as a spatiotemporal prior constraining the parameters space of task-evoked activity (Berkes et al., 2011; Raichle, 2011). Our results are consistent with a previous small-scale study (n=15) in which visual exploration eye movements were compared to eye movements recorded in darkness81. However, eye movements in darkness could reflect several factors not directly related to spontaneous visual exploration dynamics, such as posture-related information (Clemens et al., 2017) or memory-related processing

(Johansson et al., 2012). Also, pupillary responses are not controlled in the darkness. Other small-scale studies used a similar blank screen condition during a memory retrieval task (Johansson & Johansson, 2014) or while hearing sentences about a previously presented scene (Altmann, 2004). To the best of our knowledge, our work represents the first large-scale study in which spontaneous eye movement dynamics are compared to those recorded during exploration of many real-world visual scenes, and the first to show that characteristics of eye movements at rest (i.e., during blank screen viewing) can be used to classify different styles of visual exploration.

Regarding the present study's limitations, the sampling rate of the eye tracker (i.e., 120 Hz) did not allow us to investigate in detail the dynamics of microsaccades that are an important mechanism of fixation. Visual exploration could be also studied in more natural conditions without the use of a chin-rest support using algorithms for head movements correction, or wearable eye-trackers. The blank screen viewing period of observation was short (30 seconds prior to the presentation of the first image) so that we cannot rule out that some degree of expectation did influence the results. Also, longer blank screen viewing periods would allow the detection of slower fluctuations of eye movement patterns as well as pupillary responses that are related to vigilance fluctuations and could significantly impact intrinsic activity (Van Someren et al., 2011).

In conclusion, eye movement features during free visual exploration are correlated across subjects, and cluster people in two phenotypes depending on their style of exploration. The degree to which the distribution of gaze steps length resembled a power-law was the strongest predictor of the visual exploration style. We speculate that this could suggest the existence of neurological constraints that drive visual exploration behaviour and predict individual differences, e.g. patterns of anatomical connectivity and/or neural dynamics.

Another related implication of this work would be its potential as a biomarker in clinical populations. For instance, some authors have shown that neurodegenerative disorders are associated with specific patterns of eye-movements features (Anderson & MacAskill, 2013b), but *these studies have mainly used laboratory tasks (e.g., anti-saccades tasks), with some investigations during reading (Biondi et al., 2017; Fraser et al., 2017), and not focused on intrinsic dynamics. It is possible that alterations of eye movement intrinsic patterns may represent an early biomarker of neurodegeneration.*

Methods

Subjects

A sample of 120 students were recruited at the University of Padova (mean age = 23.4, SD= 2.42; 49 M). All participants had normal or corrected-to-normal (i.e., glasses, N=54) vision. We excluded individuals with excessive data loss, defined as less than 50% of usable data in more than 25% of trials (n=3 individuals excluded). Moreover, two further participants were excluded due to the interruption of the experimental session for a panic attack in one case, and for eyes irritation in the other case. Finally, one participant was excluded because of colour-blindness revealed after the experimental session was completed. Thus, 114 out of 120 participants were included in the final sample (mean age=23.52, SD=2.45, 67 F). All participants signed an informed consent before the experimental session and after it they received a remuneration of 10€ for their participation. The study was approved by the Ethical Committee of the University of Padova.

Experimental design

Each participant took part to a single session composed by five phases (total duration: 2 hours). In the first phase participants were asked to look at a grey screen without any stimulation for 30 seconds. Participants were just told to freely move their eyes within the screen boundaries.

In the second phase a set of 185 images of scenes selected from the Places 365 database (see the Stimuli paragraph for details about the dataset and the stimuli selection). Stimuli subtended 27.1° x 20.5° (width x height) degrees of visual angle on a screen subtending 31.6° x 23.9°. Participants were instructed to freely look at the pictures in a self-paced design (for min 2,000 ms – max 10,000 ms; 1500 ms ITI) and to move to the next trial by pressing the spacebar. Moreover, they were informed that they would be asked some questions at the end of the task. After the first half of the images was presented, participants had a 10 minutes break to let them relax and rest their eyes. Once all the pictures were presented, participants had another 5 minutes break before the third phase in which they were asked to recall the five repeated images. Participants were requested to describe each image for 3 minutes as accurately as possible while their verbal description was recorded by means of a voice recorder. During the recall, participants were presented with the same grey screen adopted in phase 1. For the purpose of the present paper, only phases 1 and 2 have been considered.

Stimuli

The stimuli used in the present experiment were real-world scenes selected from the Places dataset (Zhou et al., 2018a), a scenes dataset designed to train artificial systems for image recognition. Specifically, the dataset we used in this experiment is the validation set of the Places365-Standard dataset (the dataset can be downloaded here: http://places2.csail.mit.edu/download.html). All images in the dataset were categorized according to three hierarchical levels. Level 1 was the most general and subdivided the images in three categories: indoor, outdoor man-made, outdoor natural. In Level 2, each of the categories in Level 1 was split in four to six subcategories (e.g., for Level 1 category "indoor", Level 2 subcategories examples are "shopping and dining" and "home or hotel"). Finally, Level 3 encoded 365 specific categories describing the type of scene (e.g., art gallery, bakery shop, etc.)

For the purposes of the present work, only Level 1 categorization was chosen, moreover images were coded through an additional dimension, that is whether they depicted human beings or not. Thus, six categories were finally considered (i.e., indoor manmade with humans, indoor manmade without humans, outdoor manmade with humans, outdoor manmade without humans, outdoor natural with humans, outdoor natural without humans) and 30 images for each category were chosen (e.g., outdoor manmade with humans; Supplementary Figure 2). The final set of images was composed by 180 items with the add of 5 further images for the recall phase purpose. These images were taken from all the above-described categories but outdoor natural images without humans as this type of images showed a very low number of recallable details. Details about the image selection process are reported in Supplementary Figure 1.

Assessment of behaviour and personality

Participants were tested after the eye-tracker data acquisition was completed. For the cognitive assessment we decided to focus on memory (visuospatial long-term memory, working memory) and executive functions (inhibition/impulsivity) as these domains seem to mainly influence visual behaviour (Cirilli et al., 2011).

The cognitive tests employed to assess the described domains were the Digit Span (forward and backward, Monaco et al., 2013b), the brief version of the Stroop Test (A. Venneri et al., 1992), and the Rey-Osterrieth Complex Figure (ROCF, Rey & Osterrieth, 1993). Moreover, we asked participants to fill a form sent by e-mail which included three questionnaires. One of these was a personality questionnaire based on the Five Factor Model (McCrae & Costa, 1987), the Neo Five Factors Inventory (NEO-FFI, Costa & McCrae, 1989a) which evaluates the following factors: Extraversion, Agreeableness, Conscientiousness, Neuroticism, and Openness to Experience. A number of studies have shown a link between personality factors and several aspects of eye-movement such as the pattern of fixations (Mercer Moss et al., 2012), the number of fixations, *their duration, and dwelling time (Rauthmann et al., 2012). Starting from this point, in a recent paper (Hoppe et al., 2018) authors demonstrated that personality traits can be predicted from a set of visual features by means of a multivariate machine-learning approach. This result suggests an important role of individual characteristics on visual behaviour. Furthermore, in the present study we assessed impulsivity in complex behaviours by means of the Behavioral Approach System – Behavioral Inhibition Scale (BIS-BAS, Carver & White, 1994a). The relation between impulsivity and eye-movements have been previously pointed out in literature (Rauthmann et al., 2012). The information extracted from this questionnaire can be seen as complementary to those taken from the Stroop Test, thus, taken together, they allow to investigate impulsivity both from cognitive and behavioural points of view. Finally, the 21-items version of the Depression Anxiety Stress Scale (DASS-21, Lovibond & Lovibond, 1995b) was used to control for participants' state anxiety, as it can have influence visual behaviour (Vater et al., 2016). None of the participants was discarded for excessive state anxiety score. Moreover, since some participants were students of psychology, we checked their knowledge of the administered tests using a three-point scale (0= No knowledge; 1= Theoretical knowledge; 2= Theoretical and Practical knowledge). No effects of previous knowledge emerged on the subsequent models.*

Eye-tracker data acquisition, pre-processing and features extraction.

The eye-tracker adopted was the Tobii T120 (Tobii Technologies, Danderyd, Sweden) which allows to acquire gaze data with a 120Hz sampling-rate (or every 8.3ms). Participants were seated at a fixed distance of 60 cm from the screen, and their head-movements were limited by a chin-rest. Raw eye-tracking data were minimally pre-processed. We included in the analysis only gaze samples in which both eyes were assigned the highest validity value (i.e, validity code of 0, indicating that the eye is found and that the tracking quality is good). Then, we extracted a large *set of features encoding various characteristics of eye-movements to describe visual behaviour in an exhaustive way, as done in other recent studies (Hoppe et al., 2018).*

For each participant, a set of 58 features was extracted (Supplementary Table 2) which encoded four main sources of information: fixations, pupil diameter, gaze steps and exploration time. Statistics over fixations (e.g., mean duration) are frequently employed in eye tracking studies (Rauthmann et al., 2012). In the present study, fixations were detected using a velocity-based threshold algorithm (Engbert & Kliegl, 2003b; detection threshold lambda = 15), which is considered adequate and robust across several testing conditions (Stuart et al., 2019). From a cognitive point of view, fixations represent information processing and their duration is correlated with the depth of cognitive processing (Just & Carpenter, 1980). Pupil diameter (e.g., mean pupil diameter of left eye) was considered since it is not only related to environmental light and vigilance, but also to a variety of cognitive processes such as attention (Unsworth & Robison, 2016) and cognitive load (Krejtz et al., 2018). Gaze steps statistics (e.g., mean gaze step length, number of flips on x and y axes) were computed from raw gaze data as the Euclidean pixel distance between two consecutive gaze positions (Stephen & Mirman, 2010). Notably, the use of this metric allows to avoid the distinction between saccades and microsaccades, as both types of eye movements are thought to be controlled by the same neuronal mechanisms (Krauzlis et al., 2017). Finally, statistics describing exploration time were taken into account (e.g., mean duration of pictures' exploration). Moreover, for fixations and gaze steps, additional features were extracted which encoded their temporal course (e.g., mean fixation duration in the first, second, third and fourth quarter of exploration time). This set of features is largely overlapped with those adopted in previous studies that examined the relationship between eye movements and individual characteristics (Hoppe et al., 2018). The choice of these features was made to capture the spatiotemporal features of eye movements and fixations rather than their spatial distribution.

Eye-movements data reduction.

A Principal Components Analysis (PCA) was performed on the features matrix (114 subjects x 58 features) to reduce it to fewer meaningful components. Oblique rotation (promax) was adopted because of the correlation between the features. To select the optimal number of components we adopted the Kaiser's criterion (Kaiser, 1960) and selected only components with eigenvalues higher than 1. In addition, to be selected a component had to account for a percentage of variance of at least 10%.

For the image-viewing task, according to the selection criteria and after visual inspection of a scree plot, a three-component solution was chosen. The first three components globally explained roughly 60% of variance. The first component (explained variance: 31.1%) mainly loaded on fixations duration, second component (explained variance: 16.5%) mainly loaded on exploration time, number of steps and number of flips (i.e., changes of direction on X or Y axis), finally third component (explained variance: 12.2%) mainly loaded on steps' length.

For the blank screen viewing phase, a separate PCA analysis was done after computing the same set of features as before with the exception of exploration-time related features. The reason of this is that in the blank screen viewing condition the exploration time was basically the same for all participants. Since fourteen participants showed missing data in some fixation-based features (e.g., due to a single central fixation), only 100 participants were included in this analysis. Moreover, exploration time-based features were removed, as blank screen viewing had the same duration (30 s) for all subjects. Thus, the PCA on blank screen viewing data was performed on 100 subjects and 53 features.

Moreover, in the PCA on the blank screen viewing features we decided to include the first 3 components regardless of the amount of explained variance, to match the structure of the previous PCA on the image-viewing task. The first component (explained variance: 23.4%) mainly loaded on number of steps, number of flips and steps' length variability. The second component (explained *variance: 19%) mainly loaded on pupil diameter and steps' length, while the third component (explained variance: 8.4%) mainly loaded on fixations duration (Supplementary Figure 10). Interestingly, the most important features in blank screen viewing condition were mainly included in the third component extracted from the image-viewing task. This suggests that the importance of fixation-related features was lower if compared to the image-viewing condition, while more importance was assigned to pupil diameter and steps' length.*

Detection of clusters in visual behaviour and their interpretation.

Preliminarily, Silhouette method (Rousseeuw, 1987) was applied to identify the optimal number of clusters in a data-driven manner, and suggested the existence of 2 clusters in our data. Then, a k-means cluster analysis with a k value of 2 was carried out. The reliability of the two clusters solution was tested by comparing different clustering solutions obtained from k-means and hierarchical clustering algorithms, using several distance metrics. The similarity between the clustering solutions was quantified by means of the Jaccard index (Supplementary Figure 3) and revealed that the 2 clusters solution was the most reliable across different methods. Figure 3 shows the participants scores in the three-dimensional space defined by the first three principal components, coloured according to the cluster participants belonged to. The PC1 scores accounted well for the differences between the two clusters which were represented by a continuum.

Subsequently, we wanted to investigate whether the different visual exploration styles were associated with differences in the topography of the visual exploration pattern (i.e., entropy), in the distribution of gaze steps (i.e., more power-law-like) and in the informational content of fixations (i.e., whether subjects paid more attention to saliency or semantic information).

First, for each participant, 185 heatmaps were created (i.e., one for each presented picture) representing the empirical gaze maps encoding the normalized number of times the gaze was centred in each pixel. The Shannon entropy was calculated for each heatmap.

Second, the distance (i.e., euclidean distance) covered in each gaze step (i.e., gaze step length) was calculated and the distribution of their length was computed. Then, the subject-specific gaze step length distribution was fitted to a power-law distribution and their similarity was quantified by means of the Kolmogorov-Smirnov test, a well-known nonparametric test which is used to distinguish between distributions (Clauset et al., 2009). Specifically, in our case this test was used to investigate whether an empirical probability distribution (i.e., the subject-based distribution of gaze steps length) disagreed from a reference distribution (i.e., the power-law distribution), by quantifying the distance between these two distributions (Kolmogorov-Smirnov Distance, KSD). The lower the KSD, the higher the similarity between the empirical distribution and the reference power-law distribution. Importantly, this procedure was applied to each individual gaze steps distribution independently, leading to a different power-law exponent for each participant.

Third, we wanted to quantify the influence of saliency and semantic information in shaping general properties of visual exploration of real-world scenes. To this end, we created two types of heatmaps for each image: (1) a saliency map created using the classical saliency model by Itti and colleagues 1 implemented in the graph-based visual saliency (GBVS) Matlab toolbox (Harel et al., 2006); (2) a semantic map created by means of a recently published algorithm based on a Convolutional Neural Network (CNN: Residual Network, Zhou et al., 2018a). These maps were used to quantify, fixation by fixation, the quantity of saliency and semantic information included. We therefore calculated the mean amount of saliency and semantic information fixated by each subject. Supplementary Figure 6 shows a graphical explanation of this procedure. All computed heatmaps were spatially smoothed using a 2° full width at half maximum (FWHM) Gaussian Kernel.

Three nested linear regression models were built with PC1 scores (obtained in the image-viewing task) as dependent variable, and the measures described above as predictors. Specifically, the first model (M1) included only saliency in fixations, then in M2 we added semantic information, in M3 also Shannon Entropy of visual exploration was included, and finally, M4 included all previously *mentioned predictors as well as KSD. The models were compared by means of a Likelihood Ratio Test (LRT) to highlight the most plausible model given the data. The resulting best model (M4) was then tested on the whole sample, and its reliability and generalizability were tested by randomly splitting the sample in two halves, fitting the model on one half (i.e., the training set) and testing its prediction (i.e., PC1 score) on the other half data (i.e., the test set). This procedure was repeated 1,000 times and each time the correlation between actual and predicted PC1 values was collected (Fig. 6B).*

Furthermore, we built a further linear regression model with the aim to investigate whether visual exploration styles (PC1 scores) were predicted by demographic information (i.e. age, sex, education), cognitive (i.e., inhibition, visuospatial and verbal memory) or personality traits (i.e. Big Five scores). The full regression model (i.e., including all predictors; Supplementary Table 5) was tested and validated by applying the same split-half validation procedure used before (with 1,000 iterations; Fig. 6E).

Prediction of fixation topography from saliency, semantic information and KSD

In this analysis we aimed to test whether KSD could predict the topography of fixations. To this end, we first computed a Fixation Density Map (FDM) for each image and for each subject (resulting in 185x114 FDMs). A gaussian kernel (FWHM=2°) was then applied to approximate the width of the visual field saw by the fovea and to match the other maps. Then, we computed spatial KSD maps as follows: 1) since KSD is computed on a distribution of gaze-steps, it could not be computed at the pixel-level, thus we subsampled the image space (512x683 pixels) to a smaller (10x10) matrix; 2) from raw gaze data we extracted the vector of gaze-steps amplitude within each cell while watching an image at the subject-level, and we calculated corresponding KSD values, resulting in a 10x10 KSD matrix. This procedure was applied to all images and all subjects resulting in 114x185 KSD maps. Then, FDMs, saliency and semantic maps were subsampled to *match the size of the KSD maps. Finally, the resulting set of matrices were vectorized, concatenated and used to build three mixed-effect models (MM1, MM2 and MM3) to quantify the contribution of saliency, semantic information and KSD in describing the spatial distribution of fixations (FDMs). A graphical representation of this method is shown in Supplementary Figure 9. Each model included a random intercept for both images and subjects, and nested sets of fixed effects: MM1 included only saliency maps; in MM2 we added semantic maps, and in MM3 also KSD maps were included. The models were compared through LRT as described in the previous paragraph. And the results of the best model (MM3) were discussed. Notably, the model comparison was run also within each subject independently, by building the same models with random intercept only for images.*

Machine-learning classification analysis of cluster labels from blank screen viewing eye-movements' features.

We investigated whether the features extracted during blank screen viewing were informative about the visual exploration styles emerged while watching real-world scenes. To do so, we trained a Random Forest classifier to predict the two cluster labels (Static vs Dynamic, as determined in the image-viewing condition) from the blank screen viewing multivariate pattern of eye-movement features. We used a 10-fold cross-validation design, i.e. data were split into 10 folds, nine of which were used as training set and one was left out and used as test set. This procedure was repeated for 10 iterations until each fold was used once as test set, resulting in a mean accuracy value indicating the proportion of participants correctly labelled.

Moreover, we computed a features correlation matrix between subjects, thus testing the interindividual similarity in the pattern of eye-movement's features (Fig. 7B). As shown in the figure, the correlation is higher for participants falling within the same cluster (i.e., Static viewers or Dynamic viewers) than between participants with different visual exploration styles. Then, to *test the reliability of this pattern of between-subjects similarity between blank screen viewing and image-viewing conditions, the Pearson's correlation between the two matrices was computed.*

Statistics and reproducibility

Principal Component Analyses (PCA): performed on scaled and mean-centred full set of features extracted from the gaze data acquired during the exploration of images (N=114), and during blank screen viewing (N=100). Control analyses (PCA on image-viewing data): (I) splitting the images in odd/even, running a PCA on each subset and correlating the obtained PC1 scores with those found on the whole images set; (II) reconstructing the original features matrix (as well as individual patterns of features) from PC1, PC2 and PC3 scores and testing the accuracy of the reconstruction; (III) computing PC1 scores from features extracted from different image-categories (i.e., indoor, outdoor natural, outdoor manmade, with/without humans) and applying PC1 loadings calculated on all images to make scores comparable.

K-means cluster analysis: on the same input of the PCA, after computing the optimal number of clusters (k) given the data, using the silhouette method. Control analysis: the chosen k was validated by comparing different clustering solutions (i.e., different k values) and different distance measures (e.g., Euclidean, Manhattan, etc.) and testing the similarity of different solutions, with the hypothesis that if applying different distance measures would give similar results (i.e., individuals clustered together), it would suggest a more reliable solution.

Linear regression models (visual exploration features): a set of models was built to explain PC1 scores. Specifically, four nested models were compared by means of a LRT which allows to determine whether adding a predictor to a simpler model would significantly improve model fit. Control analyses on the best model resulting from the LRT: (I) split-half reliability design in which 57/114 participants were randomly selected to fit model parameters and the other half was used as test set. This was repeated for 1,000 iterations and for each iteration the Pearson's r coefficient *between actual and predicted PC1 scores was collected; (II) the reliability of the main effect of the model (i.e., KSD) was checked by recomputing KSD using different gaze-step thresholds (0.2° to 8.1°), that is gaze-steps smaller than each threshold were iteratively removed from the computation.*

Linear regression model (demographic, cognitive and personality information): only the full regression model including all test scores and demographic information was built. Control analysis: the model was validated using the split-half procedure described above with 1,000 iterations.

Linear mixed-effects models: we built a set of mixed-effects models to predict fixations topography (i.e., FDMs) from KSD, saliency and semantic maps. Three nested models were compared by means of a LRT and pointed out that adding KSD to a model including saliency and semantic information improved model explanatory power of the topographical distribution of fixations. Each model included a random term (i.e., random intercept) for both individuals and images. Control analysis: in order to assess reproducibility, the effects of interest were also measured at the individual level (i.e., within each subject separately). The same models were built with the only difference that the random intercept was set only for images.

Machine learning classification: we classified subjects as Static vs. Dynamic viewers from features computed while viewing a blank screen by means of a multivariate Random Forest classifier. Control analyses: (I) we checked the stability of viewing styles between image-viewing and blank screen viewing conditions by computing PC1 values obtained in the two conditions (applying loadings obtained in the image-viewing condition to make scores comparable); (II) we compared the between-subjects correlation of eye movement features (during visual exploration and blank screen viewing) with members of the same cluster vs. with members of the other cluster.

Finally, to foster reproducibility, in all seed-based analyses (e.g., PCA) we used seed=1234.

Reporting summary. *Further information on research design is available in the Nature Research Reporting Summary linked to this article.*

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Author Contributions

A.Z., G.C., Ma.Co., Mi.Ce. conceived the study and designed the experiment. Mi.Ce, A.Z., G.C. performed the experiments. A.Z., Mi.Ce. analyzed the data. A.Z., G.C., Ma.Co., Mi.Ce., M.Z. discussed the results and wrote the manuscript.

Data availability

The data that support the findings of this study are available from the corresponding author on reasonable request. The source data used for the main figures are available at https://osf.io/2rkx9/.

Code availability

All codes used for data analysis are available from the corresponding author on reasonable request.

Competing Interests

The authors declare no competing interests.

Chapter 4: One-year later spontaneous EEG features predict visual exploratory human phenotypes.

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One-year-later spontaneous EEG features predict visual exploratory human phenotypes.

Miriam Celli[1, 2], Ilaria Mazzonetto[3], Andrea Zangrossi[1], Alessandra Bertoldo[1, 3], Giorgia Cona[1,4], Maurizio Corbetta*[1,2,5]*

1. *Padova Neuroscience Center (PNC), University of Padova, Padova, Italy;*
2. *Department of Neuroscience, University of Padova, Padova, Italy;*
3. *Department of Information Engineering, University of Padova, Padova, Italy;*
4. *Department of General Psychology, University of Padova, Padova, Italy;*
5. *Venetian Institute of Molecular Medicine (VIMM), Padova, Italy.*

**These authors equally contributed*

Abstract:

During visual exploration, eye movements are controlled by multiple stimulus- and goal-driven factors. We recently showed that the dynamics of eye movements –how/when the eye move– during natural scenes' free viewing were similar across individuals and identified two viewing styles: static and dynamic, characterized respectively by longer or shorter fixations. Interestingly, these styles could be revealed at rest, in the absence of any visual stimulus. This result supports a role of intrinsic activity in eye movement dynamics.

Here we hypothesize that these two viewing styles correspond to different spontaneous patterns of brain activity. One year after the behavioral experiments, static and dynamic viewers were called back to the lab to record high density EEG activity during eyes open and eyes closed. Static viewers show higher cortical inhibition, slower individual alpha frequency peak, and longer memory of alpha oscillations. The opposite holds for dynamic viewers.

We conclude that some properties of spontaneous activity predict exploratory eye movement dynamics during free viewing.

Introduction

Neuroscience has traditionally examined the function of neurons and brain regions using an outside-in approach. Neural activity recorded during the presentation of stimuli or performance of behavioral tasks is correlated with stimulus or task features. This is based on the idea that the brain 'learns' during development stimuli and tasks by entraining neural activity out of random noise. However, neuron-to-behavior correlation strictly depends on the researcher's knowledge about the experimental paradigm. As recently discussed (Buzsáki, 2019), other neurons in the brain without knowledge of the experimental paradigm would have a hard time deciding if the recorded pattern of neural activity has indeed anything to do with the stimulus or task of interest, as compared to many other patterns simultaneously present.

An alternative approach to study the brain is inside-out. In this framework the brain comes with preconfigured and self-organized dynamics that constrains how it views and acts on the world. During development and individual experience, these intrinsic or endogenous patterns organize themselves to induce highly structured robust yet flexible patterns that statistically match the environment and the body. Accordingly, patterns of brain activity recorded in a data-driven manner both at rest and during tasks can be used to classify, predict, or model stimuli or behaviors. As more and more relationships are found, then it should be possible to understand how 'intrinsic' brain signals modulate during stimulus processing or behavior of interest. In this paper we employ this inside-out strategy to test whether electroencephalographic (EEG) spontaneous (resting state) activity recorded one year later from the original experiment distinguish two types of observers (static, dynamic) during free viewing exploration of naturalistic visual images.

We constantly explore the visual world using complex sequences of eye movements that are driven by multiple factors: low-level visual features (Itti et al., 1998a), contextual information (Torralba et al., 2006a), and task goals (Einhäuser & Koch, 2008). Eye movement features like latencies, accuracies, and velocities, underlie individual differences (Bargary et al., 2017a), which are stable across time periods up to two years (Bargary et al., 2017a; Calkins et al., 2003; Filin, V. A., Sidorov, S. P., Ananin, V. F., & Zagorodnikova, 1973; Gooding et al., 2004; Knox & Wolohan, 2015; Meyhöfer et al., 2016; Poynter et al., 2013a; Roy-Byrne, P. et al., 1995). This observation is consistent with fMRI data showing robust interindividual differences in functional networks that are relatively independent of task states and day-to-day variability (e.g., Gratton et al., 2018).

Classic models of visual exploration have emphasised the importance of salience, i.e. the relative sensory distinctiveness of objects in the environment, in guiding exploratory eye movements5. However, a recent study (Kümmerer et al., 2015a) showed that various stimulus-based visual exploration models account for just a small portion of the variance in eye movement patterns (i.e., the best model reaching 34% of maximum information gain). Vision also relies on temporal *strategies, and temporal neural codes to extract and represent spatial information (Rucci et al., 2018). In other words, it is not only important 'where', but also 'how' and 'when' to look.*

In a recent study (Zangrossi et al., 2021), we measured inter-individual differences in a free viewing eye movement exploration paradigm. Observers (n=120, final sample N=114) visually inspected a large number (n=185) of naturalistic pictures, some containing human or man-made figures, some outdoor/indoor visual scenes. The dynamics of eye movements (e.g., fixation duration, number, direction, and amplitude of saccade, etc) across hundreds of observers and pictures were low dimensional and were described by three principal components accounting for ~60% of variability. The first component (PC1) separated two kinds of viewers: 'static', characterized by longer fixations, and 'dynamic', characterized by shorter fixations. Critically this latent variable was independent of image saliency and semantics, and was correlated with power law similarity of eye movements suggestive of intrinsic biological constraints (Plenz & Thiagarajan, 2007b). Notably, the two kinds of observers could be also accurately classified from eye movements recorded in the absence of any stimulus (blank screen) (see also Andrews & Coppola, 1999a). These findings suggested that intrinsic dynamics, rather than stimulus content, controlled 'how/when' people looked at images. In control analyses, we showed that the location of fixations ('where' to look), in contrast, depended strongly on stimulus information (saliency, semantics).

Given the dependency of eye movement dynamics on intrinsic dynamics, here we test whether evidence for this latent variable can be identified in spontaneous recordings of brain activity. To this end, we recruited from the previous experiment (Zangrossi et al., 2021) forty-three participants who were representative of the two viewing styles and recorded high-density electroencephalographic (EEG) activity during eyes open and closed in the absence of any task 1 year after the original experiment. This activity can be considered intrinsic, not task-dependent, since it was recorded one year after the behavioral session, and subjects were unaware of the purpose of the EEG study. While we could have recorded EEG both during task and rest, we opted *for just recordings at rest to truly look at spontaneous brain activity not confounded with task activity or even instructions related to the task.*

Subjects' viewing style was operationalized based on the scores of the first principal component (PC1) in Zangrossi et al. (2021) that summarizes eye movement features stable over long periods of time (Bargary et al., 2017a; Calkins et al., 2003; Filin, V. A., Sidorov, S. P., Ananin, V. F., & Zagorodnikova, 1973; Gooding et al., 2004; Knox & Wolohan, 2015; Meyhöfer et al., 2016; Poynter et al., 2013a; Roy-Byrne, P. et al., 1995). The two groups of subjects recorded in this experiment showed the extreme positive (static) or negative (dynamic) loadings on the PC1 score.

Our hypothesis is based on the theory that spontaneous activity plays a fundamental role in cognition by providing a generative predictive model of spatiotemporal patterns of activity during behavioral tasks (Pezzulo et al., 2021a; Stringer et al., 2019). Hence, we hypothesized that differences in eye movement dynamics were related to stable individual differences in the brain's intrinsic EEG oscillatory activity. Spontaneous brain activity is behaviourally relevant in different species, and at different spatial and temporal scales (LFP in Stringer et al., 2019; EEG in Mahjoory et al., 2019; fMRI in Zou et al., 2013). Moreover, the well-known reciprocal influence of task-related and spontaneous activity (Northoff et al., 2010), makes spontaneous activity (resting state) a good candidate for the prediction of trait-like behaviours (e.g., Liégeois et al., 2019; Mahjoory et al., 2019).

We considered three EEG metrics shown to be good behavioral predictors: resting-state frequency power (MacLean et al., 2012; Pitchford & Arnell, 2019), individual alpha-frequency (Klimesch et al., 2003) and long-range temporal correlations (Palva, Zhigalov, Hirvonen, Korhonen, Linkenkaer-Hansen, et al., 2013a). The resting state frequency power is thought to reflect the baseline level of cortical activation (e.g., Laufs et al., 2003). The IAF has an established relation with inhibition and speed of processing (Klimesch et al., 2006) that could be related to the faster saccadic dynamics of the dynamic viewing style. Finally, Long Range Temporal Correlations (LRTCs) measure the *temporal structure of oscillations, and have been related to behavioral fluctuations (e.g., Palva, Zhigalov, Hirvonen, Korhonen, Linkenkaer-Hansen, et al., 2013a). Power- law form LRTCs have been suggested to represent underlying biological constraints (e.g. excitation/inhibition balance in Poil et al., 2012), and were more representative in the behavioral experiment of the more static viewing style.*

This study highlights two resting state oscillation profiles which predict different visual exploration phenotypes. These results suggest a link between resting state brain activity and oculomotor behaviour.

Results

Spectral analysis

In the eyes open condition, alpha, beta, and gamma bands showed significant differences between groups (ANOVA alpha band: F1,38 = 5.39, p = 0.04; beta band: F1,38 = 6.68, p = 0.04; gamma band: F1,38 = 4.71, p = 0.04; FDR corrected), thus all were subsequently compared at a scalp level with a nonparametric permutation approach with cluster correction. In the eyes closed condition, the beta band showed a significant difference between groups (F1,38 = 7.31, p = 0.03; FDR corrected).

In the eyes open condition, a significant cluster of electrodes, primarily located in the occipital regions, showed significantly higher t-values in the alpha band (7.5-12 Hz) in Static than in Dynamic Viewers (number of electrodes = 16, p = 0.01, FDR corrected). A Spearman's rank correlation between global alpha power and PC1 values showed a positive correlation in the significant cluster (r = 0.4919, p = 0.0014, FDR corrected).

In the eyes open condition, in the beta band (12.5-32 Hz), a significant frontal cluster of electrodes showed significantly lower t-values in Static Viewers than in Dynamic Viewers (number of

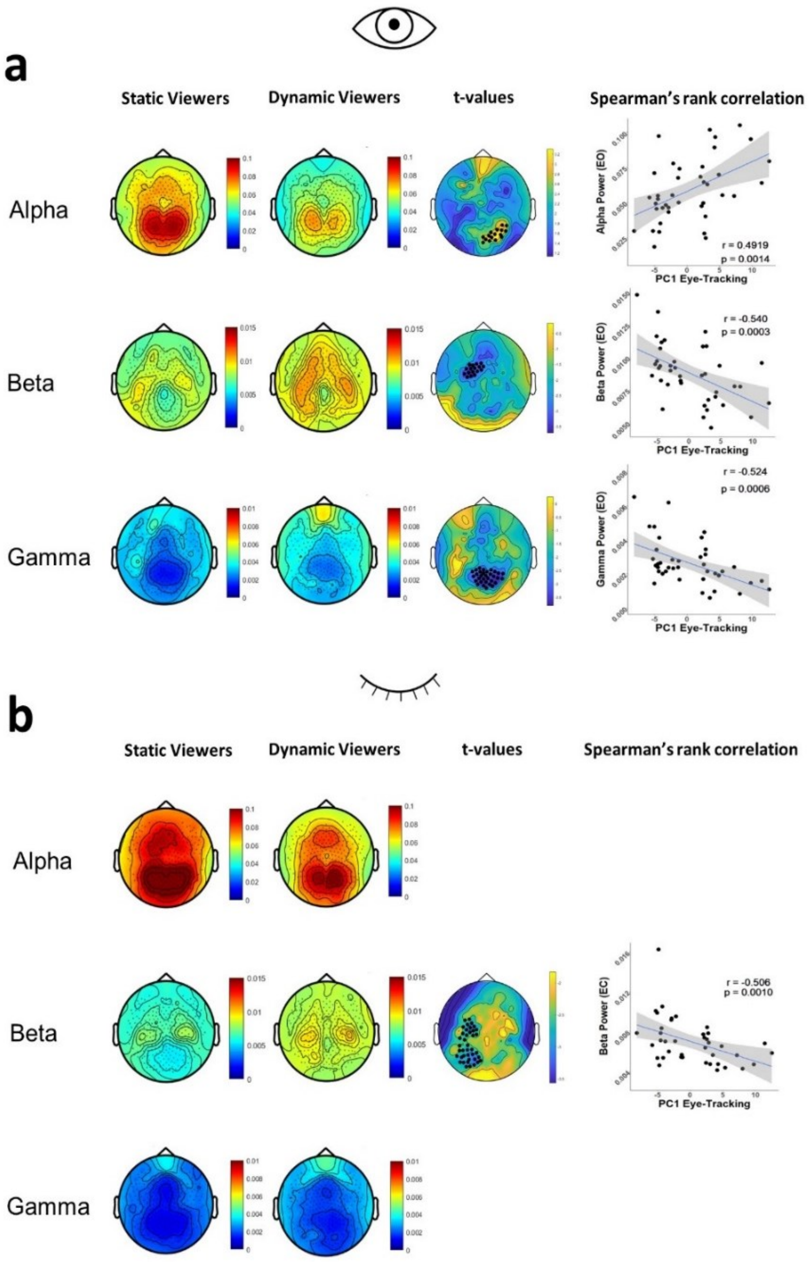

Fig.1|Spectral Analysis Results. ***a**, Group scalp maps in eyes open condition for alpha (7.5-12 Hz), beta (12.5-32 Hz) and gamma (32.5-45 Hz) relative power and t-value maps (where the comparison yielded significant results) for the cluster-based permutation analysis. Black dots index significance with cluster alpha at p<0.01 (two-tailed) and alpha p<0.05 (two-tailed). The right panel shows the Spearman's rank correlation between PC1 and averaged power in the significant cluster of electrodes (with Spearman's r, p-value and 95 % CI). N=40.* ***b,** Group scalp maps in eyes closed condition for alpha (7.5-12 Hz), beta (12.5-32 Hz) and gamma (32.5-45 Hz) relative power and t-value maps (where the comparison yielded significant results) for the cluster-based permutation analysis. Black dots index significance with cluster alpha at p<0.01 (two-tailed) and alpha p<0.05 (two-tailed). The right panel shows the Spearman's rank correlation between PC1 and averaged power in the significant cluster of electrodes (with Spearman's r, p-value and 95 % CI). N=40.*

electrodes = 17, p = 0.01, FDR corrected). Again, we computed a Spearman's rank correlation between beta power in the significant cluster and PC1. There was a negative correlation between global beta power and PC1 value (r = -0.54, p = 0.0012, FDR corrected).

In the eyes open condition, in the gamma band (32.5-45 Hz), a significant cluster of electrodes, primarily located in occipital electrodes, showed significantly lower t-values in Static Viewers than in Dynamic Viewers (number of electrodes = 32, p = 0.01, FDR corrected). The subsequent Spearman's rank correlation showed a negative correlation between global gamma power and PC1 values in the significant cluster (r = -0.524, p = 0.0012, FDR corrected).

In the eyes closed condition, in the beta band (12.5-32 Hz), a significant cluster of electrodes showed significantly lower t-values in Static Viewers than in Dynamic Viewers (number of electrodes = 40, p = 0.01, FDR corrected). A Spearman's rank correlation between beta power in the significant cluster and PC1 was significant (r = -0.506, p = 0.0013, FDR corrected).

In summary, Static viewers were characterized by stronger occipital alpha power, and weaker frontal beta and occipital gamma power (the opposite for Dynamic viewers). PC1 values were positively correlated with alpha power, but negatively correlated with beta (both eyes open and closed) and gamma power (Fig.1).

For effect sizes see Supplementary Table 1 and 2 and Supplementary Figure 1.

The direction of the correlation was confirmed even when static and dynamic viewers were considered as separate groups (Supplementary Figure 3).

Individual Alpha Frequency

Dynamic Viewers (i.e., subjects with shorter fixations) showed a significantly higher IAF than Static Viewers (i.e., subjects with longer fixations) (independent sample t=-3.324; p= 0.003). The Spearman's rank correlation between IAF values and PC1 was negatively related (r = -0.452, p = 0.003) in the direction that lower PC1 scores (i.e., shorter fixations) corresponded to higher

IAF(Fig.2).

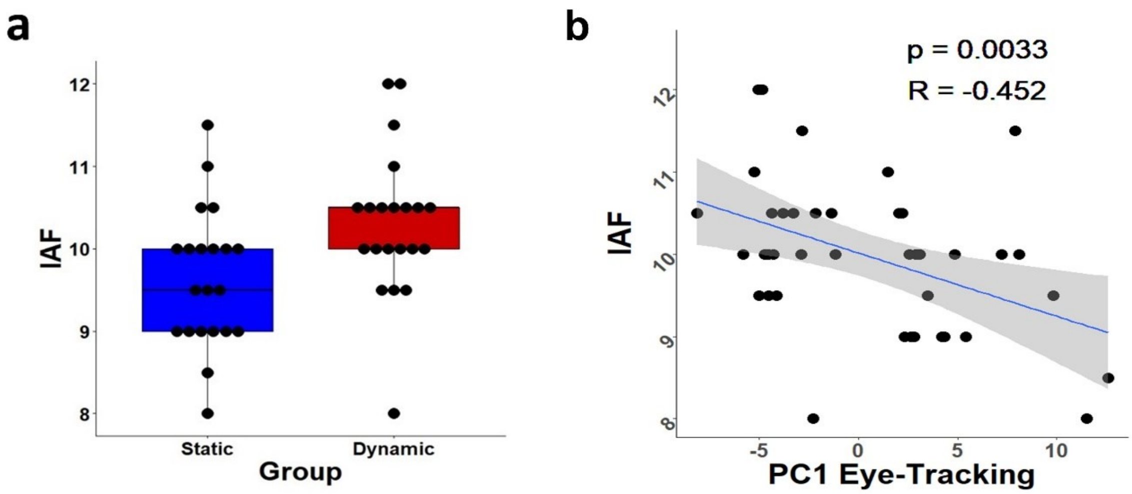

***Fig.2 | Individual Alpha Frequency Results**. a, Individual alpha frequency values by group (static n=19, median = 9.5 Hz; dynamic n=21, median = 10.5 Hz). N=40 b, Spearman's rank correlation between PC1 and Individual Alpha Frequency values (with Spearman's r, p-value and 95 % CI). N= 40.56*

Long Range Temporal Correlations

To the best of our knowledge this measure has never been examined in eye movements. As a first step, we computed a Detrended Fluctuation Analysis (DFA) on the eye-tracking time-series to test the hypothesis that eye movement time-series showed fractal properties. To fit this hypothesis the exponents are expected to fall in the range 0.5-1. All DFA exponents extracted from the eye movement time-series fell in the range 0.5-1 demonstrating long memory and LRTCs in the signal (Hardstone et al., 2012; Peng et al., 1994). The second hypothesis regarded the association between behavioural DFA exponents and PC1. These two measures partially overlap: they represent different aspects of fixation timings (i.e., PC1 is a static measure, while DFA exponents represent the temporal structure of fixations). The two measures are expected to be strongly correlated, *given the fact that they represent different aspects of the same phenomenon. The two measures were significantly correlated (Spearman's rank correlation, r=0.465, p = 0.002). The third step was to test the association between mean brain and behavioural exponents across subjects. There was a positive correlation between brain and behavioural exponents in eyes open condition*

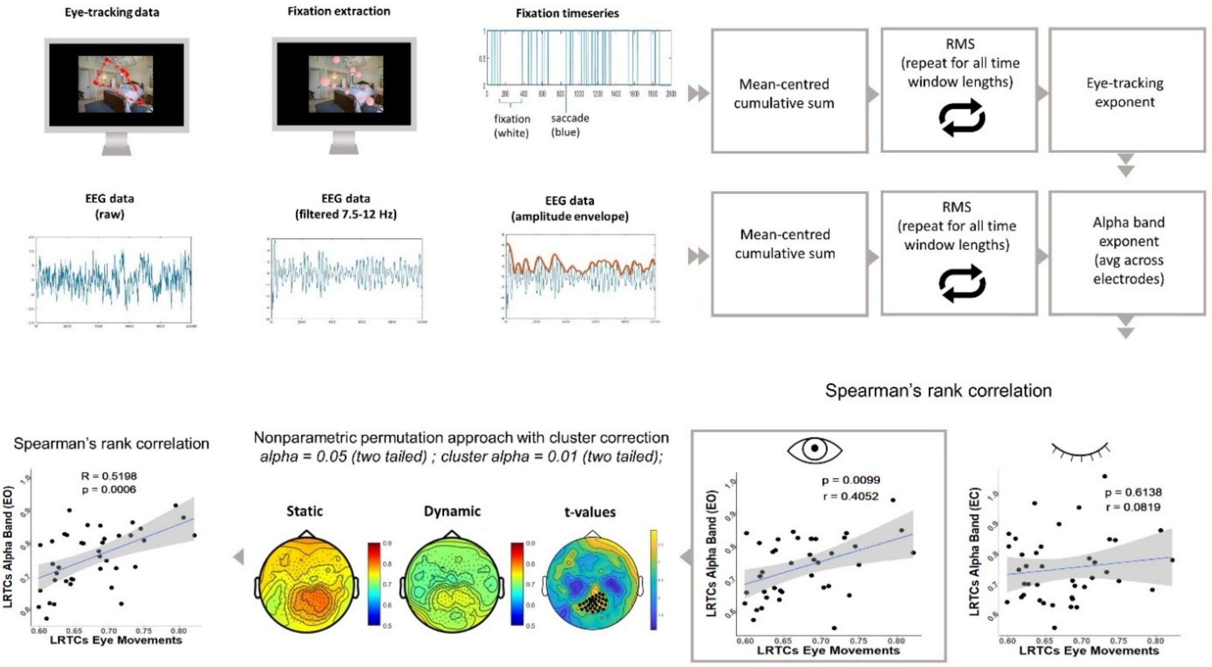

Fig. 3| Procedure and Results for DFA Analysis. *Workflow for DFA analysis. For eye-tracking data, after extracting fixations with a velocity-based algorithm, a fixation timeseries is built (where 0 = fixation; 1 = saccade). EEG data are first bandpass filtered in the frequency of interest (7.5-12 Hz, filter order = 66), then the amplitude envelope is computed. For both timeseries, DFA Analysis is performed. First, a correlation between eye tracking exponents and mean alpha band exponents (i.e., averaged across 256 channels) is computed. A significant positive correlation is found in eyes open condition (r = 0.405, p = 0.009). In this condition, Spearman's rank correlation coefficients are computed in each electrode between alpha band DFA exponents and eye tracking DFA exponents. Null hypothesis testing is conducted by using the nonparametric permutation approach with cluster correction. Black dots index significance with cluster alpha at p<0.01 (two-tailed) and alpha p<0.05 (two-tailed). Finally, a Spearman's rank correlation is computed between DFA exponents in eye movements and DFA exponents in alpha band in the significant cluster of electrodes (r = 0.455, p = 0.003). All the scatterplots show Spearman's r, p-value and 95% CI. N=40.*

LRTCs: Long Range Temporal Correlations

RMSE: Root-Mean Square Error

alpha band (Spearman's rank correlation, r = 0.40, p = 0.009). To explore the scalp topography of the effect, we computed Spearman's rank correlation on an electrode-to-electrode basis by using the nonparametric permutation approach with cluster correction. A significant positive cluster of electrodes, primarily located in occipital areas showed significantly higher correlation t-values in Static Viewers than in Dynamic Viewers (number of electrodes = 30, p = 0.007). Alpha band exponents significantly differed between static and dynamic viewers (t=2.03,p=0.04). Next, we computed a Spearman's rank correlation between alpha band DFA exponents in the significant cluster and behavioural DFA exponents. There was a positive correlation between alpha band DFA exponents and behavioural DFA exponents (r = 0.519, p = 0.0006). The correlation between alpha band DFA exponents and behavioural DFA exponents was not present in the eyes closed condition (Spearman's rank correlation, r = 0.08, p = 0.61) (Fig.3).

Control analysis on global power

To rule out the possibility that the observed differences in viewing styles were explained by differences in arousal, we contrasted global alpha power with eyes closed and the alpha reactivity index (eyes closed-eyes open), respectively a measure of baseline arousal and a measure of arousal reactivity (see Barry, Clarke, Johnstone, & Brown, 2009). There were no differences between the two groups of observers in either measure (Suppl.Fig.2).

Discussion

In a previous study (Zangrossi et al., 2021) we showed that eye movement exploration dynamics (how/when we move the eyes) in 120 (final sample N=114) observers across 185 pictures were low dimensional. Three linear components accounted for most of the variability across pictures and subjects. The first component PC1 loaded on the duration of fixation (among other features) identifying two groups of observers: Static viewers, characterized by longer fixation duration *statistics and a higher similarity of gaze steps (i.e., the Euclidean distance between two consecutive gaze positions) to a power law distribution; and, Dynamic viewers characterized by shorter more frequent fixations, and a more random distribution of gaze steps. Critically PC1 scores were not explained by the saliency and semantic information of the objects presented in each picture. Furthermore, the two viewing styles during visual exploration were successfully classified based on the eye movement features recorded when looking at a blank screen (rest). These findings indicate that how/when we move the eyes during visual exploration partly reflect intrinsic (endogenous) dynamic mechanisms. Based on the theory that spontaneous activity plays a fundamental role in cognition providing a generative model of spatiotemporal patterns of activity employed during behavioural tasks (Pezzulo et al., 2021b), we tested whether these two patterns of eye movement dynamics were related to intrinsic brain dynamics, as measured by properties of EEG oscillations at rest. Accordingly, we recruited from the previous experiment (Zangrossi et al., 2021) forty-three participants who were representative of the two viewing styles (they had opposite extreme PC1 scores) and recorded their resting state EEG one year later.*

We show that visual exploration styles have robust correlates in spontaneous EEG oscillations recorded one year later. Three different oscillatory EEG features correlated with dynamic eye movement features (PC1 scores). Static viewers showed higher alpha power and lower gamma power in occipital electrodes. They also showed lower beta power in frontal electrodes. Static viewers displayed a lower individual alpha frequency. Finally, static viewers' brain oscillations and eye movement time series were endowed with stronger long-range temporal correlation indicating a higher self-affinity and complexity.

In contrast, dynamic viewers' oscillation profile was characterized by lower alpha power and higher high-frequency power (beta and gamma). Dynamic viewers also showed a higher individual alpha frequency and weaker long-range temporal correlations, thus a less complex signal (i.e., closer to white noise) both in brain and eye fixation time series.

Our interpretation is that these intrinsic EEG features represent a trait-like constrain on exploratory eye movement dynamic features. We propose that this constrain on eye movement dynamics depends on the timing of oscillations (i.e., IAF and LRTCs) and baseline level of cortical activation, which has been proposed to index the focus of attention (e.g., Benedek et al., 2014). Herein we discuss data relevant to this interpretation.

Resting state frequency power may reflect the baseline level of cortical activation (e.g., Laufs et al., 2003). The interplay between activation (i.e., high frequency activity, typically observed in task-relevant areas (Berger, 1938; Pfurtscheller & Lopes, 1999) and inhibition (i.e., alpha activity, typically observed at rest in Berger, 1938; or in task-irrelevant areas in Pfurtscheller & Lopes, 1999), has been proposed to reflect the focus of attention, respectively directed externally to environment stimuli or internally to memory, emotion, cognitive information. For instance, in their seminal study Ray and Cole (1985) found lower alpha power during external tasks, e.g. counting words in a passage, and higher power during internal tasks, e.g. mental arithmetics. Therefore, alpha rhythms may reflect a possible index of internal vs. external attention, with alpha power decreases linked to externally directed attention (Benedek et al., 2014). In this line of thought, then, a higher alpha power (i.e., the static viewer profile) would index a heightened inhibition with regards to external stimuli.

At the other end, dynamic viewers have lower inhibition towards external stimuli and are more focused on external stimuli. Their EEG power profile is consistent with stimulus processing (Rajagovindan & Ding, 2011) and selective attention to stimuli (Wyart & Tallon-baudry, 2009): occipital alpha power decreases —alpha desynchronization (Pfurtscheller & Lopes, 1999)— and gamma power increases (Wyart & Tallon-baudry, 2009). This change in the balance of oscillatory power is thought to reflect the release of inhibition in sensory and task relevant areas. According to this interpretation, dynamic viewers start from a resting profile that is more similar to that seen during stimulus processing and selective attention to stimuli (Bartoli et al., 2020; Haegens & Ha, *2011; Pfurtscheller & Lopes, 1999; Wyart & Tallon-baudry, 2009). While the mutual relationship between inhibition and stimulus processing is widely studied during tasks, recent studies also found a correlation between alpha and beta band resting state EEG activity and visual attention (MacLean et al., 2012; Pitchford & Arnell, 2019).*

In contrast to this interpretation of alpha inhibition/gamma excitation stand the results on the frontal beta band power that was lower (more desynchronized) in static than dynamic viewers, both during eyes closed and eyes open. Beta power is classically described as the inhibitory rhythm of the motor cortex (e.g., Gaetz et al., 2010), and it becomes desynchronized during movement planning (Hwang et al., 2014). This is like alpha occipital power that is higher at rest but desynchronizes during visual processing. However, a more recent interpretation is that beta rhythms represent the status quo or maintenance of a specific task or motor set (Engel & Fries, 2010). This is based on evidence of increased beta synchronization during tasks in which a set is maintained over time (e.g., a working memory task). A related account is that beta rhythms in centrally connected regions of cortex (hubs) in multiple networks maintain a prediction or prior about the temporal structural of visual exploratory behavior (Betti et al., 2018). This is based on the similarity of beta band power fluctuation temporal structure at rest and during visual exploration. Our results suggest that static viewers maintain at rest a more reactive motor cortex. The difference with dynamic viewers support the notion that spontaneous activity patterns predict exploratory behavior as in (Zangrossi et al., 2021).

Overall then the occipital power results indicate that static viewers have a profile of baseline cortical activation biased toward cortical inhibition and internal processing, while dynamic viewers have a profile biased toward cortical excitation and external processing. This is in line with the cognitive profiles of these two types of subjects, with static observers showing a slightly stronger visual working memory, and dynamic observers a weaker inhibition to salient but irrelevant stimuli (Zangrossi et al., 2021).

In addition to power relationships, we found an association between visual exploration timings (i.e., PC1 scores and fixations time-series) and timing constraints of alpha oscillations (i.e., IAF and LRTCs).

In the literature the IAF has been correlated with speed of processing, with a weak but significant relation between IAF individual differences and reaction times (Klimesch et al., 2003). A more general interpretation is that the speed of information processing could be related to the speed or frequency of the alpha pacemaker. A more recent view (Klimesch et al., 2006) explains IAF in terms of neural inhibition timings. For instance, a higher IAF is linked to shorter P1 latencies (Schabus et al., 2004). This is also consistent with the relationship between higher alpha power and lower individual alpha frequency (e.g., Koch et al., 2008) In this view, alpha band dynamics have an active role: the inhibition serves to establish a highly selective activation pattern. Higher IAFs index stronger intra-cortical inhibition and more highly specialized activation patterns eventually resulting in faster task performance. In line with these views, dynamic viewers endowed with a higher IAF can disengage faster from fixation and generate a higher number of fixations overall. The negative relationship between IAF and PC1 scores indexing fixation duration is consistent with this interpretation. These results predict that dynamics viewers shall be faster in visual processing and attention tasks.

The final link between eye movement dynamics and brain dynamics is the observation of LRTCs in both fixation sequences and brain oscillations. Static viewers show stronger LRTCs both in the occipital alpha band and eye movement time-series. A long-range temporal correlation indicates that these signals maintain memory over time, i.e., their sequences repeat. In contrast the fixation and oscillatory sequences of dynamic viewers were closer to white noise, i.e., they have less temporal structure in time resembling more a random process. Power-law form LRTCs are thought to index intrinsic systems constraints (e.g., structural constraints Honey et al., 2009, physiological constraints Bruening et al., 2006) that may cause recursive regularities in brain signals

(Linkenkaer-Hansen, Nikouline, Matias Palva, et al., 2001) and behaviour (Palva, Zhigalov, Hirvonen, Korhonen, & Linkenkaer-hansen, 2013). The stronger link between LRTC and static viewers is highly consistent with a profile of activity and dynamics that emphasizes internal processes.

In the setting of review several important issues were raised that are worth discussing. One objection is whether the distinction between static and dynamic viewers can be considered stable one year later, at the time of EEG recordings. In other words, is it possible that we are documenting brain correlates of a 'state' recorded one year earlier not a stable 'trait', i.e., a true difference in viewing styles? The two groups were called back for EEG recordings based on their extreme (positive, negative) PC1 scores. PC1 scores were computed based on eye movement features that in the literature are stable over time (Bargary et al., 2017a; Calkins et al., 2003; Filin, V. A., Sidorov, S. P., Ananin, V. F., & Zagorodnikova, 1973; Gooding et al., 2004; Knox & Wolohan, 2015; Meyhöfer et al., 2016; Poynter et al., 2013a; Roy-Byrne, P. et al., 1995). Also in (Zangrossi et al., 2021), we carried out several controls showing that PC1 scores were stable in different sub-samples of even/odd images (i.e., all r values > 0.97); different image categories (i.e., all r values = 0.97). In addition, PC1 features measured at rest when viewing a blank screen classified with >80% accuracy static and dynamic viewers when looking at natural images, and vice versa. Nonetheless, we recognize that this is a relative limitation of the study.

Another point is that our findings may reflect differences in overall arousal/motivation between groups (e.g., Zentall, 1975). The arousal/motivation theory states that each individual has its own baseline level of arousal, with low arousal subjects showing less high frequency power and more low frequency power (Barry, Clarke, Johnstone, Mccarthy, et al., 2009), higher eyes closed alpha power (Barry et al., 2007), lower alpha reactivity (Fonseca et al., 2013). These features have been related to extraversion (Brocke & Leue, 2006) and sensation seeking (Geissler et al., 2014).

In additional control analyses we show that static and dynamic viewers do not differ in eyes closed alpha power (t = 1.58, p = 0.12), or alpha reactivity (t = 0.45, p = 0.65; eyes closed to eyes open alpha power ratio; Supplementary Figure 2). They also show no differences in extraversion (Zangrossi et al., 2021), while static viewers, those with longer fixation and higher alpha power, were more open to new experiences (Zangrossi et al., 2021).

Taken together these results do not suggest a difference in overall arousal/motivation. However, this experiment was not designed to test this hypothesis and future work is needed to clarify this issue.

An alternative hypothesis is that differences in brain rhythms, specifically alpha, can modulate on-line eye movement behavior (Popov et al., 2021). In other words, dynamically during a task, periods of lower alpha power immediately follow saccades, while periods of fixation are associated with increased alpha power. This would result in lower overall alpha power in those individuals who show high oculomotor activity (i.e., more saccades) during the recording. This interpretation is not inconsistent with our findings. Hebbian plasticity (Hebb, 1949) predicts that repeated patterns of neural activation leave a persistent trace in the brain, first in the form of synchronized spontaneous activity, later on in the form of synaptic and structural connectivity changes. Accordingly, subjects during development and/or experience might have developed a more 'static' or 'dynamic' style of eye movements during visual exploration, which have entrained in turn tonic differences in their spontaneous activity recorded in this experiment. This idea suggest that genetic differences may be partly responsible for the different developmental/experience trajectories (as in (Kennedy et al., 2017a).

That a complex behaviour like eye movement visual exploration can be summarized with a few dynamic features across many subjects and pictures was surprising(Zangrossi et al., 2021). A growing behavioral literature focused on the covariance across subjects is showing that many apparently complex behaviour underlie a low dimensionality. Apparently complicated hand *movements (Avella et al., 2003a), human navigation in cities (Pappalardo, Simini, Rinzivillo, Pedreschi, & Giannotti, 2015), and variability in reward inhibition (Cona et al., 2019b) can be all explained by a small number of latent variables. There is also growing evidence for low dimensionality of coding through correlated neuronal activity across many neurons, as in the case of face perception (Chang & Tsao, 2017), hand movements (Churchland & Cunningham, 2014), and exploratory face movements (Stringer et al., 2019). Even more unexpected, somehow, is that these dynamic eye movement features are related to resting-state oscillatory properties of EEG signals recorded one year later. We think that the results suggest that the timing of oscillations (IAF, LRTCs) and inhibition (alpha power) could be a key in controlling the duration of fixation and shifts thereof.*

Given the high temporal resolution of both eye movement and EEG recordings, it will be interesting in future studies to explored jointly EEG signals and eye movement recordings and relate resting to task dynamics.

A final consideration is the potential of eye movement and resting-state EEG recordings as a diagnostic or prognostic tool for pathologies in which structural, metabolic, or biological measures are either too expensive or invasive. We are thinking of eye movements (Anderson & MacAskill, 2013a), as well as alterations in resting state EEG metrics (Montez et al., 2009; Moretti et al., 2004) in high impact pathologies like Alzheimer disease.

Methods

Participants

Participants for the resting-state EEG session (n=43, mean age 24.11 years, sd 2.41, 16 males) were recruited from the pool of subjects of a previous study (Zangrossi et al., 2021). All participant signed an informed consent before the experimental session, and after it they received a *remuneration of 10€ for their partecipation. The study was approved by the Ethical Committee of the University of Padova.*

Participants were selected based on the PC1 scores from the previous study. The PC1 is the first principal component extracted from a PCA on 59 eye-tracking features computed on a free visual exploration task on 205 pictures and 120 (final sample N=114) subjects. Participants were chosen for this session based on PC1 values higher than 1 and lower than -1. These values represented the extremes of the distribution identifying subjects who belonged to the static vs. dynamic group. Eligibility in the previous study was based on the applicants being in good health, no history of neurological disease, no colour blindness. All participants had normal or corrected-to-normal vision. This session took place after a mean interval of 11 months (327 days ±43). Three participants were excluded due to the bad quality of the data, resulting in a final sample of 40 participants (19 static viewers and 21 dynamic viewers).

Stimuli and apparatus

*EEG activity was recorded with a high-density EEG system consisting of the 256-channel Hydrocel Geodesic Sensor Net, the high impedance amplifier Net Amp 400 and the Net Station 4.3 (Electrical Geodesics Inc.). Before testing, impedances were measured and adjusted until they were kept below 50 k***Ω***. Impedance of each channel was also measured and saved at the end of the session. All electrodes were referenced online to the electrode placed over the vertex (Cz in the 10/20 international system). EEG data were digitized with a sampling rate of 500 Hz. During the registration, the participant sat in a chair in a sound-shielded Faraday recording cage. A screen displaying a fixation cross was set on the centre of a desk in front of the participant. Two resting-state EEG sessions (eyes open and eyes closed) lasting 10 minutes each were collected. In eyes open condition, participants were asked to look at the fixation cross for the whole duration of the task* *(i.e., eye movements were discouraged); in the eyes closed condition, participants were asked to keep their eyes closed for the whole duration, to relax and not to fall asleep.*

Electrode positions were digitized by means of the Occipital 3D Structure Sensor (Occipital Inc.) mounted on an iPad Pro (225,226) at the end of the resting-state EEG session. Structural MR T1w data (TR/TE: 7.20/3.29 ms; 165 sagittal slices; voxel size: 0.53 × 0.53 × 1.1 mm; FA: 9°; acquisition matrix: 448 × 448) were acquired in a separate session using a 3T Ingenia Philips whole body scanner (Philips Medical Systems, Best, The Netherlands) equipped with a 32-channel head-coil, at the Neuroradiology Unit of the University Hospital of Padova, Italy. Anatomical images were obtained for 34 participants out of 43 recruited for the EEG session. Electrode positions and T1 structural images were acquired for a future study and will not be used in this work.

EEG Pre-processing

EEG data were pre-processed using Matlab (The MathWorks, Inc, Natick, Massachusetts, USA) scripts based on functions from the EEGLAB software (version 14.1.2b,226). First, data were band-pass filtered (cut-off frequencies: 0.5 – 47 Hz) using two zero-phase Kaiser-windowed sinc FIR filters (high-pass: transition bandwidth = 1 Hz, order = 1812, low-pass: transition bandwidth = 2, order = 908) as suggested in Widmann et al.(Widmann et al., 2015) and resampled at the 250 Hz. Then, an automated detection of the noisy channels was performed and later confirmed by visual inspection. Selection was based on the combination of the following five criteria, whose thresholds were determined with a preliminary examination of the dataset to optimize the detection: i) impedance at the end of the acquisition above 100 kΩ; ii) correlation to the surrounding channels less than 0.75, iii-iv) standard deviation bigger than 4 for the spectral and improbability tests; v) standard deviation bigger than 7 for the kurtosis test. Channels selected by the criterium i), ii) or at least two of iii-v) criteria were interpolated using spherical splines (Perrin et al., 1989). Afterwards EEG data were re-referenced to the average of all electrodes. Ocular, muscular and *movement artifacts were removed by applying Independent Component Analysis (ICA) using a deflation-based Fast fixed-point ICA algorithm (http://research.ics.aalto.fi/ica/fastica/) with the hyperbolic tangent as cost function. Independent components (ICs) were classified in seven classes (brain, muscle, eye, heart, channel noise, line noise, other) using the ICLabel toolbox (Pion-tonachini et al., 2019). All the components classified as brain or other (but with brain as the second highest probability) were kept. After this step, residual artifacts were corrected using the Artifact Subspace Reconstruction (ASR)230. Noisy data segments were identified using a 1-s sliding-window principal component analysis (PCA). If PCs exceeded 30 standard deviations of the cleanest part of the dataset, current data was repaired using a mixing matrix computed on the cleanest portion of the data.*

Spectral analysis

The power spectral density was computed using Welch's overlapped segment averaging estimator using spectopo() function on EEGLAB (Delorme & Makeig, 2004) to obtain a frequency resolution of 0.5 Hz. The power spectral density was extracted for every channel and converted from dB to µV2/Hz. Each spectrum was then normalized to the relative frequency power by dividing the spectrum by the power computed in the whole spectrum via trapezoidal integration.

Individual Alpha Frequency Peak

The individual alpha frequency peak was defined as the highest absolute value in the 7-13 Hz range. The alpha peak was first automatically detected based on this criterion. All spectra were then visually checked to ensure the selected frequency to be a true peak rather than the maximum value at the boundaries of the predefined alpha range. The analysis was performed on the average spectrum across occipital electrodes (cfr. Schartner et al., 2015) in eyes-closed condition, which is *the most stable measure of IAF according to the literature – i.e. it has the greater test-retest reliability (Grandy et al., 2013).*

LRTCs Computation

To assess long-range temporal correlations (LRTCs), we used the Detrended Fluctuation Analysis as described in (Hardstone et al., 2012). Briefly, this technique allows to extract a scale-free exponent which describes the temporal structure of the signal in terms of self-similarity (i.e., scaling of a statistical property across scales) and long-memory. This is done by assessing the rate at which fluctuations (i.e., mean-squared residuals) grow as a function of the scale (i.e., RMSE are assessed at different scales and the relation between RMSE and window length in double-log determines the DFA exponents).

Similarly to Palva (Palva, Zhigalov, Hirvonen, Korhonen, Linkenkaer-Hansen, et al., 2013a), here LRTCs are computed for both brain (i.e., alpha band filtered EEG) and behavioural data (i.e., fixation timeseries). Brain exponents (i.e., the temporal structure of the alpha rhythm) and eye movements exponents (i.e., the temporal structure of eye movements) are then correlated. The DFA scaling exponent is typically ranging between 0.5 and 1 in brain signals (Linkenkaer-Hansen, Nikouline, Matias Palva, et al., 2001) and eye movements time-series (Liang et al., 2005). While an exponent of 0.5 index an uncorrelated signal (i.e., white noise), an exponent of 1 index strong long-range temporal correlations (Hardstone et al., 2012; Peng et al., 1994).

A more detailed version of DFA computation can be found in Supplementary Methods.

Statistical Analysis (spectral analysis)

The statistical analysis was implemented in FieldTrip toolbox (Oostenveld et al., 2011).

Frequency power was first averaged into five frequency bands (delta 1-3 Hz, theta 3.5-7 Hz, alpha 7.5-12 Hz, beta 12.5-32 Hz, gamma 32.5-45 Hz). Global frequency power (i.e., averaged across all 256 channels) was then compared between groups with a bin-by-bin one-way ANOVA in both conditions separately. Null hypothesis testing was conducted comparing the results of each bin-by-bin ANOVA against a null distribution of 1000 permuted datasets. All p-values were FDR corrected(Benjamini & Hochberg, 1995). For the frequency bands showing significant between groups differences, we conducted a comparison at the scalp level by using the nonparametric permutation approach with cluster correction(Benjamini & Hochberg, 1995). This analysis was performed excluding face electrodes. We computed two-tailed independent samples t-tests with 1000 resamples, two-sided 95% confidence intervals, corresponding to an alpha level of 0.05 (two-tailed). Cluster threshold setting was based on maximum cluster size, with an alpha level set to 0.01 (two-tailed).

To check the extent to which these differences were linked to visual exploration styles, we also computed the Spearman's rank correlation between PC1 values and frequency power in alpha, beta, and gamma only for the electrodes identified in the previous contrast (FDR corrected). Spearman's rank correlation was chosen due to the distribution of PC1 values, after a Shapiro-Wilk Normality test suggested a non-gaussian distribution of the variable (p<0.001).

Statistical Analysis (Individual Alpha Frequency)

After testing for normality of the distribution of the IAF values (Shapiro-Wilk Normality test; p=0.459; p=0.051), null hypothesis testing was conducted comparing the results of the independent sample t-test against a null distribution of 1000 permuted datasets.

Subsequently, we also tested for the association between Individual Alpha Frequency and PC1 by computing Spearman's rank correlation, to confirm that the observed group difference linearly *related with the PC1 values. Spearman's rank correlation was chosen due to the non-Gaussianity of PC1 distribution.*

Statistical Analysis (LRTCs)

Brain exponents in the alpha band (7.5-12 Hz) were averaged across conditions across all 256 electrodes (cfr. Palva, Zhigalov, Hirvonen, Korhonen, Linkenkaer-Hansen, et al., 2013a). According to the literature (see for example Palva, Zhigalov, Hirvonen, Korhonen, Linkenkaer-Hansen, et al., 2013a), alpha band at rest is the band showing a more remarkable relationship with power-law-form LRTCs in behaviour.

In both eyes open and eyes closed condition, the normality test of the distribution of the DFA exponents of the alpha band amplitude time series (Shapiro-Wilk Normality test) suggested evidence for a non-gaussian distribution ($p<0.001$; $p<0.001$; $p<0.001$; $p<0.001$). As a consequence, we computed Spearman's rank correlation between brain and behavioural exponents.

In the eyes open condition only we computed the Spearman's rank correlation coefficients between alpha band DFA expontents in each electrode and behavioural DFA exponents and conducted null hypothesis statistical significance testing by using the nonparametric permutation approach with cluster correction (Maris & Oostenveld, 2007). We computed 1000 resamples; two-sided 95% confidence intervals, corresponding to an alpha level of .05. Cluster correction method: maximum cluster size. Cluster threshold (non-parametric) was set to 0.01 (two-tailed). Finally, a Spearman's rank correlation is computed between DFA behavioural exponents and DFA alpha exponents only for the cluster of electrodes identified in the previous step.

Control Analyses

To control for possible confounding effects on PC1, we contrasted between groups all available demographic information from Zangrossi et al.(2021) and the current study (see Supplementary Table 3). After accounting for multiple comparisons, Age is the only variable significantly different between the two groups (t= -3,38; p corr. = 0,03). The significant difference in Age between the two groups confirms what was already seen in the previous study with the full sample (Zangrossi et al., 2021).

To rule out that the observed differences are not explained by differences in arousal, we contrast global eyes closed alpha power and alpha reactivity index (eyes open-eyes closed alpha power ratio, (Fonseca et al., 2013) between groups. The two measures are respectively a measure of baseline arousal and a measure of arousal reactivity. For further control analyses see Supplementary Information.

Statistics and Reproducibility

R (v 4.1.0) and MATLAB (r2018b) softwares were used to perform all analyses, the required tools and packages are cited in the Methods section (see EEG Pre-processing, Spectral Analysis and Statistical Analysis). Preprocessing steps and statistical analyses are described in Methods section (see EEG Pre-processing and Statistical Analysis). All analyses are perfomed on the same sample (N=40).

Author Contributions

A.B., Mi.Ce., G.C., Ma.Co., I.M. and A.Z conceived the experiment. Mi.Ce., G.C. and I.M. performed the experiment. Mi.Ce., G.C., I.M. and A.Z. analyzed the data. A.B., Mi.Ce., G.C., Ma.Co., I.M. and A.Z discussed the results and wrote the paper.

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Data availability

The data that support the findings of this study are available from the corresponding author on reasonable request. The source data used for the main figures are available at https://osf.io/wnxkq/.

Competing Interests

The authors declare no competing interests.

***Correspondence** and requests for materials should be addressed to Maurizio Corbetta at maurizio.corbetta@unipd.it.*

Chapter 5: Characterization of a behavioural correlate of free visual exploration: visual memory recall

Introduction

In the previous chapters, we have discovered that the dynamics of eye movement exploration for natural images are relatively low dimensional and controlled by endogenous factors that are typical of an individual subject. Interestingly, the corresponding styles of eye movement (static or dynamic) interact with the sensory saliency and the semantic information contained in each image to determine where and how people look at visual scenes. The partly endogenous nature of eye movement dynamics is indicated by two observations. First, the styles can be recovered from recordings of eye movement "at rest" when observers are looking at a blank screen. Secondly, the styles relate to "trait" baseline EEG features like alpha, beta, and gamma power, or the temporal structure of EEG signals over time, recorded one year later from the behavioral observations.

We have argued that these EEG signals are the correlate of endogenous spontaneous activity that in agreement with recent theories (Buzsáki, 2019; Pezzulo et al., 2021b) provides a prior to shape subjects' behavior.

Here we take a step further to examine one of the consequences of eye movement exploration to natural visual scenes, namely whether there exists a link between eye movement patterns and memorability of specific objects/scenes.

What is the relationship between visual information attended and visual information retrieved? Visual memory recall is among the less studied cognitive processes. Here we aim to describe and characterize the spatial similarities between visual exploration and visual memory recall – an attempt to "see with the mind's eye" and compare it with what the eyes had previously seen during encoding.

Visual memory had been traditionally studied using recall paradigms, which have the clear advantage of being highly controllable at the experimental level (e.g., these paradigms allow for repeated exposure or trial averaging). In memory recall paradigms, subjects are usually shown several stimuli and later asked if they saw those stimuli before. This field of study has led to the introduction of the concept of image memorability, i.e., the fact that some images are easier to recognize based on multiple features (e.g., object atypicality in It et al., 1984). Nevertheless, classic results on image memorability in recognition had not been replicated in free recall in a recent work (Bainbridge et al., 2019a). Free recall is substantially different from recognition in its nature. In free recall, subjects are typically asked to describe previously seen stimuli (in several different ways, e.g., by talking in Marks, 1973; by writing in Lee & Chen, 2022, or by drawing in Bainbridge et al., 2019b). Moreover, this finding (Bainbridge et al., 2019a) is in line with the idea that recognition and recall do not share the same neural substrates and mechanisms (Felician & Barbeau, 2011; Staresina & Davachi, 2006).

On the other hand, recall memory necessarily entails "narrative-like" paradigms, and most experimental standards (e.g., repeated exposure) do not apply. The first attempts to study this memory component came in the 70s, when researchers asked participants to visually encode pictures and then counted the number of objects correctly reported verbally (e.g., Marks, 1973; Shiffrin, 1973). A somewhat similar implementation is that of Baker and colleagues (Bainbridge et al., 2019a; Lee & Chen, 2022), in which free recall of visual scenes is measured during drawing production. Another recent attempt to characterize the structure of memory recall required subjects to write down memories of video narratives previously encoded (Bainbridge et al., 2019b). What we learn from these two recent attempts is that 1) recollection does not necessarily follow recognition rules (Bainbridge et al., 2019a); 2) memories for scenes contain numerous objects, and the spatial relation between items is preserved (Bainbridge et al., 2019a; Lee & Chen, 2022); 3) *central events (e.g., with stronger semantic connections with other events) are more likely to be remembered in narratives (Lee & Chen, 2022).*

However, the relationship between the recall of visual memories and the patterns of visual exploration at encoding is still unclear. The main implementation of vision at the behavioral level is through eye movements. Eye movements are mainly structured in saccade-fixations sequences allowing specific points of space to be focused on the fovea, to gather high-quality visual information. In the absence of any task (i.e., free visual exploration), eye movements have been shown to be drawn to low-level image features (i.e., saliency, Itti et al., 1998a) and semantically relevant areas (Torralba et al., 2006a).

Moreover, there is evidence for bilateral interactions between vision/eye movements and visual memory both at the behavioural and neural level. This has also recently led to the idea that memory theories need to incorporate oculomotor aspects (e.g., Ryan et al., 2022). At the behavioural level, memory modulates the duration and spatial distribution of fixations, even before and without conscious awareness (i.e., a phenomenon known as preferential viewing, e.g., Hannula et al., 2007). At the same time, oculomotor functions seem to play a key role in memory retrieval: gaze scanpaths during visual mental imagery show a significant degree of match with those during encoding (i.e., a phenomenon known as gaze reinstatement, e.g., Wynn et al., 2016).

At the brain level, the two systems have been shown to reciprocally interact. Activity from the hippocampus and MTL can reach oculomotor regions within a span of a fixation (e.g., Henderson et al., 2015); while on the other hand, the hippocampus elaborates speeds signals from MTL to oculomotor regions. While there are no monosynaptic connections between memory and oculomotor systems, bi-synaptic connections are present (e.g., FEFs and hippocampus Stephan et al., 2001) and network analyses suggest that they may be functionally connected (e.g., Shen et al., 2016).

In the present, we propose a novel method to study the spatial relationship between eye movements during the encoding of a visual scene and the spatial pattern of subsequently recalled *details. To this end, we collected eye movements and memory data from a large cohort of subjects (n=120, final sample n=114) to characterize both population effects and subject-specific effects (i.e., strategies).*

Using novel methods, we compared eye movement exploration maps with memory retrieval maps. We showed that 1) gaze fixations show a higher similarity with memory maps, as compared to stimulus-related maps (i.e., saliency and semantics); 2) this unbalance between gaze fixations and stimulus-related information varies in clusters across the population.

Methods

Participants

A total sample of 120 students was recruited at the University of Padova (mean age = 23.4, SD = 2.42; 49 M) through advertisements. All participants had normal or corrected-to-normal (n=54) vision. Three subjects were excluded due to excessive data loss (i.e., less than 50% of usable data in more than 25% of the trials), two subjects were excluded due to the interruption of the experimental session and one subject was excluded due to color blindness. Thus, the final sample is composed of 114 participants (mean age = 23.52, SD = 2.45, 67 F). All the participants signed an informed content. The study was approved by the Ethical Committee of the University of Padova. All subjects received a 10€ remuneration for their participation.

Experimental Protocol

This study was part of a broader experimental protocol composed of five phases (total duration: 2 hours). For detailed information on the protocol see Zangrossi et al. (2021). For the purposes of this study, we take into consideration the second and third phases only (Figure 1A). In the second phase (i.e., visual exploration phase), subjects were instructed to look at 185 pictures selected from *the Places 365 database (see stimuli paragraph for details). Five of the pictures (i.e., target images) were repeated five times to promote incidental memorization. Stimuli subtended 27.1° × 20.5° (width × height) degrees of visual angle on a screen subtending 31.6° × 23.9°. Participants were instructed to freely explore the pictures while their gaze was recorded with a Tobi T120 eye-tracker. The experimental design was self-paced (i.e., subjects had to press the spacebar to move to the next trial) with a minimum stimulus duration set to 2 s and a maximum stimulus duration set to 10 s. The inter-trail interval was set to 1500 ms. Before the task, the subjects were informed that they will be asked some questions at the end. The visual exploration task was divided into two sessions with a 10-minute break to relax and rest the eyes. Once the visual exploration task was completed, subjects took an additional five-minute break. Participants were then asked to verbally recall these pictures in an element-by-element manner while their voice was recorded with a Sony ICD-MX20 voice recorder. During the recall, participants were presented with a grey screen without any stimulation. No a-priori recall order was set: subjects were free to recall the target images in any order. The total duration of recall for each image was set to 3 minutes, during which they were encouraged to keep thinking about that image. In case subjects didn't remember an image, they were cued with Level 3 image labels from the Places 365 dataset (see next section).*

Assessment of behaviour and personality

At the end of the session, participants were tested on memory (i.e., Rey-Osterreith's Complex Figure, Rey & Osterrieth, 1993) for visuospatial long-term memory and DigitSpan (for working memory, Monaco et al., 2013a) and executive functions (Stroop Test, Venneri et al., 1992) for inhibition/impulsivity). Moreover, participants were asked to fill an online form that contained three personality questionnaires: the Neo Five Factors Inventory (NEO-FFI, Costa & McCrae, 1989b), the Behavioral Approach and Behavioral Inhibition Scale (BIS-BAS, Carver & White, 1994b), and the 21-items version of the Depression Anxiety Stress Scale (DASS-21, Lovibond &

Lovibond, 1995a). Moreover, since some participants were students of psychology, we checked their knowledge of the administered tests using a three-point scale (0=No knowledge;1=Theoretical knowledge; 2=Theoretical and Practical knowledge).

Stimuli: image set

The stimuli used in the present study were a set of 180 real-world pictures selected from the validation set of the Places365-Standard dataset (Zhou et al., 2018b). Places365 images are categorized according to three levels: Level 1 (three levels: indoor, outdoor man-made, outdoor natural), Level 2 (six category-specific labels for each Level one category: e.g., Level 1 "indoor", Level 2 "shopping and dining"), Level 3 (scene type: e.g., Level 1 "indoor", Level 2 "shopping and dining", Level 3 "bakery shop"). For image selection, we used only Level 1 categorization and added an additional dimension (i.e., the presence or absence of human beings). Thus, we considered a final set of six categories with 30 images each (i.e., indoor manmade with humans, indoor manmade without humans, outdoor manmade with humans, outdoor manmade without humans, outdoor natural with humans, outdoor natural without humans).

Stimuli: target images

In addition to the image set, we selected five target images for recall. Target images were selected by two evaluators according to the following criteria: 1) a high number of recallable details, 2) low or medium-low overlap between saliency and semantic maps. This latter criterion was chosen since we were interested in dissociating the effect of saliency and semantic information on memory. Saliency maps were computed using Itti and Koch's saliency model (Itti et al., 1998a) implemented in graph-based visual saliency (GBVS) Matlab toolbox, while semantic maps were created using an algorithm based on a convolutional neural network for image labeling (Zhou et al., 2018b). Overlap levels were assessed using the maximum overlap criterion. The maximum overlap was defined as *the highest value between saliency overlap (intersection divided by the size of saliency map) and semantic overlap (intersection divided by the size of the semantic map). Low overlap was defined as maximum overlap being lower than 25% and medium-low overlap as maximum overlap being lower than 50%. One target image for each of the six categories was selected, except for the outdoor natural without human category. This latter category was excluded since it showed a very low number of recallable details. The final target sample contained the following real-world pictures: a bedroom (i.e., indoor manmade no humans), a laboratory (i.e., indoor manmade humans), a street (i.e., outdoor manmade humans), a hospital (i.e., outdoor manmade no humans) and a beach (i.e., outdoor natural humans).*

Stimuli: saliency and semantic maps

As mentioned in the previous paragraph, for each target image a saliency map and a semantic map were computed. The specific purpose is to control the effect of image-specific features that have been shown to attract the human gaze in free visual exploration (e.g., Itti et al., 1998, Torralba et al., 2006).

In saliency maps, multi-scale low-level image features are combined in a single topographic map to predict attended locations for human fixations. Saliency maps highlight low-level features such as spatial frequency content, local contrast, brightness, and color. In other words, saliency maps describe visually salient image areas regardless of content.

In semantic maps, the highlight is on semantically relevant areas of the image. Here, semantic maps are operationalized as image areas maximally contributing to the labelling (see previous paragraph) performed by a convolutional neural network (for further information see Zhou et al., 2018).

Eye tracking

A minimal pre-processing was performed on raw eye-tracking data. In this step only gaze samples in which both eyes were assigned the highest validity value were kept (i.e., validity code of 0, meaning that the eye is found and that the tracking quality is good). Fixations were then detected with a velocity-based threshold algorithm (Engbert & Kliegl, 2003a) with a detection threshold of lambda = 15. The fixations were then transformed into gazemaps. First, a matrix of zeros with the same size as the image was created. Each fixation corresponded to a +1 on its coordinates. Finally, a 2° FWHM Gaussian blur is applied. Gazemaps were created for each subject and image, with the five presentations collapsed into a single map.

Image Annotations (Figure 1c - row 1)

Two independent evaluators examined the five target pictures and compiled a list of elements that could be included in a verbal description of each image (i.e., image annotations).

The image annotations were then updated (if necessary) based on subject-specific verbal reports (from audio data). In other words, if some object contained in the images was not labeled in the first step, it was added at this stage (Figure 1c – row 1). This update was done by comparing the audio data with the images, and it was carried out by a different independent evaluator.

Coordinates (Figure 1c - row 2)

An evaluator drew a region of interest (ROI) for each element listed in the annotations (see previous step) directly on the image by using ImageJROI software (version 1.52a) (Figure 1c – row 2). The ROIs were subsequently imported into MATLAB and the x/y coordinates corresponding to the ROI were extracted by using the ReadImageJROI package.

The result of this procedure was a list of objects with their related coordinates on the image space. Note that all the pixels occupied by the object are reported in the coordinate list.

Recall Annotations (Figure 1c - row 3)

Three independent evaluators listened to the audio recordings and manually compiled the annotations created in the first step (Figure 1c - row 1). Recall annotations and Image Annotations were compiled by different independent evaluators. For each named element the evaluators compiled three fields: type (either correct recalled element, whether the element was already mentioned, or confabulation, I.e., an element not present in the image), order (sequence of recalled elements), and time (onset of the recalled element in the audio track). The compiled annotations created in this step will be referred to as recall annotations (Figure 1c - row 3). Recall annotations were compiled at a subject- and image-specific level and were checked by a different independent evaluator to correct errors if present (e.g., wrong type).

Memory Maps (Figure 1c - row 4)

After this check, we simulated subject-specific sets of fixations by combining individual annotations (i.e., recalled objects) and objects' coordinates (Figure 1c - row 4). In other words, each recalled element was treated as a fixation. Notably, since we considered the coordinates of all pixels in each object-specific ROI, each element was represented with as many fixations (i.e., point coordinates on a matrix with the same dimensions as the image) as the number of pixels occupied by the object. The data frame was then transformed into a 2D map with the same procedure used for eye-tracking data. Finally, the same blur used for eye-tracking data was applied (2° FWHM Gaussian blur).

With this procedure, we created a set of 5 memory maps (one per image) for each subject that could be compared with fixation maps.

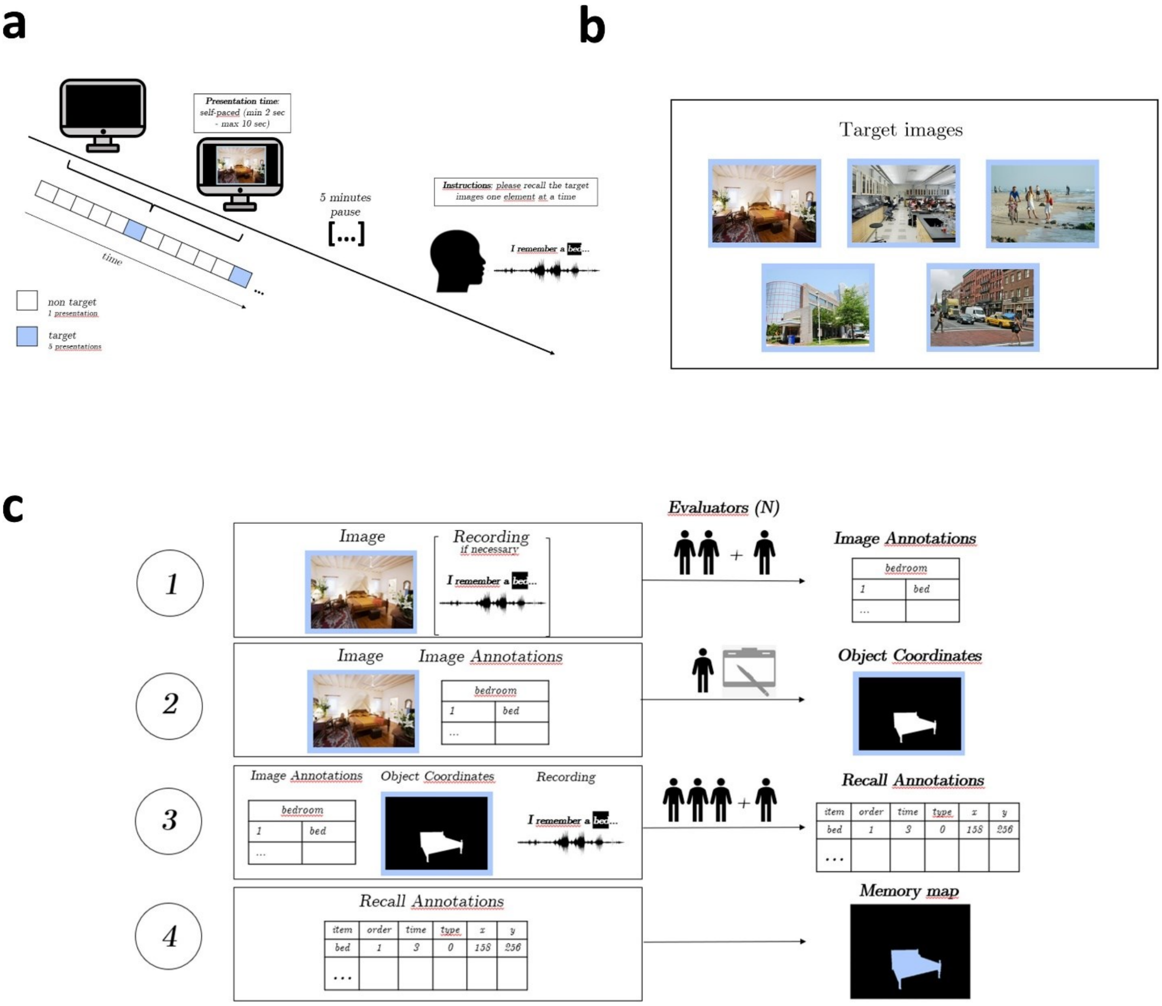


Figure 1| **a. Experimental paradigm** *Subjects were asked to explore with their eyes the picture and press a bar when ready to explore the next picture. After a five-minute break, they were asked to verbally recall the target pictures one element at a time while their voice was recorded.* **b. Target Images** *The final set of five target images for memory recall in this experiment (respectively: indoor manmade no humans, indoor manmade humans, outdoor manmade humans, outdoor manmade no humans, outdoor natural humans).* **c. Workflow for memory maps** *1) By using images and recordings (if necessary) two evaluators (+ one evaluator for check) create Image Annotations for each image. 2) By using images and Image Annotations one evaluator draws each object on the image to extract object coordinates in the image space (this is done by using ImageJROI). 3) By using Image Annotations, Object Coordinates and Recordings, three evaluators (+ one evaluator for check) compile Recall Annotations for each subject and image separately. 4) By using Recall Annotations, a Memory Map is automatically created for each subject and image separately.*

Overlap between gaze and memory maps

We compared the overlap between the gazemap and the memory map through the Actual Overlap Percentage (AOP), which was computed in two slightly different ways:

1. *Comparison between only gazemaps and memory maps (i.e., gAOP)*
2. *Comparison between multiple maps: gaze and stimulus-related maps (i.e.,gazemaps, saliency, and semantic maps) with memory maps (i.e., mAOP).*

The construction of AOPs follows three steps, two of which are common between gAOP and mAOP.

First, the distribution of the memory maps was matched to the eye movement maps (i.e., gazemaps). This was done to provide comparable size thresholded maps in the following step. To do so, we used the Matlab function imhistmatch, which approximates the integral of the memory maps to the corresponding eye-tracking maps.

Second, a threshold was applied to all maps (i.e., all values that exceed the upper 50% of values in the distribution are kept).

Third, for gAOP, we assessed the overlap (i.e., AOP between memory and eye tracking maps), defined as the number of pixels shared by the gazemap and memory map, divided by the size of the gazemap (Figure 2). For mAOP, we assessed the overlap (i.e., AOP between memory and eye tracking maps), defined as the number of pixels shared by gaze+stimulus-related maps and memory maps, divided by the size of the memory map (Figure 3).

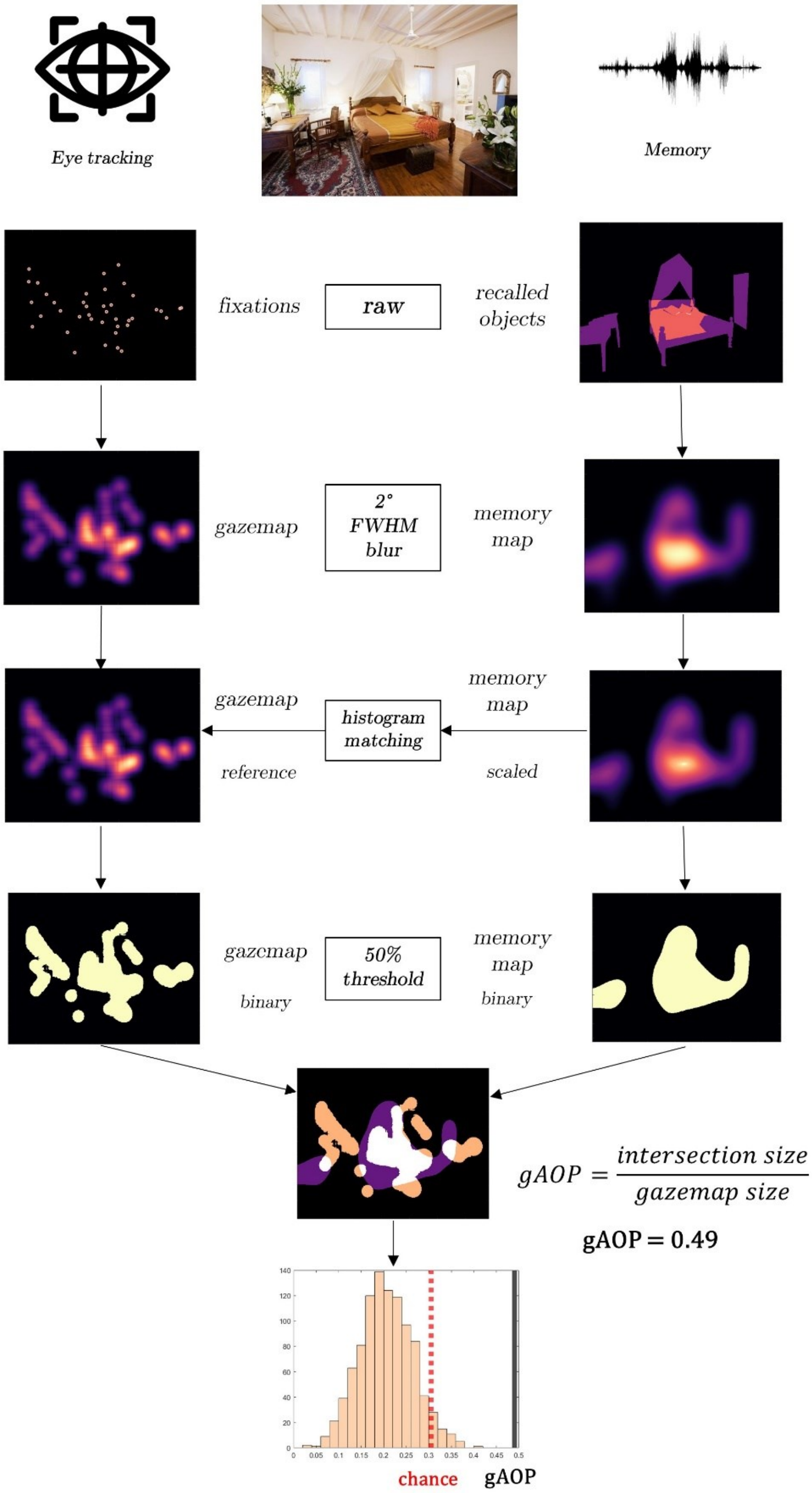
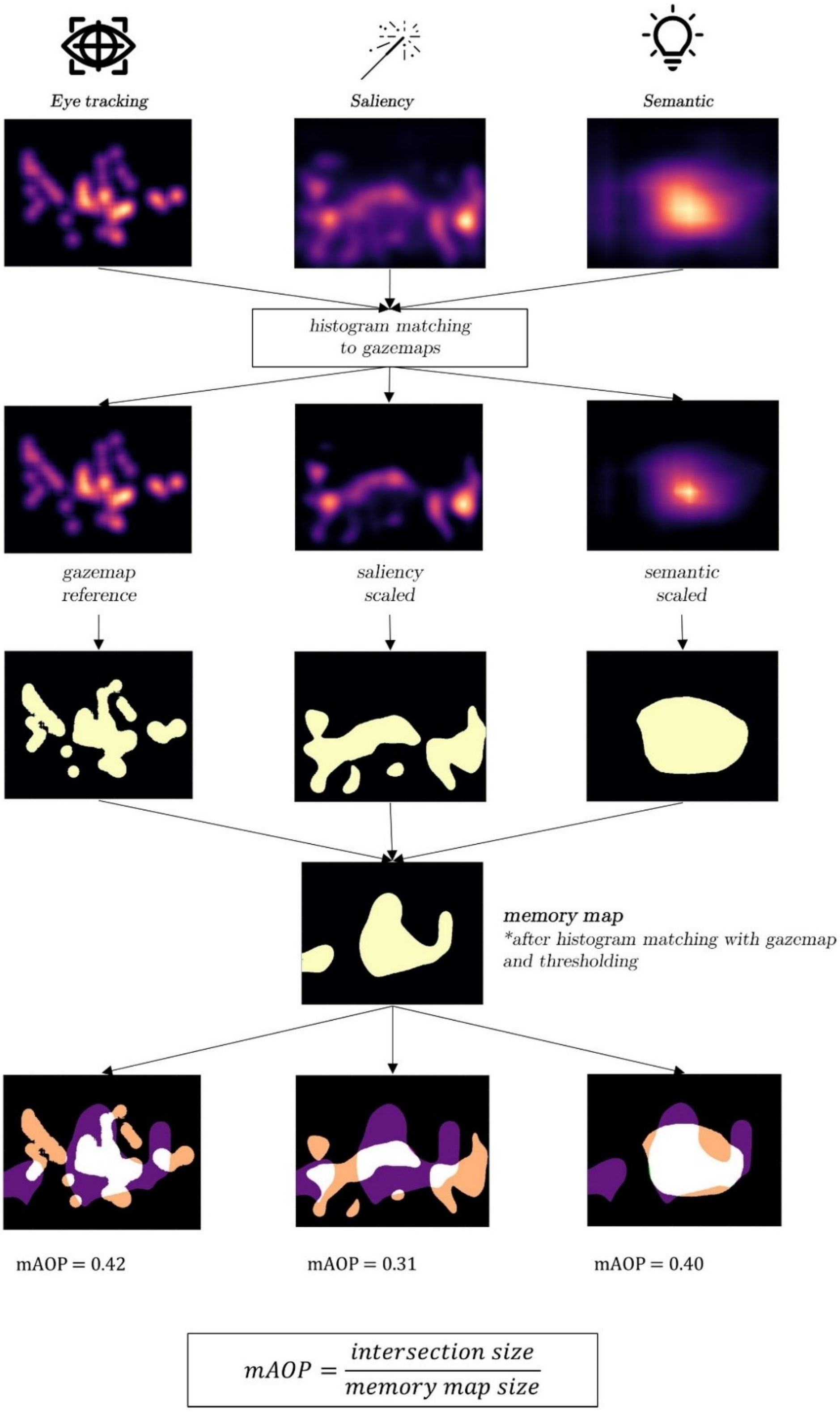


Figure 2| Workflow for gAOP computation. *First, a 2° FWHM gaussian blur is applied to raw data (fixations and recalled objects in the image space). Then, we apply histogram matching by using gazemaps as reference, so that the memory map is subsequently scaled. In the next step we apply a 50% threshold, by keeping the upper 50% of the heatmap value distribution. Finally, the gAOP is calculated (as the ratio between intersection size and gazemap size) and compared with a random distribution of AOPs computed with the FROA method to assess significance. This is done for each subject and image. Sample data from one subject are shown.*



$$mAOP = \frac{intersection\ size}{memory\ map\ size}$$

Figure 3| Workflow for mAOP computation. *Starting from blurred gaze and stimulus-related maps (i.e., gazemaps, saliency and semantic maps with a 2° FWHM gaussian blur), we apply histogram matching with gazemaps as reference. Then, we apply a 50% threshold, by keeping the upper 50% of the heatmap value distribution. Finally, the mAOP is calculated (as the ratio between intersection size and the memory map size).*

Compare overlap between maps: image level

For each image separately, a one-tailed independent sample t-test was applied to gAOPs to test the hypothesis of the mean level of overlap significantly above 0.

Compare overlap between maps: individual level

To assess the significance of the overlaps between gazemaps and memory maps (i.e., gAOP), we applied a modified version of the fixation region overlap analysis (FROA) proposed by Johnston and Leek in Johnston & Leek, 2008). The FROA method has been originally developed to test theoretical models of eye movements (e.g., Itti et al., 1998a) against human data (e.g., Ambrosini & Costantini, 2017). The assessment of significance in this method is based on the generation of a distribution of random overlaps, against which the significance of the observed overlap (i.e., the overlap between human-generated and model-generated data) is tested. In this case, the aim was to assess the significance of the overlap between eye-tracking-generated and free recall-generated data. To do so, we generated a random distribution of overlaps, as follows:

1. *The total number of fixations for each gazemap was assessed (e.g., 20).*
2. *The same number of fixations (e.g., 20) was permuted in space in an empty matrix (filled with zeros) with the same size as the image.*
3. *A smoothing was applied to the permuted gazemap (2° FWHM Gaussian blur).*
4. *The permuted map distribution was matched to the real (i.e., eye-tracking) map by using Matlab imhistmatch function.*
5. *The same threshold used for gazemaps and memory maps was applied to the permuted map (i.e., upper 50%).*
6. *Assessment of overlap (permuted and memory maps), defined as the number of pixels shared by the permuted map and memory map, divided by the size of the permuted map.*
7. *This permutation step was repeated 1000 times to build a distribution of random overlaps.*

Statistical Analysis (general)

Since there is variability both at the subject and image level, statistical analysis on gAOPs and mAOPs aimed to respond to the following questions:

1. *Are there different strategies?*
2. *What differentiates the two groups in terms of behaviour? And, can we use this information to predict significance at the individual level? (i.e., cluster profiles)*
3. *Do these strategies correlate with cognitive/personality variables? (i.e., cognitive characterization of clusters)*

Cluster Analysis (mAOP)

First, we created a data frame by vectorizing all mAOPs, which was then normalized by column. Then, the Hopkins statistic (Hopkins & Skellam, 1954) was computed with the hopkins package in R. When this is between 0.7 and 1, the data is clusterable. The obtained value was 0.97. Therefore, we searched for clusters in our AOP data employing the NbClust R function (package NbClust, Charrad et al., 2014). This function compares 30 indices to assess the most suitable number of clusters based on the dataset. Based on the majority rule, the optimal number of clusters assessed with this method was 2.

Following this step, a k-means cluster analysis with k=2 was computed on the dataset by using the R kmeans function.

Cluster profiles

To characterize cluster profiles, we build a linear mixed-effect model to predict mean mAOPs with subjects as random intercepts and cluster and map types as fixed effects. This model aimed to *predict mean mAOPs (3 for each subject, averaged by map type) based on map type and subject-specific information (i.e., cluster). This was implemented by using the R lmer function from the lmerTest package (Kuznetsova et al., 2017).*

Then, we asked if this information could be useful in predicting significance at the individual level. To do so, we used clusters, as well as image-specific (i.e., category) information, to predict whether the overlap between memory and gaze map would be significant (according to the individual- and image-specific permuted maps). We built three separate logistic mixed-effect models (i.e., one for each category) to predict significance, with subjects as random intercepts and cluster and category as fixed effects. We built these models to assess possible interactions between cluster and image categories.

Cognitive Characterization of Clusters

To characterize clusters at a cognitive level, we employed all available information from cognitive and personality testing (see Zangrossi et al., 2021) to build a stepwise logistic regression model to predict clusters by using cognitive variables.

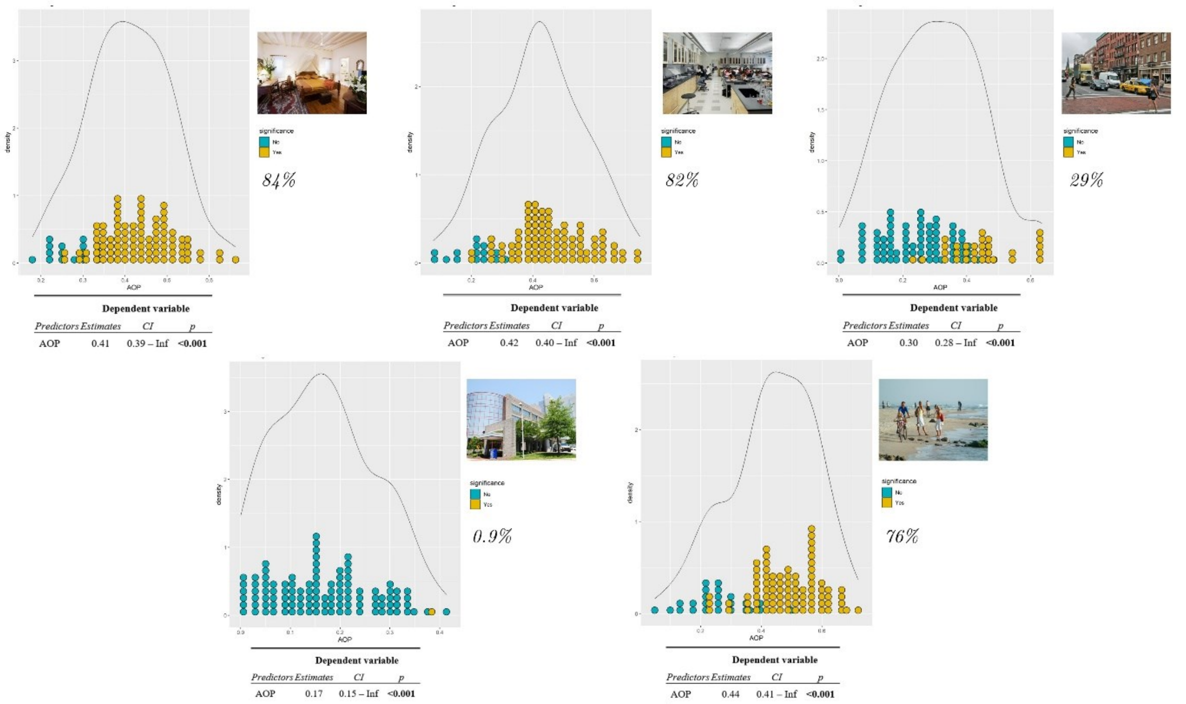
Results

Memory maps overlap with gaze maps

Since this measure has never been tested, first we asked if gAOP distributions have means greater than 0. One-tailed independent sample t-tests were computed separately for each image with $H = mu>0$*. All tests are significant with* $p<0.001$*, indicating that the means of gAOP distributions for each image were always significantly greater than 0 (Figure 4).*

Overlap between memory and fixation maps at the individual level

To assess the presence of overlap between memory and gaze at an individual- and image-specific level, we tested the significance of gAOPs against a null distribution of random AOPs based on the data. The results show that on average half of the gAOPs (across subjects and images) significantly exceeded the chance level, with the lowest at 0% and the highest 75%. The mean ratio for significance (i.e., the number of significant gAOPs/N) was 54% (averaged across images). Individual data points colour coded for significance and significance ratios for each image are shown in Figure 4.



Predictors	Estimates	CI	p
AOP	0.41	0.39 – Inf	**<0.001**

Predictors	Estimates	CI	p
AOP	0.42	0.40 – Inf	**<0.001**

Predictors	Estimates	CI	p
AOP	0.30	0.28 – Inf	**<0.001**

Predictors	Estimates	CI	p
AOP	0.17	0.15 – Inf	**<0.001**

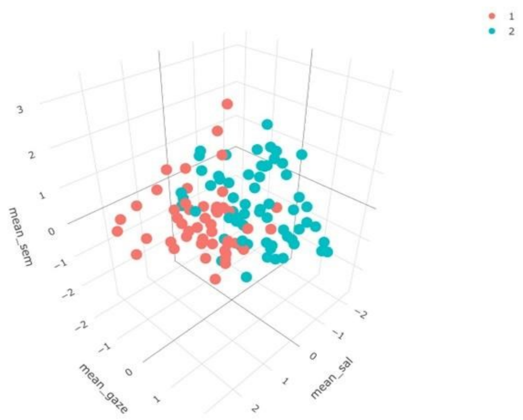
Predictors	Estimates	CI	p
AOP	0.44	0.41 – Inf	**<0.001**

Figure 4| *Distributions of image-specific gAOPs, along with individual data points (color code for significance of gAOPs according to the FROA method). Bottom panels show the results for one-sample t-tests for each image separately. N=114.*

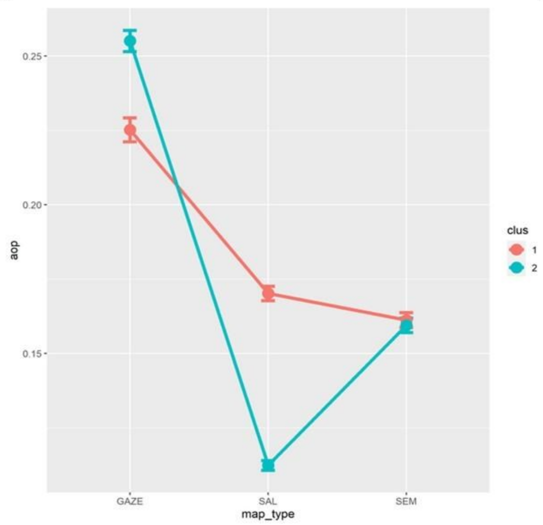
Two strategies in visual memory describe the use of gaze and stimulus-related maps across subjects

Based on the actual overlap between memory maps and gaze+stimulus-related maps (mAOP), the data appears to be clusterable in two groups. Subsequent statistical analysis showed that the two groups have a different tendency towards relying on gaze+stimulus-related maps (Figure 5). After a k-means cluster analysis with k = 2, we fitted a linear mixed-effect model to predict mAOP with

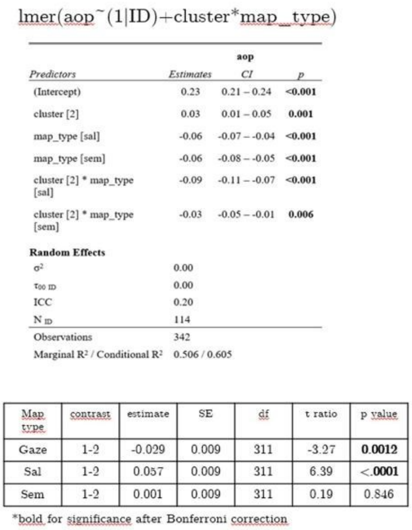
a



b



c



lmer(aop~(1|ID)+cluster*map_type)

	aop		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.23	0.21 – 0.24	**<0.001**
cluster [2]	0.03	0.01 – 0.05	**0.001**
map_type [sal]	-0.06	-0.07 – -0.04	**<0.001**
map_type [sem]	-0.06	-0.08 – -0.05	**<0.001**
cluster [2] * map_type [sal]	-0.09	-0.11 – -0.07	**<0.001**
cluster [2] * map_type [sem]	-0.03	-0.05 – -0.01	**0.006**
Random Effects			
σ^2	0.00		
$\tau_{00\ ID}$	0.00		
ICC	0.20		
N_{ID}	114		
Observations	342		
Marginal R^2 / Conditional R^2	0.506 / 0.605		

Map type	contrast	estimate	SE	df	t ratio	p value
Gaze	1-2	-0.029	0.009	311	-3.27	**0.0012**
Sal	1-2	0.057	0.009	311	6.39	<**.0001**
Sem	1-2	0.001	0.009	311	0.19	0.846

*bold for significance after Bonferroni correction

d

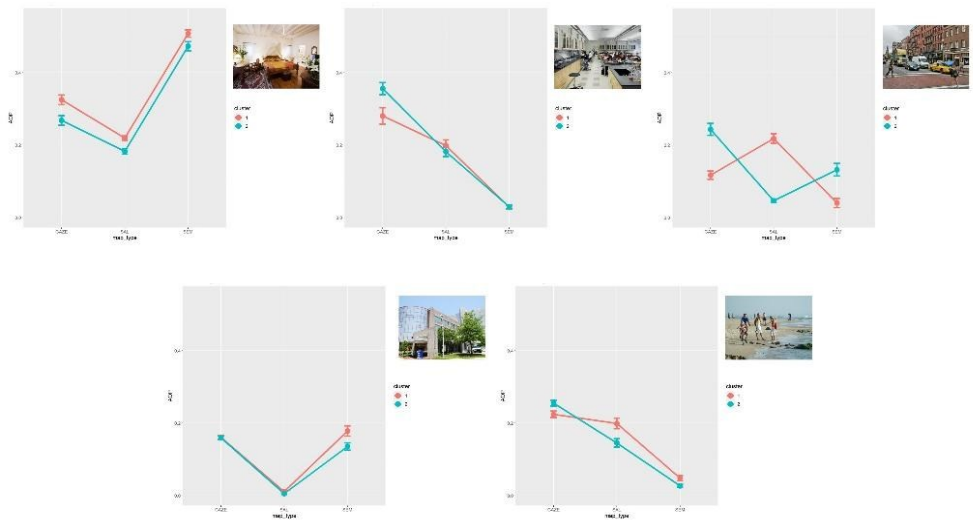


*Figure 5| **a.** Cluster projection in three-dimensional space defined by mAOP means (averaged for map type). **b.** mAOP means averaged by map. Separate lines and color code for clusters. **c.** Tables for the mixed model to predict mAOPs with map type and cluster as fixed effects and subjects as random intercepts. The bottom panel shows paired t-test for the interaction cluster*map type. Bold for significance after Bonferroni correction. **d.** mAOP means averaged by map shown separately for each image. Separate lines and color code for clusters. N=114.*

subjects as random intercepts and cluster and map type (i.e., saliency, semantic, gaze) as fixed effects. The model showed a significant effect for all tested variables.

First, there is a main effect of map type: saliency and semantic maps showed lower mAOPs than gazemaps (estimate = -0.06, p = <0.001, estimate = -0.06, p = <0.001, respectively). Since salience and semantics are purely stimulus-based, this could indicate that endogenous dynamics during visual exploration are more closely related to endogenous dynamics during visual scene recalling. Secondly, cluster 2 shows higher overall mAOPs (estimate = 0.03, p =0.001) as compared to cluster 1. Finally, the interaction between the two is significant. To explore the effect of interactions we ran pairwise t-tests (Bonferroni corrected). The interaction between gaze and cluster, as well as the interaction between saliency and cluster, remained significant after the Bonferroni correction. The results indicate that cluster 1 has a higher overlap with saliency maps (t=6.39, p <.0001), while cluster 2 has a higher overlap with gaze maps (t=-3.27, p=0.0012).

Significant overlap between gaze and memory maps is predicted by cluster and image features

Going further in the description of clusters, we built three separate logistic mixed-effect models (i.e., one for each category: indoor/outdoor, humans/no-humans, manmade/natural), to assess interactions between cluster and image categories. For the first category (indoor/outdoor), the logistic mixed-effects model showed a significant effect of cluster (chisq: 24.61, p <0.0001) and category (chisq: 105.52, p<0.0001). This means that the probability for gaze-memory overlap to be significant is overall higher for indoor scenes and for cluster 2. However, the interaction between cluster and category was not significant. For the second category (human/no human), the logistic

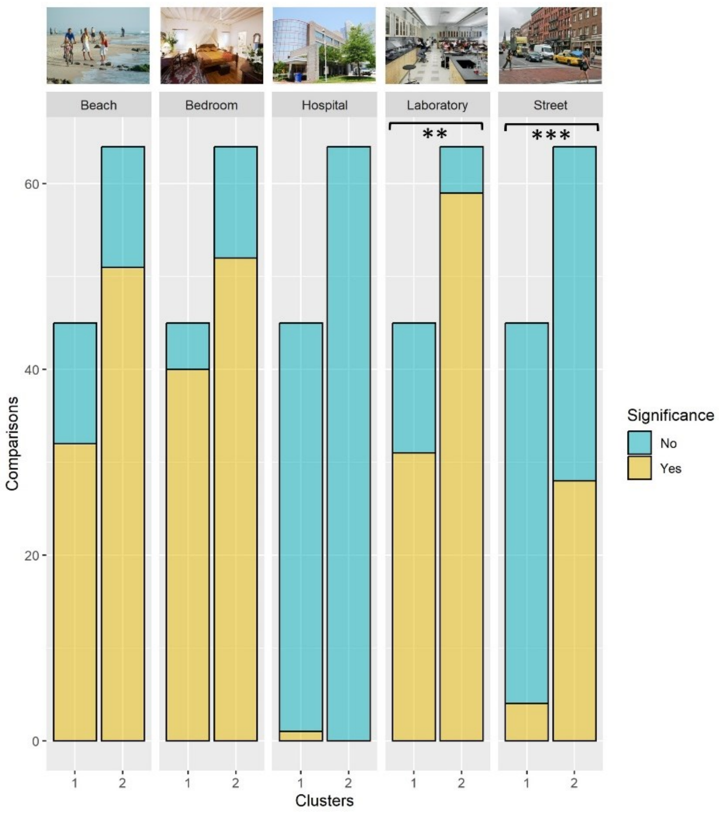


Figure 6| *Barplots for gAOP significance according to the FROA method, shown for each image separately. Color code for significance. N=114.*

mixed-effect model showed a significant effect of both cluster (chisq: 19.48, p<0.001) and category (chisq: 22.89, p<0.0001) as well as the interaction between the two. This means that the probability for gaze-memory overlap to be significant is overall higher for human scenes and for cluster 2. To assess the interaction between cluster and category we ran pairwise t-tests. When comparing clusters in the human category, there was a significant effect (estimate = 1.33, p<0.001), meaning that when humans were present it was more likely for cluster 2 subjects to show a significant memory-gaze overlap. In the no-human category, there was no significant effect when comparing clusters (estimate = 0.121, p = 0.65), meaning that when humans were not present the two clusters behaved similarly. For the third category (manmade/natural), the logistic mixed-effect model showed a significant effect of both cluster (chisq: 20.62, p<0.0001) and category (chisq: 25.62, p<0.0001). This means that the probability for gaze-memory overlap to be significant is overall higher for natural scenes and for cluster 2. However, the interaction between cluster and category was not significant. To assess the individual image-specific differences in the overlap between gaze and memory maps, chi-square independence tests were then conducted at an image-specific level (Figure 6). Two images showed a significant difference between the two clusters in the proportion of significant gAOPs. In the laboratory image (i.e., indoor manmade human) there was a significant relationship between clusters and *significance: cluster 2 subjects were more likely to have a significant gAOP (chisq: 8.412, p = 0.003). In the street image (i.e., outdoor manmade human) there was a significant relationship between clusters and significance: cluster 2 subjects were more likely to have a significant gAOP (chisq: 13.84, p = 0.0001). The other comparisons yielded non-significant results.*

Cognitive Model

To further characterize clusters from the cognitive point of view, we employed all available information from cognitive testing (see Assessment of Behaviour and Personality) in the present study, as well as PC1 (a component mainly representing dynamical features of eye movement patterns, see Chapter 3) to build a stepwise logistic regression model to predict cluster. In the resulting model, however, none of the variables had a significant effect. The final model contains three parameters: Rey-Osterreith complex figure score (estimate = 0.077, p = 0.100), Stroop error interference (estimate = -0.410, p = 0.123), and extraversion (estimate = -0.044, p = 0.150) as measured with NEO-FFI. None of them was significant in the prediction of cluster labels, meaning that none of the tested cognitive variables was significantly different between the two clusters.

Discussion

In the present study, we aim to describe the spatial relationship between the topography of eye movements during free viewing of scenes and the topography of memory recall. To this end, we designed a method to transform audio recordings into 2D maps. Then we compared those memory heatmaps with eye-tracking heatmaps obtained during encoding.

The results show that: 1) there is a significant overlap between gaze and memory; 2) the overlap with memory maps is significantly higher with the topography of fixation than with the topography of salience and semantic information in each picture; 3) Subjects can be clustered based on the degree of overlap between memory and gaze, saliency, or semantics respectively.

The % overlap between gaze maps and memory maps (gAOP) was significant on average (across subjects) 54% of the times with 84% for the bedroom; 82% for the laboratory; 76% for the beach; 29% for the street; 0.9% for the outside building. When averaged across categories: the gAOP was 83% vs. 38% for indoor vs. outdoor, 62% vs. 46% for human vs. non-humans, and 70% vs 76% for manmade vs natural (note that there is only one image in the natural category). Given only five scenes were studied in the memory paradigm, and the outside building scene clearly shows by far the smallest overlap, results that include this scene must be weighted with great caution. If we eliminate the outside building picture the average gAOP rises to 67% of significant comparisons. While it is not surprising that eye movements and memory maps do not always significantly overlap since gist-level information can be processed within the span of a fixation (Biederman et al., 1974), we think that the degree of overlap between gaze topography and memory topography is on average rather high and interestingly it shows across subjects a significant degree of variability. Through cluster analysis, we show that the data can be summarized ideally in two clusters of subjects. We tested the reliability of the cluster solution by computing the best clustering solution by comparing 30 different methods for cluster solutions (the optimal cluster solution is chosen based on the majority rule). A low dimensional solution for complex behavior at the population level is consistent with recent literature on human mobility in cities (Pappalardo, Simini, Rinzivillo, Pedreschi, & Giannotti, 2015) and eye movement visual exploration (Zangrossi et al., 2021). It is also consistent with a large body of literature reviewed above in chapter 2. That is, some behaviours that look apparently chaotic, hide a low dimensional structure across subjects: different strategies to perform a given function.

In the case of visual memory retrieval, at the general population level, gaze seems to be the preferential source of information for memory as compared to saliency and semantic maps (see Figure 5B). This is somehow not surprising considering that gaze is the mean by which we collect visual information (see above). However, we shall recall that our previous work shows that eye *movement dynamics like those used here to compute gaze maps strongly rely on endogenous dynamics, and much less on sensory or semantic salience.*

The main effect of gaze across the population suggests that in the context of visual memory, it appears that endogenous representations that guide visual exploration also contribute to memory recall. Independent of the two clusters, gaze outperforms saliency and semantics in the similarity with memory maps. This means that endogenous variables (i.e., gaze) have a more prominent role in defining memory topography, as compared to purely stimulus-driven maps such as saliency and semantics.

The k-means cluster analysis revealed an additional latent structure across subjects: two different strategies. Subjects belonging to cluster 1 seem to use less information from the gaze and more from saliency maps as compared to subjects appertaining to cluster 2. This suggests that gaze topography predicts the topography of memory recall above and beyond low-level features of the image (saliency, semantic), and the magnitude of this unbalance varies across clusters of individuals.

Moreover, these memory recall strategies seem to be interacting with the image category: in particular, whether the image contains humans or not. It is well known that human figures and faces strongly attract the human gaze (Cerf et al., 2007). Since this is quite a general mechanism across human beings, one would expect the presence of humans to make performances more homogeneous. Counterintuitively, images containing humans vs. no-human show a significant interaction with clusters. In other words, while all participants seem to behave in a very similar manner in pictures without humans, they tend to differentiate (and cluster) when humans are indeed present. However, this particular finding might be interpreted with great caution since the number of images in each category is very small.

Moreover, in the present, we show that cluster, together with image category (i.e., human/no-human) predict significance in gAOPs. In other words, individual- and image-specific information *interact in determining the overlap between gazemaps and memory maps (more in detail, if this overlap exceeds chance levels based on permuted maps). As above, since there are few images in each category, this preliminary result may be interpreted with caution.*

Finally, among all the cognitive variables tested, none seem to predict cluster labels. Surprisingly, visual exploration PC1 (see Zangrossi et al., 2021; Chapter 3) seems not to be related to visual memory strategies, since it is not contained in the final cognitive model selected with the stepwise procedure. Moreover, memory recall strategies are not related to visuospatial memory ability, as demonstrated by the non-significant estimate of Rey-Osterreith's complex figure in the cognitive model. It is possible that the chosen variables are not the most relevant for the phenomenon. Thus, future studies would require testing for other cognitive variables to complete the cluster characterization. For instance, vivid visual imagery has been shown to affect memory recall performance (i.e., the number of correctly recalled elements Marks, 1973).

Future directions of this work will involve testing the robustness of clustering across different thresholding strategies for the maps (e.g., 25%,50%,75%). Moreover, we are currently planning to exploit the additional time dimension, by comparing gaze scanpaths and memory "scanpaths" by using the ScanMatch method (Cristino et al., 2010). This will shed light on the spatiotemporal similarity between eye movements during encoding and subsequent memory recall. Finally, a limitation of this study is represented by the number of target images. Future studies will have to enlarge the sample and the number of target images encoded, in order to rule out category- and image-specific effects separately.

To sum up, here we propose a new method to study the overlap between eye movements during encoding and subsequent visual memory recall. By transforming free recall audio tracks into 2D maps, we show that there is an overlap between what we see and what we remember. In other words, we found that gaze maps show higher similarity with memory maps, as compared to stimulus-related maps (i.e., saliency and semantics). This suggests a key role of endogenous *processes in shaping visual memory recall, as compared to purely stimulus-related information. Interestingly, the unbalanced importance of gaze topography and image-related information topography shows a structured pattern of interindividual differences which could be summarized in two clusters.*

Chapter 6: Conclusions and future directions

In the present project, we aimed at characterizing using an ecological paradigm free viewing eye movement behavior during visual exploration and its relationship with spontaneous brain activity and memory performance. We selected an ecological paradigm and rich signals like eye movement dynamics, EEG, and topographic map analysis of memory and eye movements to study inter-subject variability in a relatively large number of subjects (n>100). This approach was based on recent theories supporting a role of spontaneous brain dynamics in biasing behaviour (Pezzulo et al., 2021b), and recent observations on the low dimensionality of both behaviour and neural activity. We choose to analyze and characterize eye movements during free visual exploration: an extremely variable phenomenon, although reliable on an individual basis (e.g., Poynter et al., 2013b). In addition, we analyzed EEG signals not to find correlates of pre-defined cognitive operations (outside-in), but rather to use the EEG to classify data-driven behavioral components (inside-out) following a recent distinction made by Buszaki et al. (2019).

First, we review the hypothesis of low dimensionality in behaviour (Chapter 2). We propose that the brain implements low dimensionality in behaviour (which is the primary output of the brain) and representations (to increase the efficiency of environment readability) to overcome the high dimensionality of the environment (since the resources of the brain are limited).

In the following chapters, we characterize visual exploration phenotypes and their neural correlates in healthy controls. We show that visual exploration is low dimensional and driven by intrinsic factors (Zangrossi et al., 2021). 3 PCs explained 60% of the variance in a large eye-tracking dataset (n=120 observers) and participants can be classified in one of two viewing styles (Static and Dynamic viewers). In the next study (Celli et al., 2022) we show that spontaneous brain oscillations at rest recorded one year later predict these visual exploratory phenotypes, delineating two complementary oscillation profiles.

Finally, since visual exploration is not a stand-alone process, we choose to characterize a connected behaviour: visual memory recall. In this study (Chapter 5), by transforming audio recordings into 2D maps, we quantify the overlap between visual exploration (i.e., gazemaps) and recollection (i.e., memory maps). We show that there is an overlap between memory and gaze, with gaze outperforming purely stimulus-related models (i.e., saliency and semantics). We show that this unbalance is structured in two strategies across the population: one more relying on gaze fixations, and the other more relying on saliency as compared to the other.

Future directions

Future directions of this project will take mainly three directions: 1) validation of these results on a different sample; 2) studying free visual exploration and neural signals (e.g., EEG) simultaneously; 3) studying these mechanisms in clinical populations (e.g., Alzheimer's disease).

First, it would be important to validate these results on a different sample. Since we are trying to describe the co-occurrence of several features at the population level, it would be crucial to test the reliability of our findings on new data with the aim of replicating our results and strengthening the conclusions of the present study.

About the second point, the reciprocal relationship between rest and task brain signals is well known (e.g., Northoff et al., 2010). In Chapters 3 and 4 we show two visual exploration patterns linked to two different resting state oscillation profiles. The next step would be to see how they change and develop during a task with the expectation of finding this pattern also in an active state, as suggested by Popov's study (Popov et al., 2021).

Further developments of this project will have the final goal of understanding what kind of information spontaneous eye movement patterns can give us about the brain, with potential clinically useful implementations. For instance, recent studies show that eye-movement alterations can be identified in neurodegenerative diseases (e.g., Alzheimer's, see Anderson & McAskill, 2013) *even in early stages of pathology (i.e., MCI). A goal of this line of research would be to identify non-invasive biomarkers based on eye-tracking, able to identify an ongoing neurodegenerative disease at its early stages. In the future of medicine, it would be revolutionary if simple tasks (i.e., viewing some pictures on a computer) with cheap technologies (i.e., eye tracking implemented with a webcam) could give us useful information about the brain state. Within this framework, eye movements have several advantages since 1) eye tracking is cheap and totally non-invasive; 2) viewing pictures on a screen is less effortful than performing a structured task.*

References

Alexandrov, A., Frolov, A., & Massion, J. (1998). Axial synergies during human upper trunk bending. 210–220.

Altmann, G. T. M. (2004). Language-mediated eye movements in the absence of a visual world: the 'blank screen paradigm.' Cognition, 93(2), B79–B87. https://doi.org/10.1016/j.cognition.2004.02.005

Ambrosini, E., & Costantini, M. (2017). Body Posture Differentially Impacts on Visual Attention Towards Tool, Graspable, and Non-Graspable Objects. Journal of Experimental Psychology: Human Perception and Performance, 43(2), 1–29.

Anderson, T. J., & MacAskill, M. R. (2013a). Eye movements in patients with neurodegenerative disorders. In Nature Reviews Neurology (Vol. 9, Issue 2, pp. 74–85). https://doi.org/10.1038/nrneurol.2012.273

Anderson, T. J., & MacAskill, M. R. (2013b). Eye movements in patients with neurodegenerative disorders. Nature Reviews Neurology, 9(2), 74–85. https://doi.org/10.1038/nrneurol.2012.273

Andrews, T. J., & Coppola, D. M. (1999a). Idiosyncratic characteristics of saccadic eye movements when viewing different visual environments. Vision Research, 39(17), 2947–2953. https://doi.org/10.1016/S0042-6989(99)00019-X

Andrews, T. J., & Coppola, D. M. (1999b). Idiosyncratic characteristics of saccadic eye movements when viewing different visual environments. Vision Research, 39(17), 2947–2953. https://doi.org/10.1016/s0042-6989(99)00019-x

Ausburn, L. J., & Ausburn, F. B. (1978). Cognitive Styles: Some Information and Implications for Instructional Design.

Austin, D., Bowen, W. D., & McMillan, J. I. (2004). Intraspecific variation in movement patterns: modeling individual behaviour in a large marine predator. Oikos, 105(1), 15–30. https://doi.org/10.1111/j.0030-1299.1999.12730.x

Austin, E. J., Deary, I. J., Whiteman, M. C., Fowkes, F. G. R., Pedersen, N. L., Rabbitt, P., Bent, N., & Mcinnes, L. (2002). Relationships between ability and personality: does intelligence contribute positively to personal and social adjustment? www.elsevier.com/locate/paid

Avella, A., Saltiel, P., Bizzi, E., Section, H. P., Fondazione, I., Lucia, S., & Ardeatina, V. (2003a). Combinations of muscle synergies in the construction of a natural motor behavior. Nature Neuroscience, 6(3). https://doi.org/10.1038/nn1010

Avella, A., Saltiel, P., Bizzi, E., Section, H. P., Fondazione, I., Lucia, S., & Ardeatina, V. (2003b). Combinations of muscle synergies in the construction of a natural motor behavior. 6(3). https://doi.org/10.1038/nn1010

Bainbridge, W. A., Hall, E. H., & Baker, C. I. (2019a). Drawings of real-world scenes during free recall reveal detailed object and spatial information in memory. Nature Communications, 10(1). https://doi.org/10.1038/s41467-018-07830-6

Bainbridge, W. A., Hall, E. H., & Baker, C. I. (2019b). Drawings of real-world scenes during free recall reveal detailed object and spatial information in memory. Nature Communications, 10(1). https://doi.org/10.1038/s41467-018-07830-6

Baranes, A., Oudeyer, P.-Y., & Gottlieb, J. (2015). Eye movements reveal epistemic curiosity in human observers. Vision Research, 117, 81–90. https://doi.org/10.1016/j.visres.2015.10.009

Bargary, G., Bosten, J. M., Goodbourn, P. T., Lawrance-Owen, A. J., Hogg, R. E., & Mollon, J. D. (2017a). Individual differences in human eye movements: An oculomotor signature? Vision Research, 141, 157–169. https://doi.org/10.1016/j.visres.2017.03.001

Bargary, G., Bosten, J. M., Goodbourn, P. T., Lawrance-Owen, A. J., Hogg, R. E., & Mollon, J. D. (2017b). Individual differences in human eye movements: An oculomotor signature? Vision Research, 141, 157–169. https://doi.org/10.1016/j.visres.2017.03.001

Barry, R. J., Clarke, A. R., Johnstone, S. J., & Brown, C. R. (2009). Clinical Neurophysiology EEG differences in children between eyes-closed and eyes-open resting conditions. Clinical Neurophysiology, 120(10), 1806–1811. https://doi.org/10.1016/j.clinph.2009.08.006

Barry, R. J., Clarke, A. R., Johnstone, S. J., Magee, C. A., & Rushby, J. A. (2007). EEG differences between eyes-closed and eyes-open resting conditions. Clinical Neurophysiology, 118(12), 2765–2773. https://doi.org/10.1016/j.clinph.2007.07.028

Barry, R. J., Clarke, A. R., Johnstone, S. J., Mccarthy, R., & Selikowitz, M. (2009). Electroencephalogram Theta/Beta Ratio and Arousal in Attention-Deficit / Hyperactivity Disorder : Evidence of Independent Processes. BPS, 66(4), 398–401. https://doi.org/10.1016/j.biopsych.2009.04.027

Bartoli, E., Bosking, W., & Foster, B. L. (2020). Seeing Visual Gamma Oscillations in a New Light. Trends in Cognitive Sciences, 24(7), 501–503. https://doi.org/10.1016/j.tics.2020.03.009

Battleday, R., Peterson, J., & Griffiths, T. (2020). Capturing human categorization of natural images by combining deep networks and cognitive models. Nature Communications, 1–14. https://doi.org/10.1038/s41467-020-18946-z

Benedek, M., Schickel, R. J., Jauk, E., Fink, A., & Neubauer, A. C. (2014). Alpha power increases in right parietal cortex reflects focused internal attention. Neuropsychologia, 56, 393–400. https://doi.org/10.1016/j.neuropsychologia.2014.02.010

Benjamini, Y., & Hochberg, Y. (1995). Controlling the False Discovery Rate : A Practical and Powerful Approach to Multiple Testing Author (s): Yoav Benjamini and Yosef Hochberg. Journal of the Royal Statistical Society, 57(1), 289–300.

Berger, H. (1938). Uber das Elektrenkephalogramm des Menschen. Archiv Fur Psychiatrie, 108, 408–431.

Berkes, P., Orban, G., Lengyel, M., & Fiser, J. (2011). Spontaneous Cortical Activity Reveals Hallmarks of an Optimal Internal Model of the Environment. Science, 331(6013), 83–87. https://doi.org/10.1126/science.1195870

Betti, V., Corbetta, M., de Pasquale, F., Wens, V., & Penna, S. della. (2018). Topology of functional connectivity and hub dynamics in the beta band as temporal prior for natural vision in the human brain. Journal of Neuroscience, 38(15), 3858–3871. https://doi.org/10.1523/JNEUROSCI.1089-17.2018

Betti, V., Della Penna, S., de Pasquale, F., Mantini, D., Marzetti, L., Romani, G. L., & Corbetta, M. (2013). Natural Scenes Viewing Alters the Dynamics of Functional Connectivity in the Human Brain. Neuron, 79(4), 782–797. https://doi.org/10.1016/j.neuron.2013.06.022

Biederman, I., Rabinowitz, J. C., Glass, A. L., & Stacy, E. W. (1974). On the information extracted from a glance at a scene. . Journal of Experimental Psychology, 103(3), 597.

Biondi, J., Fernandez, G., Castro, S., & Agamennoni, O. (2017). Eye-Movement behavior identification for AD diagnosis. ArXiv Preprint ArXiv:1702.00837.

Bisogno, A. L., Favaretto, C., Zangrossi, A., Monai, E., Facchini, S., de Pellegrin, S., Pini, L., Castellaro, M., Basile, A. M., Baracchini, C., & Corbetta, M. (2021). A low-dimensional structure of neurological impairment in stroke. Brain Communications, 3(2), 1–13. https://doi.org/10.1093/braincomms/fcab119

Bonner, M. F., & Epstein, R. A. (2021). Object representations in the human brain reflect the co-occurrence statistics of vision and language. Nature Communications, 12(1), 1–16. https://doi.org/10.1038/s41467-021-24368-2

Boot, W. R., Becic, E., & Kramer, A. F. (2009). Stable individual differences in search strategy?: The effect of task demands and motivational factors on scanning strategy in visual search. Journal of Vision, 9(3), 7–7. https://doi.org/10.1167/9.3.7

Box-Steffensmeier, J. M., Burgess, J., Corbetta, M., Crawford, K., Duflo, E., Fogarty, L., Gopnik, A., Hanafi, S., Herrero, M., Hong, Y. yi, Kameyama, Y., Lee, T. M. C., Leung, G. M., Nagin, D. S., Nobre, A. C., Nordentoft, M., Okbay, A., Perfors, A., Rival, L. M., ... Wagner, C. (2022). The future of human behaviour research. Nature Human Behaviour, 6(1), 15–24. https://doi.org/10.1038/s41562-021-01275-6

Broca, M. P. (1861). REMARQUES SUR LE SIÉGE DE LA FACULTÉ DU LANGAGE ARTICULÉ, SUIVIES D'UNE OBSERVATION D'APHÉMIE (PERTE DE LA PAROLE). Bulletin et Memoires de La Societe Anatomique de Paris, 6, 330–357.

Brocke, B., & Leue, A. (2006). Energetical bases of extraversion : Effort , arousal , EEG , and performance. International Journal of Psychophysiology, 62(2), 212–223. https://doi.org/10.1016/j.ijpsycho.2005.12.001

Bruening, S., Oh, E., Hetzenauer, A., Escobar-alvarez, S., Westphalen, R. I., Jr, H. C. H., Singewald, N., Shippenberg, T., & Toth, M. (2006). The anxiety-like phenotype of 5-HT 1A receptor null mice is associated with genetic background-specific perturbations in the prefrontal cortex GABA – glutamate system. Journal of Neurochemistry, 99(3), 892–899. https://doi.org/10.1111/j.1471-4159.2006.04129.x

Bullmore, E., & Sporns, O. (2009). Complex brain networks: graph theoretical analysis of structural and functional systems. Nature Reviews Neuroscience, 10(3), 186–198. https://doi.org/10.1038/nrn2575

Bundesen, C. (1990). A Theory of Visual Attention. In Psychological Review (Vol. 97, Issue 4).

Buzsáki, G. (2019). The brain from inside out. Oxford University Press.

Buzsáki, G., & Moser, E. I. (2013). Memory, navigation and theta rhythm in the hippocampal-entorhinal system. In Nature Neuroscience (Vol. 16, Issue 2, pp. 130–138). https://doi.org/10.1038/nn.3304

Calder, A. J., Burton, A. M., Miller, P., Young, A. W., & Akamatsu, S. (2001). A principal component analysis of facial expressions. Vision research, 41(9), 1179-1208.

Calkins, M. E., Iacono, W. G., & Curtis, C. E. (2003). Smooth pursuit and antisaccade performance evidence trait stability in schizophrenia patients and their relatives. International Journal of Psychophysiology, 49(2), 139–146. https://doi.org/10.1016/S0167-8760(03)00101-6

Carmi, R., & Itti, L. (2006). Visual causes versus correlates of attentional selection in dynamic scenes. Vision Research, 46(26), 4333–4345. https://doi.org/10.1016/j.visres.2006.08.019

Carver, C. S., & White, T. L. (1994a). Behavioral inhibition, behavioral activation, and affective responses to impending reward and punishment: The BIS/BAS Scales. Journal of Personality and Social Psychology, 67(2), 319–333. https://doi.org/10.1037/0022-3514.67.2.319

Carver, C. S., & White, T. L. (1994b). Behavioral Inhibition, Behavioral Activation, and Affective Responses to Impending Reward and Punishment: The BIS/BAS Scales. In Journal of Personality and Social Psychology (Vol. 67, Issue 2).

Casey, B. J., Cannonier, T., Conley, M. I., Cohen, A. O., Barch, D. M., Heitzeg, M. M., Soules, M. E., Teslovich, T., Dellarco, D. v., Garavan, H., Orr, C. A., Wager, T. D., Banich, M. T., Speer, N. K., Sutherland, M. T., Riedel, M. C., Dick, A. S., Bjork, J. M., Thomas, K. M., ... Dale, A. M. (2018). The Adolescent Brain Cognitive Development (ABCD) study: Imaging acquisition across 21 sites. In Developmental Cognitive Neuroscience (Vol. 32, pp. 43–54). Elsevier Ltd. https://doi.org/10.1016/j.dcn.2018.03.001

Castelhano, M. S., & Henderson, J. M. (2008). Stable individual differences across images in human saccadic eye movements. Canadian Journal of Experimental Psychology/Revue Canadienne de Psychologie Expérimentale, 62(1), 1–14. https://doi.org/10.1037/1196-1961.62.1.1

Celli, M., Mazzonetto, I., Zangrossi, A., Bertoldo, A., Cona, G., & Corbetta, M. (2022). One-year-later spontaneous EEG features predict visual exploratory human phenotypes. Communications Biology, 5(1). https://doi.org/10.1038/s42003-022-04294-9

Cerf, M., Harel, J., Einhäuser, W., & Koch, C. (2007). Predicting human gaze using low-level saliency combined with face detection. Advances in Neural Information Processing Systems, 20. http://www.klab.caltech.edu/

Chang, L., & Tsao, D. Y. (2017). The Code for Facial Identity in the Primate Brain Article The Code for Facial Identity in the Primate Brain. Cell, 169(6), 1013-1020.e14. https://doi.org/10.1016/j.cell.2017.05.011

Charrad, M., Ghazzali, N., Laval, U., & Niknafs, A. (2014). NbClust: An R Package for Determining the Relevant Number of Clusters in a Data Set Véronique Boiteau. In JSS Journal of Statistical (Vol. 61, Issue 6). http://www.jstatsoft.org/

Chiovetto, E., Berret, B., & Pozzo, T. (2010). Tri-dimensional and triphasic muscle organization of whole-body pointing movements. Neuroscience, 170(4), 1223–1238. https://doi.org/10.1016/j.neuroscience.2010.07.006

Chiovetto, E., Curio, C., Endres, D., & Giese, M. (2018). Perceptual integration of kinematic components in the recognition of emotional facial expressions. Journal of Vision, 18(4), 1–19. https://doi.org/10.1167/18.4.13

Chiovetto, E., & Giese, M. A. (2013). Kinematics of the coordination of pointing during locomotion. PLoS ONE, 8(11). https://doi.org/10.1371/journal.pone.0079555

Choe, K. W., Blake, R., & Lee, S.-H. (2016). Pupil size dynamics during fixation impact the accuracy and precision of video-based gaze estimation. Vision Research, 118, 48–59. https://doi.org/10.1016/j.visres.2014.12.018

Christensen, K., Danon, L., Scanlon, T., & Bak, P. (2002). Unified scaling law for earthquakes. Proceedings of the National Academy of Sciences, 99(Supplement 1), 2509–2513. https://doi.org/10.1073/pnas.012581099

Churchland, M. M., & Cunningham, J. P. (2014). A Dynamical Basis Set for Generating Reaches. Cold Spring Harbor Symposia on Quantitative Biology, LXXIX.

Cirilli, L., de Timary, P., Lefèvre, P., & Missal, M. (2011). Individual Differences in Impulsivity Predict Anticipatory Eye Movements. PLoS ONE, 6(10), e26699. https://doi.org/10.1371/journal.pone.0026699

Clauset, A., Shalizi, C. R., & Newman, M. E. J. (2009). Power-Law Distributions in Empirical Data. SIAM Review, 51(4), 661–703. https://doi.org/10.1137/070710111

Clemens, I. A. H., Selen, L. P. J., Pomante, A., MacNeilage, P. R., & Medendorp, W. P. (2017). Eye Movements in Darkness Modulate Self-Motion Perception. Eneuro, 4(1), ENEURO.0211-16.2016. https://doi.org/10.1523/ENEURO.0211-16.2016

Cole, M. W., Bassett, D. S., Power, J. D., Braver, T. S., & Petersen, S. E. (2014). Intrinsic and task-evoked network architectures of the human brain. Neuron, 83(1), 238–251. https://doi.org/10.1016/j.neuron.2014.05.014

Cona, G., Koçillari, L., Palombit, A., Bertoldo, A., Maritan, A., & Corbetta, M. (2019a). Archetypes of human cognition defined by time preference for reward and their brain correlates: An evolutionary trade-off approach. NeuroImage, 185, 322–334. https://doi.org/10.1016/j.neuroimage.2018.10.050

Cona, G., Koçillari, L., Palombit, A., Bertoldo, A., Maritan, A., & Corbetta, M. (2019b). Archetypes of human cognition defined by time preference for reward and their brain correlates: An evolutionary trade-off approach. NeuroImage, 185, 322–334. https://doi.org/10.1016/j.neuroimage.2018.10.050

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. https://doi.org/10.1016/j.neuron.2008.04.017

Corbetta, M., Ramsey, L., Callejas, A., Baldassarre, A., Hacker, C. D., Siegel, J. S., Astafiev, S. v., Rengachary, J., Zinn, K., Lang, C. E., Connor, L. T., Fucetola, R., Strube, M., Carter, A. R., & Shulman, G. L. (2015). Common behavioral clusters and subcortical anatomy in stroke. Neuron, 85(5), 927–941. https://doi.org/10.1016/j.neuron.2015.02.027

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. Nature Reviews. Neuroscience, 3(3), 201–215. https://doi.org/10.1038/nrn755

Costa, P. T., & McCrae, R. R. (1989a). NEO PI/FFI manual supplement for use with the NEO Personality Inventory and the NEO Five-Factor Inventory (FL: Psycho).

Costa, P. T., & McCrae, R. R. (1989b). NEO PI/FFI manual supplement for use with the NEO Personality Inventory and the NEO Five-Factor Inventory. Psychological Assessment Resources.

Cowen, A., Sauter, D., & Tracy, J. L. (2019). Mapping the Passions : Toward a High-Dimensional Taxonomy of Emotional Experience and Expression. https://doi.org/10.1177/1529100619850176

Cristino, F., Mathôt, S., Theeuwes, J., & Gilchrist, I. D. (2010). ScanMatch: A novel method for comparing fixation sequences. Behavior Research Methods, 42(3), 692–700. https://doi.org/10.3758/BRM.42.3.692

de Haas, B., Iakovidis, A. L., Schwarzkopf, D. S., & Gegenfurtner, K. R. (2019). Individual differences in visual salience vary along semantic dimensions. Proceedings of the National Academy of Sciences, 201820553. https://doi.org/10.1073/pnas.1820553116

Degani, A. M., & Latash, Æ. M. L. (2008). Flexible muscle modes and synergies in challenging whole-body tasks. 171–187. https://doi.org/10.1007/s00221-008-1413-x

Delorme, A., & Makeig, S. (2004). EEGLAB : an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. Journal of Neuroscience Methods, 134(1), 9–21. https://doi.org/10.1016/j.jneumeth.2003.10.009

Duffau, H. (2012). The " frontal syndrome" revisited: Lessons from electrostimulation mapping studies. In Cortex (Vol. 48, Issue 1, pp. 120–131). https://doi.org/10.1016/j.cortex.2011.04.029

Einhäuser, W., & Koch, C. (2008). Task-demands can immediately reverse the effects of sensory-driven saliency in complex visual stimuli. 8, 1–19. https://doi.org/10.1167/8.2.2.Introduction

Ekman, P., & Friesen, W. v. (1986). A New Pan-Cultural Facial Expression of Emotion 1 (Vol. 10, Issue 2).

Ekman, P., & Friesen, W. V. (1978). The facial action coding system. Environmental Psychology & Nonverbal Behavior.

Elazary, L., & Itti, L. (2008). Interesting objects are visually salient. Journal of Vision, 8(3), 3.1-15. https://doi.org/10.1167/8.3.3

Engbert, R., & Kliegl, R. (2003a). Microsaccades uncover the orientation of covert attention. Vision Research, 43(9), 1035–1045. https://doi.org/10.1016/S0042-6989(03)00084-1

Engbert, R., & Kliegl, R. (2003b). Microsaccades uncover the orientation of covert attention. Vision Research, 43(9), 1035–1045.

Engel, A. K., & Fries, P. (2010). Beta-band oscillations-signalling the status quo? Current Opinion in Neurobiology, 20(2), 156–165. https://doi.org/10.1016/j.conb.2010.02.015

Felician, O., & Barbeau, E. J. (2011). Visual Recognition Memory : A Double Anatomo-Functional Dissociation. Hippocampus, , 21(9), 929–934. https://doi.org/10.1002/hipo.20848

Filin, V. A., Sidorov, S. P., Ananin, V. F., & Zagorodnikova, T. N. (1973). INDIVIDUAL DIFFERENCES IN MICROMOVEMENTS OF EYES DURING FIXATION OF A POINT. Zhurnal Vysshei Nervnoi Deyatelnosti Imeni IP Pavlova, 23(5), 995–1002.

Floyd, R. G., Shands, E. I., Rafael, F. A., Bergeron, R., & McGrew, K. S. (2009). The dependability of general-factor loadings: The effects of factor-extraction methods, test battery composition, test battery size, and their interactions. Intelligence, 37(5), 453–465. https://doi.org/10.1016/j.intell.2009.05.003

Fodor, J. A. (1983). THE MODULARITY OF MIND. MIT press.

Fonseca, L. C., Tedrus, G. M. A. S., Bianchini, M. C., & Silva, T. F. (2013). Electroencephalographic alpha reactivity on opening the eyes in children with attention-deficit hyperactivity disorder. Clinical EEG and Neuroscience, 44(1), 53–57. https://doi.org/10.1177/1550059412445659

Foulsham, T., & Underwood, G. (2008). What can saliency models predict about eye movements? Spatial and sequential aspects of fixations during encoding and recognition. Journal of Vision, 8(2), 6. https://doi.org/10.1167/8.2.6

Fraser, K. C., Lundholm Fors, K., Kokkinakis, D., & Nordlund, A. (2017). An analysis of eye-movements during reading for the detection of mild cognitive impairment. Proceedings of the 2017 Conference on Empirical Methods in Natural Language Processing, 1016–1026. https://doi.org/10.18653/v1/D17-1107

Gabaix, X. (2016). Power Laws in Economics: An Introduction. Journal of Economic Perspectives, 30(1), 185–206. https://doi.org/10.1257/jep.30.1.185

Gaetz, W., MacDonald, M., Cheyne, D., & Snead, O. C. (2010). Neuromagnetic imaging of movement-related cortical oscillations in children and adults: Age predicts post-movement beta rebound. NeuroImage, 51(2), 792–807. https://doi.org/10.1016/j.neuroimage.2010.01.077

Gall, F. J. (1818). Anatomie et physiologie du système nerveux en gènèral, et du cerveau en particulier, avec des observations sur la possibilité de reconnaître plusieurs dispositions intellectuelles et morales de l'homme et des animaux par la configuration de leur têtes.

Gallagher, T., Bjorness, T., Greene, R., You, Y.-J., & Avery, L. (2013). The Geometry of Locomotive Behavioral States in C. elegans. PLoS ONE, 8(3), e59865. https://doi.org/10.1371/journal.pone.0059865

GBVS. (n.d.). Retrieved January 8, 2023, from https://github.com/Pinoshino/gbvs

Geissler, J., Romanos, M., & Hegerl, U. (2014). Hyperactivity and sensation seeking as autoregulatory attempts to stabilize brain arousal in ADHD and mania? ADHD Attention Deficit and Hyperactivity Disorders, 6(3), 159–173. https://doi.org/10.1007/s12402-014-0144-z

Gomez-Marin, A., Paton, J. J., Kampff, A. R., Costa, R. M., & Mainen, Z. F. (2014). Big behavioral data: Psychology, ethology and the foundations of neuroscience. Nature Neuroscience, 17(11), 1455–1462. https://doi.org/10.1038/nn.3812

Gooding, D. C., Mohapatra, L., & Shea, H. B. (2004). Temporal stability of saccadic task performance in schizophrenia and bipolar patients. Psychological Medicine, 34(5), 921–932. https://doi.org/10.1017/S003329170300165X

Gracco, V. (1994). Some Organizational Characteristics of Speech Movement Control. In Haskins Laboratories Status Report on Speech Research (Vol. 113).*

Grandy, T. H., Werkle-bergner, M., Chicherio, C., & Schmiedek, F. (2013). Peak individual alpha frequency qualifies as a stable neurophysiological trait marker in healthy younger and older adults. Psychophysiology, 50(6), 570–582. https://doi.org/10.1111/psyp.12043

Gratton, C., Laumann, T. O., Nielsen, A. N., Schlaggar, B. L., Dosenbach, N. U. F., Petersen, S. E., Gratton, C., Laumann, T. O., Nielsen, A. N., Greene, D. J., & Gordon, E. M. (2018). Functional Brain Networks Are Dominated by Stable Group and Individual Factors , Not Cognitive or Daily Article Functional Brain Networks Are Dominated by Stable Group and Individual Factors , Not Cognitive or Daily Variation. 439–452. https://doi.org/10.1016/j.neuron.2018.03.035

Haegens, S., & Ha, B. F. (2011). Top-Down Controlled Alpha Band Activity in Somatosensory Areas Determines Behavioral Performance in a Discrimination Task. Journal of Neuroscience, 31(14), 5197–5204. https://doi.org/10.1523/JNEUROSCI.5199-10.2011

Hannula, D. E., Ryan, J. D., Tranel, D., & Cohen, N. J. (2007). Rapid Onset Relational Memory Effects Are Evident in Eye Movement Behavior, but Not in Hippocampal Amnesia. Journal of Cognitive Neuroscience, 19(10), 1690–1705. http://direct.mit.edu/jocn/article-pdf/19/10/1690/1936059/jocn.2007.19.10.1690.pdf?casa_token=Shjara0r-psAAAAA:HroJ2AoVuO3Wg_auZb2ncTxDj-Y5vfN35161x-d6gxWnAL7eO44uvIVbbo85Sqpp0mMFJNGxQA

Hardstone, R., Poil, S., Schiavone, G., Jansen, R., Nikulin, V. v, Mansvelder, H. D., & Linkenkaer-hansen, K. (2012). Detrended fluctuation analysis : a scale-free view on neuronal oscillations. Frontiers in Physiology, 3(November), 1–13. https://doi.org/10.3389/fphys.2012.00450

Harel, J., Koch, C., & Perona, P. (2006). Graph-Based Visual Saliency.

He, B. J. (2014). Scale-free brain activity: past, present, and future. Trends in Cognitive Sciences, 18(9), 480–487. https://doi.org/10.1016/j.tics.2014.04.003

He, B. J., Zempel, J. M., Snyder, A. Z., & Raichle, M. E. (2010). The Temporal Structures and Functional Significance of Scale-free Brain Activity. Neuron, 66(3), 353–369. https://doi.org/10.1016/j.neuron.2010.04.020

Hebart, M. N., Zheng, C. Y., Pereira, F., & Baker, C. I. (2020a). Revealing the multidimensional mental representations of natural objects underlying human similarity judgements. Nature Human Behaviour, 4(November). https://doi.org/10.1038/s41562-020-00951-3

Hebart, M. N., Zheng, C. Y., Pereira, F., & Baker, C. I. (2020b). Revealing the multidimensional mental representations of natural objects underlying human similarity judgements. Nature Human Behaviour, 4(November). https://doi.org/10.1038/s41562-020-00951-3

Hebb, D. (1949). The Organization of Behavior.

Henderson, J. M., Choi, W., Luke, S. G., & Desai, R. H. (2015). Neural correlates of fixation duration in natural reading: Evidence from fixation-related fMRI. NeuroImage, 119, 390–397. https://doi.org/10.1016/j.neuroimage.2015.06.072

Hilt, P. M., Berret, B., Papaxanthis, C., Stapley, P. J., & Pozzo, T. (2016). Evidence for subjective values guiding posture and movement coordination in a free-endpoint whole-body reaching task. Scientific Reports, 6, 1–13. https://doi.org/10.1038/srep23868

Honey, C. J., Sporns, O., Cammoun, L., Gigandet, X., Thiran, J. P., Meuli, R., & Hagmann, P. (2009). Predicting human resting-state functional connectivity. Proceedings of the National Academy of Sciences, 106(6), 2035–2040.

hopkins. (n.d.). Retrieved January 8, 2023, from https://kwstat.github.io/hopkins/

Hopkins, B., & Skellam, J. G. (1954). A new method for determining the type of distribution of plant individuals. Annals of Botany, 18(2), 213–227.

Hoppe, S., Loetscher, T., Morey, S. A., & Bulling, A. (2018). Eye Movements During Everyday Behavior Predict Personality Traits. Frontiers in Human Neuroscience, 12. https://doi.org/10.3389/fnhum.2018.00105

Huang, L., Mo, L., & Li, Y. (2012). Measuring the interrelations among multiple paradigms of visual attention: An individual differences approach. Journal of Experimental Psychology: Human Perception and Performance, 38(2), 414–428. https://doi.org/10.1037/a0026314

Hwang, K., Ghuman, A. S., Manoach, D. S., Jones, S. R., & Luna, B. (2014). Cortical neurodynamics of inhibitory control. Journal of Neuroscience, 34(29), 9551–9561. https://doi.org/10.1523/JNEUROSCI.4889-13.2014

Ingram, J. N., Körding, K. P., Howard, I. S., & Wolpert, D. M. (2008). The statistics of natural hand movements. Experimental Brain Research, 188(2), 223–236. https://doi.org/10.1007/s00221-008-1355-3

Isaacowitz, D. M. (2005). The Gaze of the Optimist. Personality and Social Psychology Bulletin, 31(3), 407–415. https://doi.org/10.1177/0146167204271599

It, J. C. B., Hurry, S., & Thorley, W. (1984). Typicality and familiarity of faces. Memory & Cognition, 12(3), 219–228.

Itti, L. (2005). Quantifying the contribution of low-level saliency to human eye movements in dynamic scenes. Visual Cognition, 12(6), 1093–1123. https://doi.org/10.1080/13506280444000661

Itti, L., Koch, C., & Niebur, E. (1998a). A Model of Saliency-Based Visual Attention for Rapid Scene Analysis. IEEE Transactions on Pattern Analysis and Machine Intelligence, 20(11), 1254–1259. https://doi.org/10.1177/003591577707001019

Itti, L., Koch, C., & Niebur, E. (1998b). A Model of Saliency-Based Visual Attention for Rapid Scene Analysis. IEEE Trans. Pattern Anal. Mach. Intell., 1254–1259, 1254–1259.

Ivanenko, Y. P., Poppele, R. E., & Lacquaniti, F. (2004). Five basic muscle activation patterns account for muscle activity during human locomotion. 1, 267–282. https://doi.org/10.1113/jphysiol.2003.057174

Jensen, A. R. (1993). Spearman's g: Links Between Psychometrics and Biology. Annals of the New York Academy of Sciences, 702(1), 103–129. https://doi.org/10.1111/j.1749-6632.1993.tb17244.x

Johansson, R., Holsanova, J., Dewhurst, R., & Holmqvist, K. (2012). Eye movements during scene recollection have a functional role, but they are not reinstatements of those produced during encoding. Journal of Experimental Psychology: Human Perception and Performance, 38(5), 1289–1314. https://doi.org/10.1037/a0026585

Johansson, R., & Johansson, M. (2014). Look Here, Eye Movements Play a Functional Role in Memory Retrieval. Psychological Science, 25(1), 236–242. https://doi.org/10.1177/0956797613498260

Johnston, S. J., & Leek, E. C. (2008). Fixation Region Overlap : A quantitative method for the analysis of fixational eye movement patterns. Journal of Eye Movement Research, 1(1), 1–2. https://doi.org/10.16910/jemr.1.3.5

Joshi, S., Li, Y., Kalwani, R. M., & Gold, J. I. (2016). Relationships between Pupil Diameter and Neuronal Activity in the Locus Coeruleus, Colliculi, and Cingulate Cortex. Neuron, 89(1), 221–234. https://doi.org/10.1016/j.neuron.2015.11.028

Just, M. A., & Carpenter, P. A. (1980). A theory of reading: From eye fixations to comprehension. Psychological Review, 87(4), 329–354. https://doi.org/10.1037/0033-295X.87.4.329

Kaiser, H. F. (1960). The Application of Electronic Computers to Factor Analysis. Educational and Psychological Measurement, 20(1), 141–151. https://doi.org/10.1177/001316446002000116

Katsini, C., Fidas, C., Belk, M., Avouris, N., & Samaras, G. (2017). Influences of Users' Cognitive Strategies on Graphical Password Composition. Proceedings of the 2017 CHI Conference Extended Abstracts on Human Factors in Computing Systems - CHI EA '17, 2698–2705. https://doi.org/10.1145/3027063.3053217

Kennedy, D. P., D'Onofrio, B. M., Quinn, P. D., Bölte, S., Lichtenstein, P., & Falck-Ytter, T. (2017a). Genetic Influence on Eye Movements to Complex Scenes at Short Timescales. Current Biology. https://doi.org/10.1016/j.cub.2017.10.007

Kennedy, D. P., D'Onofrio, B. M., Quinn, P. D., Bölte, S., Lichtenstein, P., & Falck-Ytter, T. (2017b). Genetic Influence on Eye Movements to Complex Scenes at Short Timescales. Current Biology, 27(22), 3554-3560.e3. https://doi.org/10.1016/j.cub.2017.10.007

Kirton, M. (1976). Adaptors and Innovators: A Description and Measure. In Journal of Applied Psychology (Vol. 61, Issue 5).

Klimesch, W., Sauseng, P., & Gerloff, C. (2003). Enhancing cognitive performance with repetitive transcranial magnetic stimulation at human individual alpha frequency. European Journal of Neuroscience, 17(5), 1129–1133. https://doi.org/10.1046/j.1460-9568.2003.02517.x

Klimesch, W., Sauseng, P., & Hanslmayr, S. (2006). EEG alpha oscillations : The

inhibition – timing hypothesis. Brain Research Reviews, 53(1), 63–88. https://doi.org/10.1016/j.brainresrev.2006.06.003

Knox, P. C., & Wolohan, F. D. A. (2015). Temporal stability and the effects of training on saccade latency in "express saccade makers." PLoS ONE, 10(3), 1–16. https://doi.org/10.1371/journal.pone.0120437

Koch, S. P., Koendgen, S., Bourayou, R., Steinbrink, J., & Obrig, H. (2008). Individual alpha-frequency correlates with amplitude of visual evoked potential and hemodynamic response. Neuroimage, 41(2), 233–242. https://doi.org/10.1016/j.neuroimage.2008.02.018

Koehler, K., Guo, F., Zhang, S., & Eckstein, M. P. (2014). What do saliency models predict? Journal of Vision, 14(3), 14–14. https://doi.org/10.1167/14.3.14

Konkle, T., & Alvarez, G. A. (2022). A self-supervised domain-general learning framework for human ventral stream representation. Nature Communications, 13(1), 1–12. https://doi.org/10.1038/s41467-022-28091-4

Kozhevnikov, M. (2007). Cognitive Styles in the Context of Modern Psychology: Toward an Integrated Framework of Cognitive Style. Psychological Bulletin, 133(3), 464–481. https://doi.org/10.1037/0033-2909.133.3.464

Krauzlis, R. J. (2005). The control of voluntary eye movements: new perspectives. The Neuroscientist : A Review Journal Bringing Neurobiology, Neurology and Psychiatry, 11(2), 124–137. https://doi.org/10.1177/1073858404271196

Krauzlis, R. J., Bollimunta, A., Arcizet, F., & Wang, L. (2014). Attention as an effect not a cause. Trends in Cognitive Sciences, 18(9), 457–464. https://doi.org/10.1016/j.tics.2014.05.008

Krauzlis, R. J., Goffart, L., & Hafed, Z. M. (2017). Neuronal control of fixation and fixational eye movements. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 372(1718). https://doi.org/10.1098/rstb.2016.0205

Krejtz, K., Duchowski, A. T., Niedzielska, A., Biele, C., & Krejtz, I. (2018). Eye tracking cognitive load using pupil diameter and microsaccades with fixed gaze. PLOS ONE, 13(9), e0203629. https://doi.org/10.1371/journal.pone.0203629

Kümmerer, M., Wallis, T. S. A., & Bethge, M. (2015a). Information-theoretic model comparison unifies saliency metrics. Proceedings of the National Academy of Sciences of the United States of America, 112(52), 16054–16059. https://doi.org/10.1073/pnas.1510393112

Kümmerer, M., Wallis, T. S. A., & Bethge, M. (2015b). Information-theoretic model comparison unifies saliency metrics. Proceedings of the National Academy of Sciences, 112(52), 16054–16059. https://doi.org/10.1073/pnas.1510393112

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest Package: Tests in Linear Mixed Effects Models. Journal of Statistical Software, 82(13), 1–26. https://doi.org/10.18637/JSS.V082.I13

Larsen, R. J. , & Diener, E. (1992). Promises and problems with the circumplex model of emotion. In M. S. Clark (Ed.), Emotion (pp. 25–29). Sage Publications, Inc.

Laufs, H., Krakow, K., Sterzer, P., Eger, E., Beyerle, A., & Kleinschmidt, A. (2003). Electroencephalographic signatures of attentional and cognitive default modes in spontaneous brain activity fluctuations at rest. Proceeding of the National Academy of Sciences, 100(19), 11053–11058.

Lee, H., & Chen, J. (2022). Predicting memory from the network structure of naturalistic events. Nature Communications, 13(1). https://doi.org/10.1038/s41467-022-31965-2

Lemaitre, A. L., Herbet, G., Duffau, H., & Lafargue, G. (2018). Preserved metacognitive ability despite unilateral or bilateral anterior prefrontal resection. Brain and Cognition, 120, 48–57. https://doi.org/10.1016/j.bandc.2017.10.004

Leo, A., Handjaras, G., Bianchi, M., Marino, H., Gabiccini, M., Guidi, A., Scilingo, E. P., Pietrini, P., Bicchi, A., Santello, M., & Ricciardi, E. (2016). A synergy-based hand control is encoded in human motor cortical areas. ELife, 5(FEBRUARY2016), 1–32. https://doi.org/10.7554/eLife.13420

Lettieri, G., Handjaras, G., Ricciardi, E., Leo, A., Papale, P., Betta, M., ... & Cecchetti, L. (2019). Emotionotopy in the human right temporo-parietal cortex. Nature communications, 10(1), 5568

Liang, J., Moshel, S., Zivotofsky, A. Z., Caspi, A., Engbert, R., Kliegl, R., & Havlin, S. (2005). Scaling of horizontal and vertical fixational eye movements. Physical Review E, 71(3), 1–6. https://doi.org/10.1103/PhysRevE.71.031909

Liégeois, R., Li, J., Kong, R., Orban, C., van de Ville, D., Ge, T., Sabuncu, M. R., & Yeo, B. T. T. (2019). Resting brain dynamics at different timescales capture distinct aspects of human behavior. Nature Communications, 10(1), 1–9. https://doi.org/10.1038/s41467-019-10317-7

Linkenkaer-Hansen, K., Nikouline, V. v, Matias Palva, J., & Ilmoniemi, R. J. (2001). Long-Range Temporal Correlations and Scaling Behavior in Human Brain Oscillations. Journal of Neuroscience, 21(4), 1370–1377. http://paos.colorado.edu/research/wavelets

Linkenkaer-Hansen, K., Nikouline, V. V., Palva, J. M., & Ilmoniemi, R. J. (2001). Long-Range Temporal Correlations and Scaling Behavior in Human Brain Oscillations. The Journal of Neuroscience, 21(4), 1370–1377. https://doi.org/10.1523/JNEUROSCI.21-04-01370.2001

Lovibond, P. F., & Lovibond, S. H. (1995a). THE STRUCTURE OF NEGATIVE EMOTIONAL STATES: COMPARISON OF THE DEPRESSION ANXIETY STRESS SCALES (DASS) WITH THE BECK DEPRESSION AND ANXIETY INVENTORIES. In BehaP. Res. Ther (Vol. 33, Issue 3).

Lovibond, P. F., & Lovibond, S. H. (1995b). The structure of negative emotional states: comparison of the Depression Anxiety Stress Scales (DASS) with the Beck Depression and Anxiety Inventories. Behaviour Research and Therapy, 33(3), 335–343.

Luque, J., Luque, B., & Lacasa, L. (2015a). Scaling and universality in the human voice. 1–6.

Luque, J., Luque, B., & Lacasa, L. (2015b). Scaling and universality in the human voice. 1–6.

MacLean, M. H., Arnell, K. M., & Cote, K. A. (2012). Resting EEG in alpha and beta bands predicts individual differences in attentional blink magnitude. Brain and Cognition, 78(3), 218–229. https://doi.org/10.1016/j.bandc.2011.12.010

Mahjoory, K., Cesnaite, E., Hohlefeld, F. U., Villringer, A., & Nikulin, V. v. (2019). Power and temporal dynamics of alpha oscillations at rest differentiate cognitive performance involving sustained and phasic cognitive control. NeuroImage, 188(November 2018), 135–144. https://doi.org/10.1016/j.neuroimage.2018.12.001

Marie, P. (1906). Troisieme Circonvolution.

Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. Journal of Neuroscience Methods, 164(1), 177–190. https://doi.org/10.1016/j.jneumeth.2007.03.024

Marks, D. F. (1973). Visual imagery differences in the recall of pictures. British Journal of Psychology, 64(1), 17–24. https://doi.org/10.1111/j.2044-8295.1973.tb01322.x

Maselli, A., Dhawan, A., Russo, M., Cesqui, B., Lacquaniti, F., & Andrea D'avella, X. (2019). A whole body characterization of individual strategies, gender differences, and common styles in overarm throwing. J Neu-Rophysiol, 122, 2486–2503. https://doi.org/10.1152/jn.00011.2019.-Overarm

McCrae, R. R., & Costa, P. T. (1987). Validation of the five-factor model of personality across instruments and observers. Journal of Personality and Social Psychology, 52(1), 81–90.

Mercer Moss, F. J., Baddeley, R., & Canagarajah, N. (2012). Eye Movements to Natural Images as a Function of Sex and Personality. PLoS ONE, 7(11), e47870. https://doi.org/10.1371/journal.pone.0047870

Meyhöfer, I., Bertsch, K., Esser, M., & Ettinger, U. (2016). Variance in saccadic eye movements reflects stable traits. Psychophysiology, 53(4), 566–578. https://doi.org/10.1111/psyp.12592

Michelini, G., Barch, D. M., Tian, Y., Watson, D., Klein, D. N., & Kotov, R. (2019). Delineating and validating higher-order dimensions of psychopathology in the Adolescent Brain Cognitive Development (ABCD) study. Translational Psychiatry, 9(1). https://doi.org/10.1038/s41398-019-0593-4

Monaco, M., Costa, A., Caltagirone, C., & Carlesimo, G. A. (2013a). Forward and backward span for verbal and visuo-spatial data: Standardization and normative data from an Italian adult population. Neurological Sciences, 34(5), 749–754. https://doi.org/10.1007/s10072-012-1130-x

Monaco, M., Costa, A., Caltagirone, C., & Carlesimo, G. A. (2013b). Forward and backward span for verbal and visuo-spatial data: standardization and normative data from an Italian adult population. Neurological Sciences, 34(5), 749–754. https://doi.org/10.1007/s10072-012-1130-x

Montez, T., Poil, S., Jones, B. F., Manshanden, I., Verbunt, J. P. A., Dijk, B. W. van, Brussaard, A. B., Ooyen, A. van, Stam, C. J., Scheltens, P., & Linkenkaer-hansen, K. (2009). Altered temporal correlations in parietal alpha and prefrontal theta oscillations in early-stage Alzheimer disease. Proceedings of the National Academy of Sciences, 106(5), 1614–1619.

Moretti, D. v, Babiloni, C., Binetti, G., Cassetta, E., Dal, G., Ferreric, F., Ferri, R., Lanuzza, B., Miniussi, C., Nobili, F., Rodriguez, G., Salinari, S., & Rossini, P. M. (2004). Individual analysis of EEG frequency and band power in mild Alzheimer ' s disease. Clinical Neurophysiology, 115(2), 299–308. https://doi.org/10.1016/S1388-2457(03)00345-6

Mullen, T. R., Kothe, C. A. E., Chi, Y. M., Ojeda, A., Kerth, T., Makeig, S., Jung, T., & Cauwenberghs, G. (2015). Real-Time Neuroimaging and Cognitive Monitoring Using Wearable Dry EEG. IEEE Transactions on Biomedical Engineering, 62(11), 2553–2567.

Munoz, D. P., Armstrong, I. T., Hampton, K. A., & Moore, K. D. (2003). Altered Control of Visual Fixation and Saccadic Eye Movements in Attention-Deficit Hyperactivity Disorder. Journal of Neurophysiology, 90(1), 503–514. https://doi.org/10.1152/jn.00192.2003

Northoff, G., Qin, P., & Nakao, T. (2010). Rest-stimulus interaction in the brain : a review. Trends in Neurosciences, 33(6), 277–284. https://doi.org/10.1016/j.tins.2010.02.006

O'Keefe, J., & Dostrovsky, J. (1971). The hippocampus as a spatial map: Preliminary evidence from unit activity in the freely-moving rat. . Brain Research.

Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. (2011). FieldTrip : Open Source Software for Advanced Analysis of MEG , EEG , and Invasive Electrophysiological Data. Computational Intelligence and Neuroscience. https://doi.org/10.1155/2011/156869

Palva, J. M., Zhigalov, A., Hirvonen, J., Korhonen, O., & Linkenkaer-hansen, K. (2013). Neuronal long-range temporal correlations and avalanche dynamics are correlated with behavioral scaling laws. Proceedings of the National Academy of Sciences, 110(9), 3585–3590. https://doi.org/10.1073/pnas.1216855110

Palva, J. M., Zhigalov, A., Hirvonen, J., Korhonen, O., Linkenkaer-Hansen, K., & Palva, S. (2013a). Neuronal long-range temporal correlations and avalanche dynamics are correlated with behavioral scaling laws. Proceedings of the National Academy of Sciences of the United States of America, 110(9), 3585–3590. https://doi.org/10.1073/pnas.1216855110

Palva, J. M., Zhigalov, A., Hirvonen, J., Korhonen, O., Linkenkaer-Hansen, K., & Palva, S. (2013b). Neuronal long-range temporal correlations and avalanche dynamics are correlated with behavioral scaling laws. Proceedings of the National Academy of Sciences, 110(9), 3585–3590. https://doi.org/10.1073/pnas.1216855110

Pang, R., Lansdell, B. J., & Fairhall, A. L. (2016). Dimensionality reduction in neuroscience. Current Biology, 26(14), 656–660. https://doi.org/10.1016/j.cub.2016.05.029

Papale, P. (2018). Global time-size distribution of volcanic eruptions on Earth. Scientific Reports, 8(1), 6838. https://doi.org/10.1038/s41598-018-25286-y

Pappalardo, L., Simini, F., Rinzivillo, S., Pedreschi, D., & Giannotti, F. (2015). Returners and explorers dichotomy in human mobility. 6(1), 1–8. https://doi.org/10.1038/ncomms9166

Pappalardo, L., Simini, F., Rinzivillo, S., Pedreschi, D., Giannotti, F., & Barabási, A.-L. (2015). Returners and explorers dichotomy in human mobility. Nature Communications, 6(1), 8166. https://doi.org/10.1038/ncomms9166

Parkhurst, D., Law, K., & Niebur, E. (2002). Modeling the role of salience in the allocation of overt visual attention. Vision Research, 42(1), 107–123. https://doi.org/10.1016/s0042-6989(01)00250-4

Peng, C. K., Buldryrev, S. V., Havlin, S., Simons, M., Stanley, H. E., & Goldberger, A. L. (1994). Mosaic organization of DNA nucleotides. Physical Review E, 49(2), 1685–1689.

Perrin, F., Pernier, J., Bertrand, O., & Echallier, J. F. (1989). Spherical Splines for Scalp Potential and Current Density Mapping. Electroencephalography Clinical Neurophysiology, 72, 184–187.

Pezzulo, G., Zorzi, M., & Corbetta, M. (2021a). The secrect life of predictive brains : what's spontaneous activity for? PsyArxiv, 1–18.

Pezzulo, G., Zorzi, M., & Corbetta, M. (2021b). The secret life of predictive brains: what's spontaneous activity for? Trends in Cognitive Sciences, 25(9), 730–743. https://doi.org/10.1016/j.tics.2021.05.007

Pfurtscheller, G., & Lopes, F. H. (1999). Event-related EEG / MEG synchronization and desynchronization : basic principles. Clinical Neurophysiology, 110, 1842–1857.

Philippi, C. L., Mehta, S., Grabowski, T., Adolphs, R., & Rudrauf, D. (2009). Damage to association fiber tracts impairs recognition of the facial expression of emotion. Journal of Neuroscience, 29(48), 15089–15099. https://doi.org/10.1523/JNEUROSCI.0796-09.2009

Pion-tonachini, L., Kreutz-delgado, K., & Makeig, S. (2019). ICLabel: An automated electroencephalographic independent component classifier, dataset and website. NeuroImage, 198, 181–197. https://doi.org/10.1016/j.neuroimage.2019.05.026.ICLabel

Pitchford, B., & Arnell, K. M. (2019). Resting EEG in alpha and beta bands predicts individual differences in attentional breadth. Consciousness and Cognition, 75(July), 102803. https://doi.org/10.1016/j.concog.2019.102803

Plenz, D., & Thiagarajan, T. C. (2007a). The organizing principles of neuronal avalanches: cell assemblies in the cortex? Trends in Neurosciences, 30(3), 101–110. https://doi.org/10.1016/j.tins.2007.01.005

Plenz, D., & Thiagarajan, T. C. (2007b). The organizing principles of neuronal avalanches: cell assemblies in the cortex? In Trends in Neurosciences (Vol. 30, Issue 3, pp. 101–110). https://doi.org/10.1016/j.tins.2007.01.005

Poil, S., Hardstone, R., Mansvelder, H. D., & Linkenkaer-hansen, K. (2012). Critical-State Dynamics of Avalanches and Oscillations Jointly Emerge from Balanced Excitation / Inhibition in Neuronal Networks. Journal of Neuroscience, 32(29), 9817–9823. https://doi.org/10.1523/JNEUROSCI.5990-11.2012

Popov, T., Miller, G. A., Rockstroh, B., & Jensen, O. (2021). Alpha oscillations link action to cognition : An oculomotor account of the brain ' s dominant rhythm. ArXiv.

Poynter, W., Barber, M., Inman, J., & Wiggins, C. (2013a). Individuals exhibit idiosyncratic eye-movement behavior profiles across tasks. Vision Research, 89, 32–38. https://doi.org/10.1016/j.visres.2013.07.002

Poynter, W., Barber, M., Inman, J., & Wiggins, C. (2013b). Individuals exhibit idiosyncratic eye-movement behavior profiles across tasks. Vision Research, 89, 32–38. https://doi.org/10.1016/j.visres.2013.07.002

Poynter, W., Barber, M., Inman, J., & Wiggins, C. (2013c). Individuals exhibit idiosyncratic eye-movement behavior profiles across tasks. Vision Research, 89, 32–38. https://doi.org/10.1016/j.visres.2013.07.002

Privitera, C. M., & Stark, L. W. (2000). Algorithms for defining visual regions-of-interest: comparison with eye fixations. IEEE Transactions on Pattern Analysis and Machine Intelligence, 22(9), 970–982. https://doi.org/10.1109/34.877520

Raichle, M. E. (2011). The Restless Brain. Brain Connectivity, 1(1), 3–12. https://doi.org/10.1089/brain.2011.0019

Rajagovindan, R., & Ding, M. (2011). From Prestimulus Alpha Oscillation to Visual-evoked Response : An Inverted-U Function and Its Attentional Modulation. Journal of Cognitive Neuroscience, 23(6), 1379–1394.

Ramos-Fernández, G., Mateos, J. L., Miramontes, O., Cocho, G., Larralde, H., & Ayala-Orozco, B. (2004). Lévy walk patterns in the foraging movements of spider monkeys (Ateles geoffroyi). Behavioral Ecology and Sociobiology, 55(3), 223–230.

Ramsay, J. O., Munhall, K. G., & Gracco, V. L. (2017). Functional data analyses of lip motion. 3718(1996). https://doi.org/10.1121/1.414986

Rauthmann, J. F., Seubert, C. T., Sachse, P., & Furtner, M. R. (2012). Eyes as windows to the soul: Gazing behavior is related to personality. Journal of Research in Personality, 46(2), 147–156. https://doi.org/10.1016/j.jrp.2011.12.010

Ray, W. J., & Cole, H. W. (1985). EEG Alpha Activity Reflects Attentional Demands , and Beta Activity Reflects Emotional and Cognitive Processes. Science, 1, 750–752.

Rayner, K., Li, X., Williams, C. C., Cave, K. R., & Well, A. D. (2007). Eye movements during information processing tasks: Individual differences and cultural effects. Vision Research, 47(21), 2714–2726. https://doi.org/10.1016/j.visres.2007.05.007

Reed, T. E. (1988). A neurophysiological basis for the heritability of vertebrate intelligence. In Intelligence and evolutionary biology (pp. 429–436).

Rey, A., & Osterrieth, P. A. (1993). Translations of excerpts from Andre Rey"s Psychological examination of traumatic encephalopathy and P. A. Osterrieth"s The Complex Figure Copy Test. Clinical Neuropsychologist, 7(1), 4–21.

Rhodes, T., Kello, C. T., & Kerster, B. (2014). Intrinsic and extrinsic contributions to heavy tails in visual foraging. Visual Cognition, 22(6), 809–842. https://doi.org/10.1080/13506285.2014.918070

Risko, E. F., & Kingstone, A. (2011). Eyes wide shut: implied social presence, eye tracking and attention. Attention, Perception, & Psychophysics, 73(2), 291–296. https://doi.org/10.3758/s13414-010-0042-1

Rousseeuw, P. J. (1987). Silhouettes: A graphical aid to the interpretation and validation of cluster analysis. Journal of Computational and Applied Mathematics, 20, 53–65. https://doi.org/10.1016/0377-0427(87)90125-7

Roy-Byrne, P., Radant, A., Wingerson, D., & & Cowley, D. S. (1995). Human oculomotor function: reliability and diurnal variation. Biological Psychiatry, 38(2), 92–97.

Rucci, M., Ahissar, E., & Burr, D. (2018). Temporal Coding of Visual Space. Trends in Cognitive Sciences, 22(10), 883–895. https://doi.org/10.1016/j.tics.2018.07.009

Russell, J. A., & Barrett, L. F. (1999). Core Affect , Prototypical Emotional Episodes , and Other Things Called Emotion : Dissecting the Elephant. 76(5).

Ryan, J. D., Wynn, J. S., Shen, K., Liu, Z., Ryan, J. D., Wynn, J. S., Shen, K., & Aging, Z. L. (2022). Aging changes the interactions between the oculomotor and memory systems ABSTRACT. Aging, Neuropsychology, and Cognition, 29(3), 418–442. https://doi.org/10.1080/13825585.2021.2007841

Sanger, T. D. (2000). Human arm movements described by a low-dimensional superposition of principal components. Journal of Neuroscience, 20(3), 1066–1072. https://doi.org/10.1523/jneurosci.20-03-01066.2000

Santello, M., Bianchi, M., Gabiccini, M., Ricciardi, E., Salvietti, G., Prattichizzo, D., ... & Bicchi, A. (2016). Hand synergies: Integration of robotics and neuroscience for understanding the control of biological and artificial hands. Physics of life reviews, 17, 1-23.

Schabus, M., Doppelmayr, M., Klimesch, W., Gruber, W., & Sauseng, P. (2004). Phase-locked alpha and theta oscillations generate the P1 – N1 complex and are related to memory performance. Cognitive Brain Research, 19(3), 302–316. https://doi.org/10.1016/j.cogbrainres.2003.11.016

Schafer, E. W. (1985). Neural adaptability: A biological determinant of g factor intelligence. Behavioral and Brain Sciences, 8(2), 240–241.

Schartner, M., Seth, A., Noirhomme, Q., Boly, M., Bruno, A., Laureys, S., & Barrett, A. (2015). Complexity of Multi-Dimensional Spontaneous EEG Decreases during Propofol Induced General Anaesthesia. PloS One, 10(8), 1–21. https://doi.org/10.1371/journal.pone.0133532

Scoviille, W. B., & Milner, B. (1957). LOSS OF RECENT MEMORY AFTER BILATERAL HIPPOCAMPAL LESIONS. J. Neurol. Neurosurg. Psychiat, 20(1), 11.

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, 28(11), 1772–1783. https://doi.org/10.1162/jocn_a_01007

Shiferaw, B., Downey, L., & Crewther, D. (2019). A review of gaze entropy as a measure of visual scanning efficiency. Neuroscience & Biobehavioral Reviews, 96, 353–366. https://doi.org/10.1016/j.neubiorev.2018.12.007

Shiffrin, R. M. (1973). Visual Free Recall. Science, 180(4089), 980–982.

Shriki, O., Alstott, J., Carver, F., Holroyd, T., Henson, R. N. A., Smith, M. L., Coppola, R., Bullmore, E., & Plenz, D. (2013). Neuronal Avalanches in the Resting MEG of the Human Brain. Journal of Neuroscience, 33(16), 7079–7090. https://doi.org/10.1523/JNEUROSCI.4286-12.2013

Smith, S. M., Fox, P. T., Miller, K. L., Glahn, D. C., Fox, P. M., Mackay, C. E., Filippini, N., Watkins, K. E., Toro, R., Laird, A. R., & Beckmann, C. F. (2009). Correspondence of the brain's functional architecture during activation and rest. Proceedings of the National Academy of Sciences, 106(31), 13040–13045. https://doi.org/10.1073/pnas.0905267106

Soechting, J. F., & Flanders, M. (1997). Flexibility and Repeatability of Finger Movements During Typing : Analysis of Multiple Degrees of Freedom. 46, 29–46.

Spadone, S., Della Penna, S., Sestieri, C., Betti, V., Tosoni, A., Perrucci, M. G., Romani, G. L., & Corbetta, M. (2015). Dynamic reorganization of human resting-state networks during visuospatial attention. Proceedings of the National Academy of Sciences, 112(26), 8112–8117. https://doi.org/10.1073/pnas.1415439112

Spearman, C. (1961a). The Abilities of Man.

Spearman, C. (1961b). The Abilities of Man.

Sporns, O., Tononi, G., & Kötter, R. (2005). The human connectome: A structural description of the human brain. In PLoS Computational Biology (Vol. 1, Issue 4, pp. 0245–0251). Public Library of Science. https://doi.org/10.1371/journal.pcbi.0010042

Staresina, B. P., & Davachi, L. (2006). Differential encoding mechanisms for subsequent associative recognition and free recall. Journal of Neuroscience, 26(36), 9162–9172. https://doi.org/10.1523/JNEUROSCI.2877-06.2006

Stephan, K. E., Kamper, L., Bozkurt, A., Burns, G. A. P. C., Young, M. P., & Kötter, R. (2001). Advanced database methodology for the Collation of Connectivity data on the Macaque brain

(CoCoMac). *Philosophical Transactions of the Royal Society B: Biological Sciences, 356(1412), 1159–1186. https://doi.org/10.1098/rstb.2001.0908*

Stephen, D. G., & Mirman, D. (2010). Interactions dominate the dynamics of visual cognition. Cognition, 115(1), 154–165. https://doi.org/10.1016/j.cognition.2009.12.010

Stringer, C., Pachitariu, M., Steinmetz, N., Reddy, C. B., Carandini, M., & Harris, K. D. (2019). Spontaneous behaviors drive multidimensional, brainwide activity. Science, 364(6437). https://doi.org/10.1126/science.aav7893

Stuart, S., Hickey, A., Vitório, R., Welman, K. E., Foo, S., Keen, D., & Godfrey, A. (2019). Eye-tracker algorithms to detect saccades during static and dynamic tasks: a structured review. Physiological Measurement. https://doi.org/10.1088/1361-6579/ab02ab

Szekely, P., Korem, Y., Moran, U., Mayo, A., & Alon, U. (2015). The Mass-Longevity Triangle: Pareto Optimality and the Geometry of Life-History Trait Space. PLOS Computational Biology, 11(10), e1004524. https://doi.org/10.1371/journal.pcbi.1004524

Taberna, G. A., Guarnieri, R., & Mantini, D. (2019). SPOT3D : Spatial positioning toolbox for head markers using 3D scans. Scientific Reports, 9, 1–9. https://doi.org/10.1038/s41598-019-49256-0

Takei, T., Confais, J., Tomatsu, S., Oya, T., & Seki, K. (2017). Neural basis for hand muscle synergies in the primate spinal cord. Proceedings of the National Academy of Sciences of the United States of America, 114(32), 8643–8648. https://doi.org/10.1073/pnas.1704328114

Tanzarella, S., Muceli, S., Santello, M., & Farina, D. (2021). Synergistic organization of neural inputs from spinal motor neurons to extrinsic and intrinsic hand muscles. Journal of Neuroscience, 41(32), 6878-6891.

Thayer, R. E. (1989). The biopsychology of mood and activation.

Thompson, E. H. (1997). The Fallacy of the Misplaced Concreteness: Its Importance for Critical and Creative Inquiry. Interchange, 28(2), 219–230.

Thorndike, R. L. (1987). Stability of factor loadings. Person. Individ. Diff., 8(4), 585–586.

Titze, I. R. , & Martin, D. W. (1998). Principles of voice production. The Journal of the Acoustical Society of America, 104, 1148.

Todder, D., Avissar, S., & Schreiber, G. (2001). Dynamic analysis of inter-words time intervals : a method to analyze the structure of communicative signals. 57, 772–779. https://doi.org/10.1054/mehy.2001.1492

Tomasi, D. G., Shokri-Kojori, E., & Volkow, N. D. (2017). Brain Network Dynamics Adhere to a Power Law. Frontiers in Neuroscience, 11. https://doi.org/10.3389/fnins.2017.00072

Torralba, A., Oliva, A., Castelhano, M. S., & Henderson, J. M. (2006a). Contextual guidance of eye movements and attention in real-world scenes: The role of global features in object search. Psychological Review, 113(4), 766–786. https://doi.org/10.1037/0033-295X.113.4.766

Torralba, A., Oliva, A., Castelhano, M. S., & Henderson, J. M. (2006b). Contextual guidance of eye movements and attention in real-world scenes: the role of global features in object search. Psychological Review, 113(4), 766–786. https://doi.org/10.1037/0033-295X.113.4.766

Treisman, A. M., & Gelade, G. (1980). A Feature-Integration Theory of Attention. In COGNITIVE PSYCHOLOGY (Vol. 12).

Unsworth, N., & Robison, M. K. (2016). Pupillary correlates of lapses of sustained attention. Cognitive, Affective, & Behavioral Neuroscience, 16(4), 601–615. https://doi.org/10.3758/s13415-016-0417-4

Van Someren, E. J. W., Van Der Werf, Y. D., Roelfsema, P. R., Mansvelder, H. D., & Lopes da Silva, F. H. (2011). Slow brain oscillations of sleep, resting state, and vigilance (pp. 3–15). https://doi.org/10.1016/B978-0-444-53839-0.00001-6

Vater, C., Roca, A., & Williams, A. M. (2016). Effects of anxiety on anticipation and visual search in dynamic, time-constrained situations. Sport, Exercise, and Performance Psychology, 5(3), 179–192. https://doi.org/10.1037/spy0000056

Venneri, A. , Molinari, M. A., Pentore, R., Cotticelli, B., Nichelli, P., & Caffarra, P. (1992). Shortened Stroop color-word test: its application in normal aging and Alzheimer's disease. Neurobiology of Aging, 13.

Venneri, A., Molinari, M. A., Pentore, R., Cotticelli, B., Nichelli, P., & Caffarra, P. (1992). Shortened stroop color-word test: Its application in normal aging and Alzheimer's disease. Neurobiology of Aging, 13, S3–S4. https://doi.org/10.1016/0197-4580(92)90135-K

Vidal, P. P., & Lacquaniti, F. (2021a). Perceptual-motor styles. In Experimental Brain Research (Vol. 239, Issue 5, pp. 1359–1380). Springer Science and Business Media Deutschland GmbH. https://doi.org/10.1007/s00221-021-06049-0

Vidal, P. P., & Lacquaniti, F. (2021b). Perceptual-motor styles. In Experimental Brain Research (Vol. 239, Issue 5, pp. 1359–1380). Springer Science and Business Media Deutschland GmbH. https://doi.org/10.1007/s00221-021-06049-0

Wallot, S., Coey, C. A., & Richardson, M. J. (2015). Interdependence of Saccadic and Fixational Fluctuations. Ecological Psychology, 27(1), 68–86. https://doi.org/10.1080/10407413.2015.991666

Wallot, S., & Kelty-Stephen, D. (2014). Constraints are the solution, not the problem. Frontiers in Human Neuroscience, 8. https://doi.org/10.3389/fnhum.2014.00324

Wang, C.-A., & Munoz, D. P. (2021). Coordination of Pupil and Saccade Responses by the Superior Colliculus. Journal of Cognitive Neuroscience, 33(5), 919–932. https://doi.org/10.1162/jocn_a_01688

Watson, D., & Tellegen, A. (1985). Toward a Consensual Structure of Mood. Psychological Bulletin, 98(2), 219–235.

Widmann, A., Schröger, E., & Maess, B. (2015). Digital filter design for electrophysiological data – a practical approach. Journal of Neuroscience Methods, 250, 34–46. https://doi.org/10.1016/j.jneumeth.2014.08.002

Witkin, H. A., & Asch, S. E. (1948). Studies in space orientation. IV. Further experiments on perception of the upright with displaced visual fields. Journal of Experimental Psychology, 38(6), 762.

Wolfe, J. M. (1994). Guided Search 2.0 A revised model of visual search. Psychonomic Bulletin & Review, 1(2), 202–238. https://doi.org/10.3758/BF03200774

Wyart, V., & Tallon-baudry, C. (2009). How Ongoing Fluctuations in Human Visual Cortex Predict Perceptual Awareness : Baseline Shift versus Decision Bias. Journal of Neuroscience, 29(27), 8715–8725. https://doi.org/10.1523/JNEUROSCI.0962-09.2009

Wynn, J. S., Bone, M. B., Dragan, M. C., Hoffman, K. L., Buchsbaum, B. R., & Ryan, J. D. (2016). Selective scanpath repetition during memory-guided visual search. Visual Cognition, 24(1), 15–37. https://doi.org/10.1080/13506285.2016.1175531

Yarbus, A. L. (1967). Eye Movements and Vision. Plenum Press.

Yoo, K., Rosenberg, M. D., Kwon, Y. H., Lin, Q., Avery, E. W., Sheinost, D., Constable, R. T., & Chun, M. M. (2022). A brain-based general measure of attention. Nature Human Behaviour, 6(6), 782–795. https://doi.org/10.1038/s41562-022-01301-1

Zangrossi, A., Cona, G., Celli, M., Zorzi, M., & Corbetta, M. (2021). Visual exploration dynamics are low-dimensional and driven by intrinsic factors. Communications Biology, 4(1), 1–14. https://doi.org/10.1038/s42003-021-02608-x

Zentall, S. (1975). Optimal stimulation as theoretical basis of hyperactivity. American Journal of Orthopsychiatry, 45(4), 549–563. https://doi.org/10.1111/j.1939-0025.1975.tb01185.x

Zhou, B., Lapedriza, A., Khosla, A., Oliva, A., & Torralba, A. (2018a). Places: A 10 Million Image Database for Scene Recognition. IEEE Transactions on Pattern Analysis and Machine Intelligence, 40(6), 1452–1464. https://doi.org/10.1109/TPAMI.2017.2723009

Zhou, B., Lapedriza, A., Khosla, A., Oliva, A., & Torralba, A. (2018b). Places: A 10 Million Image Database for Scene Recognition. IEEE Transactions on Pattern Analysis and Machine Intelligence, 40(6), 1452–1464. https://doi.org/10.1109/TPAMI.2017.2723009

Zou, Q., Ross, T. J., Gu, H., Geng, X., Zuo, X. N., Hong, L. E., Gao, J. H., Stein, E. A., Zang, Y. F., & Yang, Y. (2013). Intrinsic resting-state activity predicts working memory brain activation and behavioral performance. Human Brain Mapping, 34(12), 3204–3215. https://doi.org/10.1002/hbm.22136