When style matters: visual exploration is low dimensional and driven by intrinsic dynamics.

Andrea Zangrossi  
University of Padua  https://orcid.org/0000-0001-7832-1953

Giorgia Cona  
University of Padua

Miriam Celli  
University of Padua

Marco Zorzi  
University of Padua

Maurizio Corbetta ( maurizio.corbetta@unipd.it )  
Università di Padova

Article

Keywords: eye movements, visual exploration

DOI: https://doi.org/10.21203/rs.3.rs-275754/v1

License: This work is licensed under a Creative Commons Attribution 4.0 International License. Read Full License
Abstract

It is often assumed that we look at objects that are salient and behaviorally relevant, and that we pay attention differently depending on individual genetics, development, and experience. This view should imply high interindividual variability in eye movements. Conversely, we show that 60% of eye movements variance of more than a hundred observers looking at hundreds of different visual scenes could be summarized by a few components. The first component was not related to image-specific information and identified two kinds of observers during visual exploration: "static" and "dynamic". These viewing styles were accurately identifiable even when observers looked at a blank screen and were described by the degree of similarity to a power-law distribution of eye movements, which is thought to be a measure of intrinsic dynamics. This suggests that eye movements during visual exploration of real-world scenes are relatively independent of the visual content and may underlie intrinsic dynamics.

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 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 or pictures). A cognitive model for the control of visual attention during search is also based on the parallel analysis of visual features.

However, since the seminal studies of Yarbus, it has been known that the patterns of eye movements depend not only on low-level features, but also on the behavioural 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. In general, these accounts fit the classic view of the brain as a sensory-motor analyser whose activity is mainly driven by the analysis and transformation of sensory stimuli into motor decisions. However, a recent study comparing different visual exploration models showed that they account only for a small portion of variance of eye movement patterns. This suggests the presence of other, still unknown, mechanisms that drive eye movement exploration.

Part of the difficulty in explaining the variability of visual exploration might be related to individual differences. Indeed, observers exhibit consistent individual differences in eye movement parameters that generalize across tasks (e.g., visual search vs. fixation) or different versions of the same picture. One study found that eye movement parameters 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\textsuperscript{12}.

These results led to the idea that eye movement patterns may reflect an intrinsic or endogenous ‘signature’ relatively independent of visual input or goal\textsuperscript{9}. Indeed, these patterns relate to individual cognitive styles\textsuperscript{13} and personality traits\textsuperscript{14}, and are in part under genetic influence\textsuperscript{15}.

In this study we aimed to quantify the role of stimulus-driven vs. intrinsic factors in visual exploration by examining eye movement patterns in a large group of healthy participants while they viewed a large set of real-world scenes vs. when they viewed a blank screen devoid any structure visual stimulus.

First, we asked if the variability of eye movements across subjects and visual scenes could be explained with a relatively low number of dimensions. A low dimensionality independent of the visual content of the images would be consistent with the importance of endogenous factors. Second, we asked whether eye movement patterns during exploration were accounted for by the sensory features of the images, their semantic content, or the power law distribution of gaze steps\textsuperscript{16}. Power laws relations are ubiquitously found in nature and predict many complex phenomena such as earthquakes\textsuperscript{17}, volcanic eruptions\textsuperscript{18}, stock market\textsuperscript{19}, and foraging behavior of many species\textsuperscript{20,21}. The identification of a power-law behavior in biological systems is thought to reflect intrinsic constraints of the organization, e.g. anatomical connection or neural dynamics in the case of the brain\textsuperscript{22–25}. Power-law scaling relations have been also found in eye movement patterns during visual search\textsuperscript{16}. Finally, to further test the intrinsic dynamics of eye movements, we investigated whether specific visual exploration patterns could be identified during spontaneous visual exploration in the absence of visual stimuli, i.e., when looking at a blank screen.

**Results**

Healthy participants (n = 120) were recruited at the University of Padova, with n = 114 satisfying exclusion criteria (Supplementary Table 2 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 pictures\textsuperscript{26} (Supplementary Fig. 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 Fig. 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 (Fig. 1). A large set of eye movement features (i.e., 58) were extracted including: fixation duration and position, gaze step amplitude and direction, pupil diameters, etc. (Supplementary
Table 3). A battery of behavioural tests and questionnaires were then administered to evaluate working memory, visuospatial memory, impulsivity, anxiety, and personality traits (Supplementary Table 2 for a list of the measures).

All volunteers received 10 € for their participation.

**Low Dimensionality In Visual Exploration**

The first question we addressed is whether eye movement patterns during visual exploration are ‘different’ or ‘similar’ across individual observers. We examined the pattern of correlation across eye movement features 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 (Fig. 2 and Supplementary Table 4).

The first component (30.5%) mainly loaded on fixation duration, the second (16.4%) on gaze step direction, 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).

We then performed a k-means cluster analysis splitting the sample in two clusters. The k = 2 clustering solution was chosen by comparing the similarity between k-means and hierarchical clustering labels obtained with different distance measures and values of k (Supplementary Fig. 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 (Fig. 3b).

Participants with high PC1 scores were nicknamed “Static Viewers”, because they showed a lower fixation rate but longer fixations. Participants with low PC1 scores were nicknamed “Dynamic Viewers”, because they showed more frequent but shorter fixations (Fig. 3c).

More generally, static viewers also tended to explore images for longer, 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 tended to focus less on spatial location with more semantic and saliency information (see Methods section and Supplementary Fig. 6 for details on the extraction of semantic and saliency information). Dynamic viewers showed an opposite pattern of features. Figure 4 shows a characterization of the viewing styles in terms of individual features by the effect size of each variable (Cohen d).

The robustness of this solution was tested by splitting the images in odd and even, computing a PCA in each subset, and then 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 Fig. 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.

As further control analyses, first we used PC1, PC2 and PC3 to reconstruct the original features matrix and compared the similarity of the resulting reconstruction (Supplementary Fig. 5A).
The most accurate reconstruction was obtained using PC1, compared to other components.

Next, we reconstructed individual pattern of features of exemplar Dynamic and Static viewers. The PC1-reconstructed patterns showed the highest similarity with the original ones, measured with Pearson's correlation coefficient (Supplementary Fig. 5B; Static viewer $r = .86$; Dynamic viewer $r = .77$). This suggests that PC1 component scores allow to accurately reconstruct prototypical eye-movements patterns from the two viewing styles.

The reliability of PC1 scores in describing visual exploration styles was also tested across different image-categories. Specifically, 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. The results showed a high similarity (Pearson's $r = .97$) between PC1 scores obtained from all images and from category-specific features (Fig. 5), suggesting that the visual exploration style is stable and relatively independent from image category.

Overall, these findings support the low dimensionality of eye movement exploration patterns across many subjects and types of visual scene.

**Relative influence of sensory, semantic, and endogenous variables on visual exploration styles**

Next, we examined if visual exploration eye movements 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 sensory saliency values across fixations (SAL), computed as an estimate of the overlap between the positions of fixations and the salience-based map derived for each scene from the Itti and Koch model\(^1\); (2) the mean of semantic values (SEM), computed similarly on semantic maps for each scene derived from a convolution neural network trained on 10,000,000 images\(^2\) (see Methods sections for further details, and Supplementary Fig. 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\(^27,28\); (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\(^22\), we used this measure to study the intrinsic component of eye movements dynamics, as previously suggested\(^29,30\).

The full regression model (i.e., including all predictors; model $F[4, 109] = 7.59, p < .001$, adjusted $R^2 = .19$) showed a significant effect of KSD ($t=-3.79, p < .001$; Fig. 6a and Supplementary Fig. 7) and a trend to significance for the effects of ShEn ($t = 1.76, p = .081$). In contrast, SEM and SAL were not significant even though the pictures were significantly different in their semantic and saliency content (Supplementary Fig. 6 bottom), and these factors would be expected to drive eye movements. See Visual Exploration model in Supplementary Table 1 for further details.
Control Analyses

The 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; Fig. 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 Fig. 8).

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

Identification of visual exploration styles in blank screen viewing condition

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 in the center of the screen and did not show any exploratory eye movements to the blank screen. The blank screen viewing data analysis was thus conducted on a sample of N = 100 subjects.

The PCA on blank screen viewing data (Supplementary Table 4 and Supplementary Fig. 9) 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 of blank screen viewing as dependent variable, and PC 1–3 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 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 (Fig. 7a). Inspection of the between-subjects correlation matrix of eye movement features during visual exploration and blank screen viewing shows that individuals tend to correlate more with members of the same cluster than with members of the other cluster (Fig. 7b). Moreover, the structure of the between-subjects similarity in visual exploration (Fig. 7b left matrix) significantly correlated with that in blank screen viewing (Fig. 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.

Importantly, to be sure that participants were actually exploring the images, after the free viewing phase, they were asked to recall and describe a subset of images which were repeated five times. 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.

**Visual Exploration Styles Are Related To Cognition And Personality**

The final analysis investigated whether visual exploration styles (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 has suggested that eye-movements are influenced by personality traits\(^\text{14,31–34}\), and that Openness seems to be related to longer fixations\(^\text{32}\).

The full regression model (see Cognitive-Personality model in Supplementary Table 1) included all test scores listed in Supplementary Table 2 as predictors, with the exception of the DASS scores and the 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 its delayed recall. The model
was significant \( F[16, 81] = 1.84, p = .03, \text{adjusted-}R^2 = .12 \) and highlighted a significant effect of Age \( (t = 2.66, p = .009; \text{Fig. } 6c) \) and impulsivity (i.e., Stroop test score; \( t = -2.36, p = .021; \text{Fig. } 6d) \) emerged, with only a trend to 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) and showed higher impulsivity (i.e., lower inhibition of automatic responses at Stroop test). Moreover, our results suggest a tendency of dynamic viewers to be less open, even if this result did not reach the significance threshold of .05. Finally, to validate the model, we applied the split-half procedure described before with 1,000 iterations (Fig. 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 parameters were strongly correlated across pictures and participants, with three components explaining roughly 60% of the variance of eye movements and fixations. This low dimensional structure of eye movement patterns, especially the duration and number of fixation (PC1) identified two viewing styles: static and dynamic. The interindividual variability of PC1 scores was predicted by their similarity to a power-law distribution, an intrinsic property of non-linear 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 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 movements during visual exploration, and the role of intrinsic dynamics vis-a-vis sensory salience and semantic information in guiding eye movements.

The low dimensionality of eye movements is not an entirely novel result. Poynter and colleagues\(^{12}\), in a study on \( n = 40 \) subjects, found that eye movement parameters were 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 patients, static and dynamic, who differed not only in terms of rate or duration of fixation, but also pupil diameter, spontaneous viewing time, amplitude and number of gaze steps, and number of gaze ips (Fig. 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, explored images for longer, 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\textsuperscript{35}. At the neural level, fixation and saccadic activity are inter-related at multiple levels in the brain (frontal eye field, superior colliculus, brainstem\textsuperscript{36–38}). At the cortical level, different neural systems, the dorsal and ventral attention networks\textsuperscript{39,40}, 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 dynamic viewers tend to be more impulsive.

The presence of low dimensionality and “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)\textsuperscript{14}. Similarly, studies of human mobility have revealed two distinct styles\textsuperscript{41} 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\textsuperscript{42}. 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\textsuperscript{43} or biological circuits\textsuperscript{44}.

Next, we asked what controls the low dimensionality of eye movement patterns across subjects? Sensory salience was quantified using a classic saliency model\textsuperscript{1}, while semantic information was quantified based on a deep learning neural network\textsuperscript{26}. These variables were 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\textsuperscript{22}, is thought to reflect intrinsic dynamics\textsuperscript{29,30}. 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 “common” eye movements. Rather, estimates of saliency and semantic information were computed fixation by fixation, therefore taking into account eye movement patterns in each picture separately. Our results are consistent with recent studies suggesting that free viewing is not best predicted by saliency.
Saliency models may be more important when the task strongly constrains the search strategy (e.g. search for a red target) but seem to weaken their predictive power in free exploration conditions.

In contrast, similarity to a power law distribution predicted a significant fraction of PC1 score variability in our free-viewing task. Power laws have been ubiquitously found in physics, 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. Moreover, behavioral performance fluctuations also follow a power law, including eye movements, 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. 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.

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 and frequency; during blank screen viewing, eye movement variability 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, with the relative correlation within and between networks adjusted during different tasks. This is consistent with the idea that spontaneous neural dynamics function as a spatiotemporal prior constraining the parameters space of task-evoked activity.

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 darkness. However, eye movements in darkness could reflect several factors not directly related to spontaneous visual exploration dynamics, such as posture-related information or memory-related processing. Also, pupillary responses are not controlled in the darkness. Other small-scale studies used a similar blank screen condition during a memory retrieval task or while hearing sentences about a previously presented scene. 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. 

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, but these studies have mainly used laboratory tasks (e.g., anti-saccades tasks), with some investigations during reading, and not focused on intrinsic dynamics. It is possible that alterations of eye movement intrinsic patterns may represent an early biomarker of degeneration.

**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). The first phase was called “blank screen viewing” as participants were asked to look at a grey screen without any stimulation for 30 seconds. Participants were just told to freely move their gaze within the screen boundaries.

In the second phase (“Free visual exploration”) 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) were shown on the computer screen. 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 (“Recall”) 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 phase, 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, 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 Fig. 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 Fig. 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.

The cognitive tests employed to assess the described domains were the Digit Span (forward and backward), the brief version of the Stroop Test, and the Rey-Osterrieth Complex Figure (ROCF).

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, the Neo Five Factors Inventory (NEO-FFI) 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, the number of fixations, their duration, and dwelling time. Starting from this point, in a recent paper 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). The relation between impulsivity and eye-movements have been previously pointed out in literature. 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) was used to control for participants’ state anxiety, as it can have influence visual behaviour.

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.

Analysis

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. For each participant, a set of 58 features was extracted (Supplementary Table 3) which encoded four main sources of information:

1. Fixations (e.g., mean duration of fixations): statistics over fixations are frequently employed in eye tracking studies. In the present study, fixations were detected using a velocity-based threshold algorithm (detection threshold lambda = 15), which is considered adequate and robust across several testing conditions. From a cognitive point of view, fixations represent information processing and their duration is correlated with the depth of cognitive processing.

2. Pupil diameter (e.g., mean pupil diameter of left eye) which is not only related to environmental light and vigilance, but also to a variety of cognitive processes such as attention and cognitive load.

3. Gaze steps (e.g., mean gaze step length, number of flips on x and y axes) in raw gaze data, i.e., the Euclidean pixel distance between two consecutive gaze positions. 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.

4. Exploration time (e.g., mean duration of pictures' exploration).

Moreover, for fixations and gaze steps, some features were extracted which encoded their temporal course (e.g., mean fixation duration in the first, second, third and fourth quarter of exploration time).

**Eye-movements data reduction.**

A Principal Components Analysis (PCA) was performed to reduce the number of features to a smaller number of meaningful components. Oblique rotation was adopted because of the correlation between the features. To select the optimal number of components we adopted the Kaiser's criterion 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 following the same procedure and the same 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 Fig. 9).

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.

Finally, the same set of features were extracted also from the eye-movements data acquired during the blank screen viewing condition.

Detection of clusters in visual behaviour and their interpretation.

Preliminarily, Silhouette method 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 Fig. 3) and revealed that the 2 clusters solution was the most reliable across different methods. Figure 2 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. 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 driving 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 implemented in the graph-based visual saliency (GBVS) Matlab toolbox; (2) a semantic map created by means of a recently published algorithm based on a Convolutional Neural Network (CNN: Residual Network). 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 Fig. 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.

A linear regression model was built with PC1 scores (obtained in the image-viewing task) as dependent variable, and the measures described above as predictors. The full model was tested on the whole sample, then 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. 5B).

Then we built a new linear regression analysis 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 4) was tested and validated by applying the same procedure used before (i.e., split-half validation with 1,000 iterations; Fig. 5E).

**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. 6B). 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.

**Declarations**

**Acknowledgments**

M.C. was supported by NIH R01NS095741 and a Strategic Grant from the University of Padova (FC Neuro).

This work was supported by the “Departments of Excellence 2018-2022” initiative of the Italian Ministry of Education (MIUR) awarded to the Department of Neuroscience (University of Padua).

Moreover, M.C. and A.Z. were supported by BIAL Foundation grant (No. 361/18).

We are grateful to Luca Semenzato for the technical support on the Tobii eye-tracker.

**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 and code availability**

The data that support the findings of this study and the codes are available from the corresponding author on reasonable request.

**Declaration of Interests**

The authors declare no competing interests.

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

2. Carmi, R. & Itti, L. Visual causes versus correlates of attentional selection in dynamic scenes. *Vision Res.* **46**, 4333–4345 (2006).

3. Elazary, L. & Itti, L. Interesting objects are visually salient. *J. Vis.* **8**, 3.1-15 (2008).

4. Wolfe, J. M. Guided Search 2.0 A revised model of visual search. *Psychon. Bull. Rev.* **1**, 202–38 (1994).

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

6. Torralba, A., Oliva, A., Castelhano, M. S. & Henderson, J. M. Contextual guidance of eye movements and attention in real-world scenes: the role of global features in object search. *Psychol. Rev.* **113**, 766–786 (2006).

7. Itti, L. Quantifying the contribution of low-level saliency to human eye movements in dynamic scenes. *Vis. cogn.* **12**, 1093–1123 (2005).

8. Kümmerer, M., Wallis, T. S. A. & Bethge, M. Information-theoretic model comparison unifies saliency metrics. *Proc. Natl. Acad. Sci.* **112**, 16054–16059 (2015).

9. Andrews, T. J. & Coppola, D. M. Idiosyncratic characteristics of saccadic eye movements when viewing different visual environments. *Vision Res.* **39**, 157–169 (2004).

10. Castelhano, M. S. & Henderson, J. M. Stable individual differences across images in human saccadic eye movements. *Can. J. Exp. Psychol. Can. Psychol. expérimentale* **62**, 1–14 (2008).

11. Privitera, C. M. & Stark, L. W. Algorithms for defining visual regions-of-interest: comparison with eye fixations. *IEEE Trans. Pattern Anal. Mach. Intell.* **22**, 970–982 (2000).

12. Poynter, W., Barber, M., Inman, J. & Wiggins, C. Individuals exhibit idiosyncratic eye-movement behavior profiles across tasks. *Vision Res.* **89**, 32–38 (2013).

13. Bargary, G. *et al.* Individual differences in human eye movements: An oculomotor signature? *Vision Res.* **141**, 157–169 (2017).

14. Hoppe, S., Loetscher, T., Morey, S. A. & Bulling, A. Eye Movements During Everyday Behavior Predict Personality Traits. *Front. Hum. Neurosci.* **12**, (2018).

15. Kennedy, D. P. *et al.* Genetic Influence on Eye Movements to Complex Scenes at Short Timescales. *Curr. Biol.* **27**, 3554-3560.e3 (2017).

16. Stephen, D. G. & Mirman, D. Interactions dominate the dynamics of visual cognition. *Cognition* **115**, 154–65 (2010).

17. Christensen, K., Danon, L., Scanlon, T. & Bak, P. Unified scaling law for earthquakes. *Proc. Natl. Acad. Sci.* **99**, 2509–2513 (2002).

18. Papale, P. Global time-size distribution of volcanic eruptions on Earth. *Sci. Rep.* **8**, 6838 (2018).

19. Gabaix, X. Power Laws in Economics: An Introduction. *J. Econ. Perspect.* **30**, 185–206 (2016).

20. Austin, D., Bowen, W. D. & McMillan, J. I. Intraspecific variation in movement patterns: modeling individual behaviour in a large marine predator. *Oikos* **105**, 15–30 (2004).
21. Ramos-Fernández, G. *et al.* Lévy walk patterns in the foraging movements of spider monkeys (*Ateles geoffroyi*). *Behav. Ecol. Sociobiol.* **55**, 223–230 (2004).

22. Plenz, D. & Thiagarajan, T. C. The organizing principles of neuronal avalanches: cell assemblies in the cortex? *Trends Neurosci.* **30**, 101–10 (2007).

23. He, B. J. Scale-free brain activity: past, present, and future. *Trends Cogn. Sci.* **18**, 480–487 (2014).

24. Tomasi, D. G., Shokri-Kojori, E. & Volkow, N. D. Brain Network Dynamics Adhere to a Power Law. *Front. Neurosci.* **11**, (2017).

25. Bullmore, E. & Sporns, O. Complex brain networks: graph theoretical analysis of structural and functional systems. *Nat. Rev. Neurosci.* **10**, 186–198 (2009).

26. Zhou, B., Lapedriza, A., Khosla, A., Oliva, A. & Torralba, A. Places: A 10 Million Image Database for Scene Recognition. *IEEE Trans. Pattern Anal. Mach. Intell.* **40**, 1452–1464 (2018).

27. Katsini, C., Fidas, C., Belk, M., Avouris, N. & Samaras, G. Influences of Users’ Cognitive Strategies on Graphical Password Composition. in *Proceedings of the 2017 CHI Conference Extended Abstracts on Human Factors in Computing Systems - CHI EA ’17* 2698–2705 (ACM Press, 2017).

doi:10.1145/3027063.3053217

28. Shiferaw, B., Downey, L. & Crewther, D. A review of gaze entropy as a measure of visual scanning efficiency. *Neurosci. Biobehav. Rev.* **96**, 353–366 (2019).

29. Wallot, S. & Kelty-Stephen, D. Constraints are the solution, not the problem. *Front. Hum. Neurosci.* **8**, (2014).

30. Rhodes, T., Kello, C. T. & Kerster, B. Intrinsic and extrinsic contributions to heavy tails in visual foraging. *Vis. Cogn.* **22**, 809–842 (2014).

31. Isaacowitz, D. M. The Gaze of the Optimist. *Personal. Soc. Psychol. Bull.* **31**, 407–415 (2005).

32. Rauthmann, J. F., Seubert, C. T., Sachse, P. & Furtner, M. R. Eyes as windows to the soul: Gazing behavior is related to personality. *J. Res. Pers.* **46**, 147–156 (2012).

33. Risko, E. F. & Kingstone, A. Eyes wide shut: implied social presence, eye tracking and attention. *Attention, Perception, Psychophys.* **73**, 291–296 (2011).

34. Baranes, A., Oudeyer, P.-Y. & Gottlieb, J. Eye movements reveal epistemic curiosity in human observers. *Vision Res.* **117**, 81–90 (2015).

35. Wallot, S., Coey, C. A. & Richardson, M. J. Interdependence of Saccadic and Fixational Fluctuations. *Ecol. Psychol.* **27**, 68–86 (2015).

36. Krauzlis, R. J. The control of voluntary eye movements: new perspectives. *Neuroscientist* **11**, 124–37 (2005).

37. Krauzlis, R. J., Bollimunta, A., Arcizet, F. & Wang, L. Attention as an effect not a cause. *Trends Cogn. Sci.* **18**, 457–64 (2014).

38. Krauzlis, R. J., Goffart, L. & Hafed, Z. M. Neuronal control of fixation and fixational eye movements. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **372**, (2017).
39. Corbetta, M. & Shulman, G. L. Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neurosci.* **3**, 201–215 (2002).

40. Corbetta, M., Patel, G. & Shulman, G. L. The Reorienting System of the Human Brain: From Environment to Theory of Mind. *Neuron* **58**, 306–324 (2008).

41. Pappalardo, L. *et al.* Returners and explorers dichotomy in human mobility. *Nat. Commun.* **6**, 8166 (2015).

42. Cona, G. *et al.* Archetypes of human cognition defined by time preference for reward and their brain correlates: An evolutionary trade-off approach. *Neuroimage* **185**, 322–334 (2019).

43. Gallagher, T., Bjorness, T., Greene, R., You, Y.-J. & Avery, L. The Geometry of Locomotive Behavioral States in C. elegans. *PLoS One* **8**, e59865 (2013).

44. Szekely, P., Korem, Y., Moran, U., Mayo, A. & Alon, U. The Mass-Longevity Triangle: Pareto Optimality and the Geometry of Life-History Trait Space. *PLOS Comput. Biol.* **11**, e1004524 (2015).

45. Koehler, K., Guo, F., Zhang, S. & Eckstein, M. P. What do saliency models predict? *J. Vis.* **14**, 14–14 (2014).

46. Linkenkaer-Hansen, K., Nikouline, V. V., Palva, J. M. & Ilmoniemi, R. J. Long-Range Temporal Correlations and Scaling Behavior in Human Brain Oscillations. *J. Neurosci.* **21**, 1370–1377 (2001).

47. He, B. J., Zempel, J. M., Snyder, A. Z. & Raichle, M. E. The Temporal Structures and Functional Significance of Scale-free Brain Activity. *Neuron* **66**, 353–369 (2010).

48. Shriki, O. *et al.* Neuronal Avalanches in the Resting MEG of the Human Brain. *J. Neurosci.* **33**, 7079–7090 (2013).

49. Palva, J. M. *et al.* Neuronal long-range temporal correlations and avalanche dynamics are correlated with behavioral scaling laws. *Proc. Natl. Acad. Sci.* **110**, 3585–3590 (2013).

50. de Haas, B., Lakovidis, A. L., Schwarzkopf, D. S. & Gegenfurtner, K. R. Individual differences in visual salience vary along semantic dimensions. *Proc. Natl. Acad. Sci.* 201820553 (2019). doi:10.1073/pnas.1820553116

51. Smith, S. M. *et al.* Correspondence of the brain’s functional architecture during activation and rest. *Proc. Natl. Acad. Sci.* **106**, 13040–13045 (2009).

52. Cole, M. W., Bassett, D. S., Power, J. D., Braver, T. S. & Petersen, S. E. Intrinsic and task-evoked network architectures of the human brain. *Neuron* **83**, 238–51 (2014).

53. Betti, V. *et al.* Natural Scenes Viewing Alters the Dynamics of Functional Connectivity in the Human Brain. *Neuron* **79**, 782–797 (2013).

54. Spadone, S. *et al.* Dynamic reorganization of human resting-state networks during visuospatial attention. *Proc. Natl. Acad. Sci.* **112**, 8112–8117 (2015).

55. Berkes, P., Orban, G., Lengyel, M. & Fiser, J. Spontaneous Cortical Activity Reveals Hallmarks of an Optimal Internal Model of the Environment. *Science (80-. ).* **331**, 83–87 (2011).

56. Raichle, M. E. The Restless Brain. *Brain Connect.* **1**, 3–12 (2011).
57. Clemens, I. A. H., Selen, L. P. J., Pomante, A., MacNeilage, P. R. & Medendorp, W. P. Eye Movements in Darkness Modulate Self-Motion Perception. *eneuro* **4**, ENEURO.0211-16.2016 (2017).

58. Johansson, R., Holsanova, J., Dewhurst, R. & Holmqvist, K. Eye movements during scene recollection have a functional role, but they are not reinstatements of those produced during encoding. *J. Exp. Psychol. Hum. Percept. Perform.* **38**, 1289–1314 (2012).

59. Johansson, R. & Johansson, M. Look Here, Eye Movements Play a Functional Role in Memory Retrieval. *Psychol. Sci.* **25**, 236–242 (2014).

60. Altmann, G. T. M. Language-mediated eye movements in the absence of a visual world: the ‘blank screen paradigm’. *Cognition* **93**, B79–B87 (2004).

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

62. Anderson, T. J. & MacAskill, M. R. Eye movements in patients with neurodegenerative disorders. *Nat. Rev. Neurol.* **9**, 74–85 (2013).

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

64. Biondi, J., Fernandez, G., Castro, S. & Agamennoni, O. Eye-Movement behavior identification for AD diagnosis. *arXiv Prepr. arXiv1702.00837* (2017).

65. Cirilli, L., de Timary, P., Lefèvre, P. & Missal, M. Individual Differences in Impulsivity Predict Anticipatory Eye Movements. *PLoS One* **6**, e26699 (2011).

66. Monaco, M., Costa, A., Caltagirone, C. & Carlesimo, G. A. Forward and backward span for verbal and visuo-spatial data: standardization and normative data from an Italian adult population. *Neurol. Sci.* **34**, 749–754 (2013).

67. Venneri, A. *et al.* Shortened stroop color-word test: Its application in normal aging and Alzheimer’s disease. *Neurobiol. Aging* **13**, S3–S4 (1992).

68. Rey, A. & Osterrieth, P. A. Translations of excerpts from Andre Rey’s Psychological examination of traumatic encephalopathy and P. A. Osterrieth’s The Complex Figure Copy Test.. *Clin. Neuropsychol.* **7**, 4–21 (1993).

69. McCrae, R. R. & Costa, P. T. Validation of the five-factor model of personality across instruments and observers. *J. Pers. Soc. Psychol.* **52**, 81–90 (1987).

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

71. Mercer Moss, F. J., Baddeley, R. & Canagarajah, N. Eye Movements to Natural Images as a Function of Sex and Personality. *PLoS One* **7**, e47870 (2012).
72. Carver, C. S. & White, T. L. Behavioral inhibition, behavioral activation, and affective responses to impending reward and punishment: The BIS/BAS Scales. *J. Pers. Soc. Psychol.* **67**, 319–333 (1994).

73. Lovibond, P. F. & Lovibond, S. H. The structure of negative emotional states: comparison of the Depression Anxiety Stress Scales (DASS) with the Beck Depression and Anxiety Inventories. *Behav. Res. Ther.* **33**, 335–43 (1995).

74. Vater, C., Roca, A. & Williams, A. M. Effects of anxiety on anticipation and visual search in dynamic, time-constrained situations. *Sport. Exerc. Perform. Psychol.* **5**, 179–192 (2016).

75. Engbert, R. & Kliegl, R. Microsaccades uncover the orientation of covert attention. *Vision Res.* **43**, 1035–45 (2003).

76. Stuart, S. *et al.* Eye-tracker algorithms to detect saccades during static and dynamic tasks: a structured review. *Physiol. Meas.* (2019). doi:10.1088/1361-6579/ab02ab

77. Just, M. A. & Carpenter, P. A. A theory of reading: From eye fixations to comprehension. *Psychol. Rev.* **87**, 329–354 (1980).

78. Unsworth, N. & Robison, M. K. Pupillary correlates of lapses of sustained attention. *Cogn. Affect. Behav. Neurosci.* **16**, 601–615 (2016).

79. Krejtz, K., Duchowski, A. T., Niedzielska, A., Biele, C. & Krejtz, I. Eye tracking cognitive load using pupil diameter and microsaccades with fixed gaze. *PLoS One* **13**, e0203629 (2018).

80. Kaiser, H. F. The Application of Electronic Computers to Factor Analysis. *Educ. Psychol. Meas.* **20**, 141–151 (1960).

81. Rousseeuw, P. J. Silhouettes: A graphical aid to the interpretation and validation of cluster analysis. *J. Comput. Appl. Math.* **20**, 53–65 (1987).

82. Clauset, A., Shalizi, C. R. & Newman, M. E. J. Power-Law Distributions in Empirical Data. *SIAM Rev.* **51**, 661–703 (2009).

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