Multivariate patterns and long-range temporal correlations of alpha oscillations are associated with flexible manipulation of visual working memory representations.

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ABSTRACT

The ability to flexibly manipulate memory representations is embedded in visual working memory (VWM) and can be tested using paradigms with retrospective cues. While valid retrospective cues often facilitate memory recall, invalid ones may or may not result in performance costs. We investigated individual differences in utilising retrospective cues and evaluated how these individual differences are associated with brain oscillatory activity at rest.

At the behavioural level, we operationalised flexibility as the ability to make effective use of retrospective cues or disregard them if required. At the neural level, we tested whether individual differences in such flexibility were associated with properties of resting-state alpha oscillatory activity (8-12 Hz). To capture distinct aspects of these brain oscillations, we evaluated their power spectral density and temporal dynamics using long-range temporal correlations (LRTC). In addition, we performed multivariate patterns analysis (MVPA) to classify individuals' level of behavioural flexibility based on these neural measures. We observed that alpha power alone (magnitude) at rest was not associated with flexibility. However, we found that the participants' ability to manipulate VWM representations was correlated with alpha LRTC and could be decoded using MVPA on patterns of alpha power. Our findings suggest that alpha LRTC and multivariate patterns of alpha power at rest may underlie some of the individual differences in using retrospective cues in working memory tasks.

Keywords: Working Memory (WM); Electroencephalography (EEG); Alpha resting-state; Neuronal oscillations; Retro-cues.

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Introduction

Visual Working memory (VWM) relies on flexibly manipulating memory representations by directing attention towards goal-relevant stimuli and inhibiting irrelevant ones (Nobre et al., 2004; Zanto & Gazzaley, 2009). This ability can be assessed with paradigms based on retrospective cues (retro-cues) presented during the retention period, i.e. between the offset of a memory array and the onset of a probe (Bays, Catalao, & Husain, 2009; Griffin & Nobre, 2003). Retro-cue studies consistently show that retro-cues matching a probe to be remembered (i.e. *valid retro-cues)* are associated with better memory recall when compared to neutral retro-cues, which provide no information about the probed item (Pertzov, Bays, Joseph, & Husain, 2013; Rerko, Souza, & Oberauer, 2014; Zokaei, Manohar, Husain, & Feredoes, 2014). This advantage is known as the retro-cue benefit (Gözenman, Tanoue, Metoyer, & Berryhill, 2014). Some past studies have also used *invalid retro-cues,* which reinforce an item not subsequently probed. Therefore, this type of retro-cue requires participants to shift their attention back to the initial memory array, discard the invalidly cued item and recall an uncued one. This additional cognitive effort in trials with invalid relative to neutral retro-cues is often associated with slower responses (Astle, Summerfield, Griffin, & Nobre, 2012; Gressmann & Janczyk, 2016; Li & Saiki, 2015), and also with a cost in memory recall accuracy (namely, retro-cue cost). However, this result is less consistent (Astle et al., 2012; Gözenman et al., 2014; Griffin & Nobre, 2003; Pertzov et al., 2013) because invalid retro-cues have been either associated with reduced magnitude of the retro-cue benefit (Gözenman et al., 2014), but also with no detrimental effect (Gressmann & Janczyk, 2016). Therefore, invalid retro-cue performance can be grouped into three categories: the presence of a retro-cue cost (higher performance in neutral relative to invalid retro-cues), no cost (higher performance in invalid relative to neutral retro-cues), and lack of cue effect (no difference between invalid and neutral cues).

Several non-mutually exclusive theoretical accounts attempted to explain the ability to manipulate retro-cue information (Gressmann & Janczyk, 2016). For instance, the invalid retro-cue cost can be explained by the *removal, protection* and *prioritisation* hypotheses, suggesting that uncued items tend to be removed from the central WM store or to decay, or that cognitive resources are redistributed following the presentation of a retro-cue, leaving fewer for the uncued items (Astle et al., 2012; Kuo & Astle, 2014; Matsukura, Luck, & Vecera, 2007; Myers, Stokes, & Nobre, 2017; Souza, Rerko, & Oberauer, 2014). In contrast, no cost may depend on the set size (if the number of encoded elements exceeds the individual VWM capacity) or cue reliability (when valid retro-cues are in an above-chance proportion compared to invalid ones) (Souza & Oberauer, 2016), which may lead participants to disregard the information carried by the retro-cue.

These accounts and past data are yet to focus on the factors underlying the ability to flexibly manipulate retro-cue information. Here, we suggested two ways to address these issues: (i) a task-dependent behavioural measure and (ii) task-independent neural measures. At the behavioural level, we used a VWM retro-cue task to examine performance in valid retro-cue trials and the invalid ones. If lack of cost reflects the suppression of the retro-cue information, then the no-cost group may show a reduced benefit from the information carried by valid cues relative to the cost group. Alternatively, if the lack of cost reflects effective and flexible processing of the retro-cue, then the no-cost group may benefit from the valid cue.

We investigated the neural factors underlying flexibility in memory representations by studying power and temporal correlation properties of the spontaneous, task-free neural activity, namely resting-state EEG (rsEEG) (Klimesch, 2012; MacLean, Arnell, & Cote, 2012). Without tasks-specific restrictions, rsEEG provides critical information on how intrinsic neural activity is linked to behavioural performance across different cognitive domains (Heister et al., 2013; MacLean et al., 2012; Oswald et al., 2017; Prat, Yamasaki, Kluender, & Stocco, 2016; Wu, Srinivasan, Kaur, & Cramer, 2014). To capture the specific electrophysiological features underlying the variability in processing retro-cues we conducted two types of analysis (univariate and multivariate) on two measures of oscillatory activity that provide distinct yet complementary information about the rsEEG: Power spectral density (PSD) and long-range temporal correlations (LRTC). 1) PSD informs about the synchronous activity of neurons averaged across several minutes of rsEEG within a specific frequency band (Klimesch, Russegger, Doppelmayr, & Pachinger, 1998)**;** Long-range temporal correlations (LRTC) is a feature of the temporal dynamics of amplitude fluctuations of neural oscillations. LRTC represents long-term memory processes across different time scales (Klaus Linkenkaer-Hansen, Nikouline, Palva, & Ilmoniemi, 2001)**.** These measures were first used in univariate analyses focusing on the statistical assessment of neural measures (alpha PSD, alpha LRTC) at each electrode separately. In addition, complementing the univariate analyses, we conducted multivariate patterns analysis (MVPA). MVPA assesses whether information about specific classes of events or participants can be decoded from patterns of activity across multiple spatiotemporal dimensions (i.e. electrodes or frequency bands) (Haxby, Connolly, & Guntupalli, 2014a). Here, we used MVPA to classify participants into our sub-groups using as features the above-mentioned measures: power spectral density and LRTC.

We capitalised on two cognitive functions required for flexible manipulation of memory representations: attentional resources to inhibit task-irrelevant information and memory, both linked to alpha oscillations (8-12Hz) (Bonnefond & Jensen, 2012; Canuet et al., 2012; Clark et al., 2004; Garrett et al., 2013; Klimesch, 2012; Poch, Campo, & Barnes, 2014). Alpha power at rest is considered a biomarker of individual trait and state-like cognitive processes such as vigilance and arousal, supporting memory and attentional tasks (Klimesch, Vogt, & Doppelmayr, 1999; MacLean et al., 2012; Mahjoory, Cesnaite, Hohlefeld, Villringer, & Nikulin, 2019; Pitchford & Arnell, 2019)**.** The relationship between the magnitude of resting oscillations and task performance is regulated by a distinct directionality (Klimesch, Vogt, et al., 1999).

Specifically, alpha at rest positively correlates with memory retention, such that participants with larger alpha power at rest memorise items better and faster (Babiloni et al., 2007; Mahjoory et al., 2019). Consistent with this, high alpha power at rest has been linked to attention directed to internally-oriented information, such as memories, rather than to external stimuli, such as distractors (Cooper, Croft, Dominey, Burgess, & Gruzelier, 2003; MacLean et al., 2012). Given the link between alpha oscillations, the inhibition of distractor, and memory performance, we expected that these neural patterns might also mediate retro-cue processing since this relies on inhibitory and memory processes.

More specifically, we predicted that a lower cost in processing invalid retro-cues might be associated with larger alpha power, compared to increased cost or lack of retro-cue effect. This scenario may account for the neural mechanisms underlying individual differences in retro-cue costs.

As mentioned above, given the flexible manipulation of information required by our paradigm, we used a measure that assesses the temporal dynamics of resting state activity: LRTC. The presence of LRTC in neural activity has been interpreted to reflect the processing, integration and manipulation of information required in executive functions, including inhibitory control and flexible adaptation to changing task demands (Bhattacharya, Edwards, Mamelak, & Schuman, 2005; Chaudhuri, Knoblauch, Gariel, Kennedy, & Wang, 2015; Honey et al., 2012; Kahana, Seelig, & Madsen, 2001; Nakao et al., 2019; Palva, Zhigalov, Hirvonen, Korhonen, & Linkenkaer-Hansen, 2013; Simola, Zhigalov, Morales-Muñoz, & Palva, 2017). Additional support for an association between LRTC and information processing is suggested by studies proposing that LRTC might be an indicator of a neural system operating close to a critical regime (Palva et al., 2013). Furthermore, recent empirical evidence suggests that a strong degree of LRTC corresponds to better task performance in higher cognitive functions, such as working memory and decision-making (Colosio, Shestakova, Nikulin, Blagovechtchenski, & Klucharev, 2017; Mahjoory et al., 2019; Nakao et al., 2019; Palva, Monto, Kulashekhar, &

Palva, 2010). In particular, in a recent rsEEG study, while alpha-band power was related to short-term memory performance, alpha-band LRTC showed a positive correlation with working memory behavioural outcome (Mahjoory et al., 2019). Additionally, high alpha LRTC at rest have been used as a proxy of neuronal noise that modulates decision-making processes (Nakao et al., 2019). Based on this evidence, we predicted that higher alpha LRTC might also be associated with higher flexibility in manipulating memory representations, possibly by suppressing the “noise” deriving from invalid cues.

In the present study, we evaluated power and LRTC on the amplitude fluctuations of alpha oscillatory activity to characterise the neuronal processes underlying the flexible manipulation of memory representations. We expected a positive relationship between the lower cost in invalid retro-cue trials and both the magnitude of alpha power and the degree of LRTC.

Given that the flexible manipulation of memory representation is unlikely be linked to specific topography, we investigated whether different performance in response to retro-cues processing could be decoded from patterns of activity using a machine learning methods, as MVPA.

Methods

Participants

Sixty-two healthy human adults (44 females, mean ± SD age: 24.36 ± 3.81 years) provided written informed consent to participate in this study. All participants completed the retro-cue paradigm. Resting-state EEG (rsEEG) were obtained from thirty participants (21 females, mean

± SD age: 23 ± 3.6 years), divided into three equal subgroups (*N*=10 each), based on individual differences in performance in invalid retro-cue trials relative to the neutral ones, which can be reflected in (i) cost, (ii) no-cost, and (iii) no-cue effect (no-cue difference). The experimental protocol was approved by the Ethics Committee at Goldsmiths, University of London.

Experimental Procedure

Participants were seated in front of a 21” CRT monitor at a viewing distance of 60 cm in a darkened and soundproof room. The task was programmed in MatLab® v.8.4 (http://www.mathworks.co.uk) using the Cogent toolbox (http://www.vislab.ucl.ac.uk/cogent.php). The resting-state fixation cross was programmed and run on E-Prime software (Schneider, Eschman, & Zuccolotto, 2002).

Before the experimental task, we recorded 5-minutes resting-state EEG during which participants kept their eyes open while looking at a white cross (visual angle 6°) presented on a black screen. Subsequently, a practice block was included to familiarise participants with the task procedure.

Experimental Design

The retro-cue WM task consisted of three blocks of 42 trials each, with 21 valid, 12 neutral and 9 invalid retro-cues in each block (Bays et al., 2009; Borghini et al., 2018). In each trial, a stimulus array followed a black fixation cross (0.8° diameter) centrally presented on a grey background. The stimulus array consisted of four arrows presented for 1s in a random orientation and in four out of five possible colours (yellow, blue, red, green and white); two arrows were presented on the right and two on the left of the fixation cross. After stimulus presentation, the fixation cross (retro-cue) could either remain on the monitor with no change of colour (neutral cue) or change for 100 ms into a colour that either correctly (valid retro-cue) or incorrectly (invalid retro-cue) matched the colour of the probe, followed by a 1 sec delay. After a 3 s interval, participants had a maximum of 3500 ms to match the probe's orientation to the item with the same colour in the initial display using a computer mouse. See Figure 1.

It's important to note that the relatively small number of invalid trials represents an intrinsic feature of retro-cues paradigms (Gressmann & Janczyk, 2016). By being persuaded to ‘trust’ the more numerous and predictable valid cues, participants use different cognitive strategies when presented with less numerous and unpredictable invalid cues. Furthermore, previous studies have shown that the ratio of valid and invalid trials plays a crucial role in producing a cost in performance (Gözenman et al., 2014; Gunseli, van Moorselaar, Meeter, & Olivers, 2015).

Figure1

WM performance indices

WM performance was measured in terms of accuracy, source of errors and response time (RTs). RTs corresponded to the difference between the probe onset and the response. However, RTs also reflected the time spent rotating the mouse (before the actual answer), and therefore should be interpreted with caution. The measures reflecting the source of errors were obtained using an established probabilistic model (see Bays & Husain, 2008; Bays, Wu, & Husain, 2011).

Accuracy

Recall precision: was calculated as the inverse of the circular standard deviation of the error in response, namely the discrepancy between the veridical and the participant’s orientation of each arrow stimulus. These values were calculated separately for the three retro-cue conditions.

Source of error

Probability to respond to the target stimulus, pT: referred to the Gaussian variability in reporting the orientation of the target item, namely the variability between the veridical orientation of the target item and the orientation reported by the participant.

Probability to respond to the non-target stimulus, pNT: measured the probability of responding to a non-probed item, considered an index of misbinding. This refers to conditions whereby not probed items (non-target items) corrupted the memory of the probe such that participants reported the orientation of an item of a colour different from the target one.

Random guess, pU: corresponded to the probability of responding to an item with a random orientation.

Kappa, κ: defined as 'concentration parameter', it provided a measure of the variability of recall of the target feature, whereby higher κ corresponds to lower variability.

Among the measures of WM performance, here we mostly referred to the probability of responding to the target item (pT) because of its link to the cognitive processes involved in the retro-cue effect (for a review, see Souza & Oberauer, 2016).

EEG acquisition and pre-processing

Participants' resting-state EEG activity was acquired using a 64 channel BioSemi Active Two amplifier system with 64 Ag/AgCl electrodes, with a sampling rate of 1024 Hz. We also recorded vertical and horizontal electrooculograms. The EEG data were re-referenced to the average of two earlobe electrodes. Offline pre-processing was conducted using EEGLAB toolbox version 14.1.1b for MatLab ® (Delorme & Makeig, 2004). The 5 min EEG recording was initially visually inspected to remove large muscle artefacts, high-pass filtered at 0.5 Hz, and down-sampled at 512 Hz. An Independent Component Analysis (ICA) was subsequently used to correct for eye-blink and saccadic movements.

Power spectral density

The power spectral density (from 2 to 115 Hz, simply termed “power” or “spectral power” thereafter) was estimated by Welch’s periodogram with a Hamming window and a 50% overlap. Power values were normalised (dB), using the log-transformation, with respect to the average power of two intervals (81-95 and 105-115 Hz) belonging to the upper gamma band (Herrojo Ruiz, Brücke, Nikulin, Schneider, & Kühn, 2014) in order to compensate for inter-individual differences in the absolute power (Grandchamp & Delorme, 2011). Next, power values were extracted for the alpha band (8-12 Hz) from the estimated broadband spectrum.

Long-range temporal correlations

Neural activity exhibits scale-free properties across different scales of spatial or temporal organisation (Bak & Bak, 2013). In electro- or magnetoencephalography, scale-free properties are best characterised by measuring correlations in the amplitude of oscillations across different temporal scales from milliseconds to seconds, known as LRTC (Nikulin & Brismar, 2005). For non-stationary time series, as in EEG signals, LRTC can be assessed using detrended fluctuation analysis, DFA (Lux & Marchesi, 1999; Palva et al., 2013; Peng, Havlin, Stanley, & Goldberger, 1995). The DFA provides a scaling exponent within range 0-1, with a value of 0.5 reflecting random temporal correlations and values from 0.5 to 1 indicating LRTC in the time series (Lux & Marchesi, 1999).

Here we evaluated the relationship between the LRTC of resting alpha-band oscillation and retro-cue processing. Following previous studies (Herrojo Ruiz et al., 2014; Nikulin et al., 2012), continuous EEG data (~3 minutes after artefact correction) were band-pass filtered in the alpha band (8-12 Hz, two-way least-squares FIR filter) using the function *eegfilt.m* implemented in the EEGLAB toolbox (Delorme & Makeig, 2004). Next, we applied the Hilbert transform on the filtered signal to extract the alpha-band amplitude envelope. The DFA analysis was then applied to the envelope of alpha oscillations as follows:

1. The cumulative sum (integral) of the signal shifted by the mean was first calculated. This data was then partitioned using 20 non-overlapping windows of equal size T in the logarithmic scale; these ranged from 1 to 18 seconds, with the maximum window (18 seconds) being 1/10 of the total length (i.e. 180 seconds), as recommended in the previous studies (Herrojo Ruiz et al., 2014; Klaus Linkenkaer-Hansen et al., 2001).
2. In each window, the signal was locally fit using the least-squares method to obtain a linear function. This linear function was subtracted from the signal in each window, thus effectively detrending the signal by removing the local linear trend. The mean-squared residual (fluctuation) function F was extracted and subsequently estimated across different time scales (see Herrojo Ruiz et al., 2014 for details).
3. A log-log plot of F vs window size T revealed a linear relationship corresponding to power-law scale-free behaviour. The slope of the linear fit, which corresponds to the scaling exponent (DFA coefficient), was extracted for each channel and each participant.

Multivariate pattern analysis (MVPA)

Next, we conducted two types of MVPA to investigate whether different features of alpha oscillatory activity carried information about two subgroups of participants showing a cost or no-cost effect (Haynes & Rees, 2006a; Norman, Polyn, Detre, & Haxby, 2006)**.** MVPA allowed us to quantify class-related information in the multivariate (multi-channel) EEG oscillatory signals in terms of decoding accuracy. In each type of MVPA, we used either alpha-band normalised spectral power or LRTC coefficients across the 64 EEG channels as features. The computations were performed in Matlab® (The MathWorks Inc., Natick, Massachusetts) with a standard library for Support-Vector Machine (libsv) (Chang & Lin, 2011). MVPA was implemented using a 2-fold leave-one-out cross-validation procedure, using single participants as "trials", to assess the effectiveness of the model. The 2-fold leave-one-out cross-validation was used as the sample size of our groups limited the analysis with higher k-folds (Kohavi, 1995).

Statistical inference on MVPA used permutation tests to assess whether the cross-participants classification accuracy (between cost and no-cost groups) was significantly above chance. We estimated the chance level by performing MVPA 1000 times after randomly shuffling the class (group) labels in the data. This generated a Null distribution on the classification accuracies. Next, we obtained a *P*-value as the proportion (%) of accuracy values from the Null distribution that were greater than or equal to the empirical decoding accuracy obtained in the cross-validation procedure (Bury, García-Huéscar, Bhattacharya, & Ruiz, 2019).

Statistical analyses

Behavioural data

Across all performance indexes obtained from the probabilistic model, 20 data points for the large sample (N=62) (.02%) and 9 for sub-sample (N=30) (.02%) were excluded from the analyses as over 2.5 standard deviations (SD) from the group mean.

Non-parametric (Wilcoxon signed-rank) test was used for planned paired comparison between the retro-cue conditions since the assumption of normality based on the Kolmogorov-Smirnov test was violated. Since these data were not normally distributed, response time between retro-cue conditions was compared using the Kruskal-Wallis Test, with retro-cue condition (valid, invalid and neutral retro-cue) included as a factor. Spearman-based correlation analyses were also carried out between retro-cue cost and benefit and between retro-cue cost and alpha-range

LRTC.

Electrophysiological data

Significant differences in the *univariate analysis* of the spectral power and LRTC in the alpha band were assessed using two-sided cluster-based permutation (1000 permutations; alpha level=.025) (Maris & Oostenveld, 2007). This test was implemented to assess differences between subgroups of participants, which had been defined based on different types of behavioural performance, namely cost, no cost and no-cue effect. Spectral power and LRTC analyses involved the entire sample (i.e. three subgroups, N=30), to provide a descriptive power and DFA distribution across the whole sample. Multivariate analyses with MVPA, however, focused on participants belonging to cost or no-cost subgroups exclusively. Indeed, to investigate the variability in the flexible manipulation of memory representations, we had to limit the focus on subgroups where the retro-cue effect was present, either expressed in cost or no cost in performance.

As a control analysis, to assess the specificity of our electrophysiological results, we extended our investigation to theta oscillations (4-7 Hz) because of their link with memory abilities and cognitive flexibility (Gevins, Smith, McEvoy, & Yu, 1997; Gladwin & De Jong, 2005; Riddle, Scimeca, Cellier, Dhanani, & D'Esposito, 2020; Sauseng et al., 2006). We computed the control analysis for theta oscillatory activity both in terms of power and neuronal dynamics applied to the univariate and multivariate approaches.

Data availability statement

Data and resources will be provided from the corresponding author upon request.

RESULTS

Behavioural data

Group effects

Data from the whole sample showed a significantly higher probability to respond to the target orientation (pT) in trials with valid compared to invalid retro-cues (Z=2.435, p=.015), but not in neutral relative to invalid (Z=1.879, p=.060), see Table 1. No other effects reached significance (p<.05). The sub-sample for which EEG data was recorded showed a similar tendency, although no significant retro-cue effect was found in any of the measures used (precision, pT, pNT, pU, Kappa) (Table 1).

Table1

For the whole sample, response times were not significantly modulated by retro-cue type (p >.05), although on average, they followed the expected trend because they were faster for the valid condition, followed by neutral and invalid, Table 1. Similar results were found in the smaller sample with no significant effect of retro-cue type (p >.05), Table 1.

Individual differences in invalid retro-cue trials

The lack of significant retro-cue effects at the group-level may be due to large inter-individual variability (Lim, Wöstmann, Geweke, & Obleser, 2018). Indeed, an inspection of the data, specifically in the invalid retro-cue condition, indicated that some participants had higher retro-cue cost values and slower response times than others (up to 2 standard deviations from the group average). Low or no retro-cue cost in some participants may be because they either ignored the information carried by retro-cue (either valid or invalid) or because they used it effectively, which may reflect higher flexibility in manipulating memory representations. This means that participants with high flexibility may more strongly benefit from valid retro-cue and at the same time be less affected by the cost associated with invalid retro-cues. In line with this prediction, we observed a significant positive correlation between reduced retro-cue cost and benefit values (r_s=.48, p=.007), indicating that lower retro-cue cost values were associated with higher retro-cue benefit values (Figure 2).

Figure 2

Next, we divided the EEG sample into three subgroups, corresponding to the three behavioural patterns based on their response to invalid retro-cues, specifically cost, no-cost and no cue-effect

This aimed to further explore individual variability in retro-cue processing and match the electrophysiological analysis methods' requirements, which demand balanced group sizes. To standardise the values to a normal distribution**,** our EEG sample (N=30) was normalised by subtracting each value to the mean and dividing it by the standard deviation of the larger sample (N=62, including all the participants for which behavioural data was available). After normalisation, we tested whether differences between the cost and no-cost subgroups may be driven by an overall tendency of the no-cost group to suppress the retro-cue. We reasoned that in that case, the no-cost subgroup who showed no invalid retro-cue cost may also exhibit less benefit from the valid retro-cue trials, compared to the cost group. Results did not support this hypothesis. Interestingly, we found that the cost and no-cost groups differed significantly in terms of retro-cue benefit ($t_{(9)}$ = 3.80, p = .004), with higher benefit in the no-cost group (M: .21, SD: .22 information vs M: -.06, SD: .09). A similar benefit was observed when the no-cue group was compared to the no-cost group in terms of retro-cue benefit (M: -.05, SD: .13; $t_{(9)}$ = -4.57, p = .001).

These results indicate that individual variability in retro-cue cost is unlikely to result from suppressing all retro-cue information, as participants in the no-cost group showed a behavioural benefit from valid retro-cue, which crucially was stronger compared to the other sub-groups. This suggests that the flexible manipulation of memory representations allowed participants in the no-cost group to effectively use and disregard information presented during the maintenance period, depending on the retro-cue conditions.

Electrophysiological data

Power spectral density analysis

Cluster-based permutation tests assessed differences between all pairs of subgroups in resting-state spectral power in the alpha band. None of the comparisons reached significance at a corrected value of p= <.01<.008 (Bonferroni correction of the alpha level for a two-sided test at 0.025). From a visual inspection of the power data, a larger alpha power magnitude in the no-cost relative to the cost subgroup emerged over parieto-occipital electrodes, but it was not statistically significant (p=.08) (Figure 3a and 3b).

Control analysis

No differences between subgroups were found when cluster-based permutation tests were applied to rsEEG power in theta band.

Figure 3

Long-Range Temporal Correlations

The DFA exponents in the alpha frequency band were extracted and averaged across channels for each subject from the entire EEG sample (N=30) The distribution of scaling exponents in the population was in the range .51 and .91 (M: .66, SE:.02), which supports the presence of LRTC in the amplitude of alpha oscillations. Next, we correlated the DFA exponents with pT cost scores (invalid minus neutral retro-cue). We found a significant positive non-parametric Spearman correlation (r_s=.40, p=.02), such that higher DFA exponents (indicating a higher degree of LRTC) were associated with lower cost values. See Figure 4a.

Next, we contrasted the DFA exponents between the cost and no-cost subgroups using cluster-based permutation tests. No significant difference emerged (p>.05), although the no-cost group showed overall higher DFA coefficients compared to the cost (M:.67, SE:.01 vs M:.61, SE:.03), see Figure 4 b.

Control analysis

No significant relationship between DFA exponents extracted for theta oscillations and pT cost scores was found.

Figure 4

Multivariate pattern classification analysis

MVPA investigated whether group membership (cost and no-cost) could be classified from the multivariate patterns of spectral alpha-band power or, separately, from the LRTC exponents, distributed across 64 channels. With alpha band power as features, we observed a significant, decoding accuracy (2-fold leave-one-out cross-validation, accuracy: 70%, p=.03), chance level estimated from the Null permutation distribution). This outcome suggested that the distribution of alpha power values across the scalp was informative of individual participants' task performance (measured as cost or no-cost effects). Finally, using LRTC exponents as features, we observed a significant above-chance classification accuracy corresponding to 75% (2-fold leave-one-out cross-validation, p = .01).

Control analysis

When theta band power and LRTC were used as features, no significant classification accuracy was reached using multivariate pattern analysis.

DISCUSSION

This study investigated the ability to flexibly manipulate memory representations by studying flexibility in the context of WM-based retrospective attention (via retro-cues) and the corresponding neuronal signatures in terms of spontaneous alpha oscillations. We specifically tested whether flexibility in WM may be linked and predicted by measures of spontaneous resting-state alpha oscillations, spectral power, long-range temporal correlation (LRTC) and multivariate pattern analysis (MVPA).

Variability in manipulating memory representations

We found a significantly lower probability of target responses (pT) –an index of inhibitory abilities – in invalid relative to valid retro-cues in our larger sample and a trend in the subsample for which EEG data was recorded. This may reflect a detrimental effect of misinformative (invalid) compared to informative (valid) retro-cue on performance, consistently with past findings (Borghini et al., 2018; Gunseli et al., 2015; Pertzov, Dong, Peich, & Husain, 2012; Rerko et al., 2014).

Across participants, performance was poorer in invalid relative to valid trials, although there was no significant difference between target responses in invalid relative to neutral retro-cues (i.e. a retro-cue cost). However, this lower probability of target responses (pT) in invalid relative to neutral retro-cues was observed in some but not all participants. To better understand whether such variability in performance may be explained by differences in the flexible manipulation of memory representations, retro-cue performance was characterised as: retro-cue cost (or 'cost' subgroup), reduced cost ('no-cost' subgroup) and no-cue effect ('no-cue' subgroup). These distinct performance patterns may reconcile the inconsistent past results on the retro-cue cost, displaying how different behavioural outcomes may co-exist in the same sample. Some participants showed invalid retro-cue cost, possibly due to the decay or removal of un-cued items in WM; differently, other participants did not show a cost effect, possibly supporting the prioritisation hypothesis (i.e. cued items are prioritised without altering the noncued ones) (Gressmann & Janczyk, 2016; Pertzov et al., 2013). Furthermore, to rule out the possibility that reduced retro-cue cost merely reflects the suppression of the information carried by the retro-cue (either valid or invalid), we also investigated the benefits in validly-cued trials in the no-cost compared to the cost group. Results showed that the no-cost group showed a benefit when the retro-cue was informative and that this behavioural effect was stronger than in the other sub-groups. We considered this pattern as reflecting the most flexible manipulation of memory representations, as it reveals an efficient use of the information carried by the retro-cue, which could either be ignored (with invalid cues) or used to benefit performance (with valid cues).

Association between Power Spectral Density, Long-Range Temporal Correlation and retro-cue effect

We focused on task-free, spontaneous oscillatory activity in the alpha band to characterise the neuronal processes underlying the flexible manipulation of memory representations, by using two types of analysis: univariate and multivariate (MVPA) analysis of averaged alpha power and alpha LRTC. We found a positive correlation between cost in retro-cue performance and the degree of LRTC, such that the higher the DFA exponents –indicating a higher degree of LRTC– the lower the performance cost. Furthermore, the MVPA conducted on alpha power and LRTC separately demonstrated significant above-chance classification accuracies, supporting that individual cost and no-cost performance can be classified from the corresponding alpha profiles. On the other hand, however, the univariate analysis of alpha power at each electrode separately did not significantly differ between performance groups. This outcome was unexpected, as previous findings reported increased resting alpha power as an indicator of better performance in memory and attention tasks (Klimesch, Doppelmayr, Schwaiger, Auinger, & Winkler, 1999; MacLean et al., 2012; Mahjoory et al., 2019). We had therefore expected alpha power to be higher in participants with lower cost. The lack of significant results should be interpreted with caution, given that our statistical approach does not allow us to make inferences on null results. Importantly, however, the MVPA findings suggest that information about individual cost and no-cost performance might be distributed across multivariate patterns of alpha power and LRTC values across electrodes.

The MVPA alpha-power results highlighted that distributed patterns of neural activity differentiate flexible manipulation of memory representations. This finding is in support of the increasing body of literature arguing that the synchronous activity of neurons averaged across time, within a specific frequency band at each separate may not reflect how information is encoded and transmitted in patterns, thus resulting in inconsistent findings (Haxby et al., 2014a; Haynes & Rees, 2006b). Furthermore, anatomical and functional variability between subjects may amplify differences in spatial characteristics, making univariate, cluster-based analysis less reliable (Wang et al., 2015). Instead, by simultaneously assessing distributed information across electrodes, multivariate analyses can successfully identify patterns of neural activity with higher sensitivity to a particular group or condition (Haxby, 2012; Haxby, Connolly, & Guntupalli, 2014b; Kamitani & Tong, 2005; List, Rosenberg, Sherman, & Esterman, 2017).

A limitation of our study is that our MVPA results originate from 2-fold leave-one-out cross-validation, which may lead to an overestimation of the model's skills (Kohavi, 1995). Although we considered conducting cross-validation with higher k-folds, our participant sample size was small, and a 2-fold leave-one-out cross-validation was more suitable to decode participants from each small group. Accordingly, these results should be interpreted, taking this limitation into consideration.

The LRTC analysis showed that greater resistance to invalidly-cued items in the no-cost subgroup corresponded to greater scaling exponents (DFA). This positive correlation is in line with evidence that efficient executive functions –here in terms of resisting to misinformation carried by the invalid retro-cue – typically involve stronger temporal coordination of neuronal activity across time scales and cortical areas (Kwok, Cardy, Allman, Allen, & Herrmann, 2019; Poil, Hardstone, Mansvelder, & Linkenkaer-Hansen, 2012; Simola et al., 2017). Similar to the link between behaviour and cortical excitability (Haegens, Luther, & Jensen, 2012; Herrmann, Strüber, Helfrich, & Engel, 2016), stronger LRTCs in neuronal oscillations may relate to a balance between cortical inhibitory and excitatory states and reduction of neural randon noise, resulting in optimal performance (K. Linkenkaer-Hansen, 2005; Poil et al., 2012; Samek et al., 2016). Our results align with previous findings that link stronger LRTC and higher performance in working memory and decision-making tasks (Mahjoory et al., 2019; Nakao et al., 2019; Simola et al., 2017). These findings demonstrated a correlation between switching capacity in working memory tasks (Mahjoory et al., 2019) and random noise suppression that may affect internal criteria in the decision-making process (Nakao et al., 2019). The current study extends such evidence to VWM and the ability to retrospectively and flexibly manipulate visual memory representations depending on probe identity, suppressing invalidly-cued item. We, therefore, propose that dynamic measures at rest, specifically LRTC in the amplitude of alpha oscillations, provides the first characterisation of individual flexibility in manipulating memory representation.

CONCLUSIONS

This study used a working memory retro-cueing paradigm to investigate individual flexibility in manipulating memory representations and its relationship with properties of resting-state EEG alpha oscillations. Such flexibility corresponded to a reduced cost and a greater benefit when processing invalid and valid retro-cues, respectively, and was decoded from distributed patterns of spontaneous alpha neural activity recorded prior to task execution.

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Conflict of interest statement

The authors declare that there is no conflict of interest.

Authors' contribution

Mara Golemme collected, analysed the data and drafted the paper. Elisa Tatti designed the study, collected the data and edited the draft. Caroline Di Bernardi Luft provided guidance for the data analysis and edited the draft. Joydeep Bhattacharya provided suggestions for the data analysis and edited the draft. Maria Herrojo Ruiz analysed, interpreted the data and edited the draft. Marinella Cappelletti designed the study and edited the draft.

Abbreviations

rsEEG - Resting-state electroencephalogram
VWM -Visual Working Memory
LRTC - Long range temporal correlation
pT - Probability to respond to the target stimulus
MVPA- Multivariate pattern classification analysis

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