The underlying brain networks of superior memory

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ABSTRACT: People can employ mnemonic techniques to achieve better memory skills. Memory athletes of the World Memory Championships train in these mnemonic techniques for years and have stated to use one mnemonic technique in particular called the method of loci. In a previous study by Dresler et al., 23 of the world's memory athletes and 51 participants, of which as small part newly trained in the method of loci, were selected to perform a memory test [1]. It was shown that the athletes possess specific functional brain networks to support their superior memory performances and that similar connectivity patterns were present in the trained group. However, it remains an open question which exact changes occurred in the functional connectivity patterns of the newly trained participants. In this paper, a new method is applied to the datasets used by Dresler et al. to verify the results previously published and to uncover the areas responsible for the increase in memory capabilities in the newly trained group. The algorithm is called Spatial Patterns for Discriminative Estimation (SPADE). SPADE produces linear filters that can discriminate two groups optimally in terms of their covariance patterns, which are associated with functional connectivity networks. The results demonstrate that the SPADE filters can be used to classify the athletes and their controls accurately. Moreover, the classification could be extended to the newly trained group in the method of loci, separating their pre-post-training stage. In this work, we present unique spatial patterns of brain activity connected with the athletes and controls during encoding. In conclusion, the results reinforce that memory athletes and controls differ in their functional connectivity networks and that they can be classified based on these differences. Finally, it is confirmed that this classification can be extended to a newly trained group before and after training.

Keywords Brain networks; Superior memory; Method of loci; SPADE; Cognitive training; Memory athletes

Introduction

It is still not fully understood if people inherently have better memory or if superior memory can be trained. Memory can be subdivided into different types such as episodic memory, which is related to autobiographical events, and working memory, which holds temporarily relevant information [2], [3]. In recent years, it is believed that the use of specific memory techniques can explain a large part of superior working memory [4]. These memory techniques are called mnemonics and are utilised to help people remember certain structured information such as names, numbers, word-lists etc. Memory is usually understood of consisting of three different processes: encoding, storage and retrieval [5]. Mnemonic skills are based on practising techniques that assist with the encoding and retrieval steps that can then support better memory performance [1]. The fact that one can practice these skills indicates that ordinary people overall can achieve these capabilities and increase their memory capacity for specific information.

Exceptional people train for years in mnemonic techniques to become so-called memory athletes and compete in the World Memory Championships [6]. One of the main approaches applied by the memory athletes is the method of loci [7]. The technique involves people imagining a known spatial path and at specific locations (loci) make imaginary associations with the items they want to remember [8], [9]. Afterwards, when the person decides to revisit the route, they will encounter the retained information in order of placement. When applying this method, different skills are essential. First, the athletes need to be able to create explicit spatial scenes with precise loci. Second, they need to affiliate the to-be-remembered information to these loci by employing imaginative associations. Lastly, they need to be able to move from loci to loci in a smooth manner.

In a previous study by Dresler et al., 23 of the world's memory athletes were recruited to perform a memory test [1]. Their functional connectivity networks were analysed, using functional magnetic resonance imaging (fMRI). These athletes all confirmed that they made extensive use of the method of loci to perform the memory test. It was demonstrated that specific functional connectivity patterns support the superior memory displayed by the athletes. Afterwards, Dresler et al. recruited 51 students to see if they could be trained in the method of loci in a six weeks time frame [1]. It was confirmed that the trained group had a significant increase in their capability to remember different types of word lists.

Furthermore, by comparing the functional brain data of the memory athletes and controls to the group of novice subjects before and after training, Dresler et al. confirmed that a similar connectivity profile could be established in the trained group [1]. The paper highlighted certain areas as displaying noticeable increases in functional connectivity for the athletes and the novice subjects after mnemonic practice. These regions included the right dorsolateral prefrontal cortex (DLPFC), the medial prefrontal cortex (MPFC) and the medial temporal lobe (MTL). However, it could not be determined, using univariate methods, where the trained group differed in their network pre-post-training. Therefore, it is still not clear which exact connectivity patterns changed in the trained group that allows for the increase in memory performance.

In a follow-up analysis, by Müller et al., the functional connectivity networks of the athletes were reanalysed using a more hypothesis-driven approach [10]. The main connectivity profile shown to be predictive of the athletes rank in the World Memory Championships was the anterior hippocampus to the posterior hippocampus and the caudate nucleus. These two areas have been linked to stimulus-response learning and the spatial component of the method of loci [10]. The strength of the method of loci has been hypothesised to be the cooperative utilisation of the caudate nucleus and the hippocampus [10].

In conclusion, these two papers found distinct functional brain networks present in the athletes, that support their superior memory performance. Moreover, similar brain network patterns have been found when comparing the pre-post-training group connectivity profiles to the athletes-controls connectivity profiles. Nevertheless, it remains an open question which exact changes occur in the functional connectivity patterns of novice participants trained in the method of loci.

In this paper, a new method is applied to the datasets previously used by Dresler and Müller et al. to confirm the earlier published results and to uncover the areas responsible for the increase in memory capabilities in the newly trained group [1], [10]. The algorithm is called Spatial Patterns for Discriminative Estimation (SPADE) [11]. Developed by Llera et al., SPADE has demonstrated to be able to identify different cognitive states or experimental conditions based on functional connectivity variations. SPADE produces linear filters that can discriminate two groups optimally in terms of their covariance. These filters can be back-projected onto the brain to show which connectivity profiles are present during different tasks. The method was illustrated using the 0-back and 2-back working memory tasks. It was determined that brain areas frequently related to working memory were present for the 2-back task and areas primarily involved with the attention and salience networks were present for the 0-back task [11]. Therefore, confirming that the 2-back task is more related to memory processing and the 0-back task more to attention sustainment.

Furthermore, it was established that the discriminative filters could be used to classify different cognitive states accurately. The SPADE algorithm was able to detect the subtle network changes during similar tasks and classify them, as it relies on the covariance between regions of the brain instead of the mean signal differences, such as used in a general linear model (GLM) analysis [11]. For distributed network changes, the covariance data can contain more information than the mean signal.

In this study, we expect the same brain regions previously demonstrated by Dresler et al. as being related to superior memory, to be represented by the SPADE filters for the athletes. With the filters being a representation of the connectivity patterns. These areas include the DLPFC, MPFC, MTL and the hippocampus, as this region has previously been shown to be essential for encoding tasks and applying the method of loci [1], [4], [10], [12]. For the LOC group, the network changes after extensive training in the method of loci seem to be distributed in nature [1]. The SPADE method is highly sensitive to these distributed connectivity changes. Therefore, it is hypothesised that the SPADE algorithm can provide us with more insight into the distributed connectivity changes of the newly trained participants that could not be detected with previous methods. We anticipate that SPADE can distinguish the connectivity profile of the novice group pre-post-training in the method of loci and demonstrate similarity to some of the athletes' network connectivity mentioned above. Three main questions will be addressed in this paper:

1. Is it possible to reproduce the results demonstrated by Dresler et al. that the athletes can be distinguished from their controls based on their functional connectivity profile using SPADE?
2. Can we distinguished the novice group practising the method of loci pre-post-training based on their functional connectivity profile and can we visualise the changes in network connectivity?
3. Can it be demonstrated that the connectivity profile of the athlete-control group, captivated by the SPADE-filters, can classify the group practising the method of loci pre-post-training?

For the first question, we will explore the difference in functional connectivity networks between athletes and controls during encoding using SPADE. SPADE will be utilised to make discriminative filters. These filters indicate which ROIs combined explain most of the connectivity for the athlete group or their controls. Then, we will examine if the participants of the two groups can be accurately classified based on their SPADE filters. For the second question, the same will be done for the pre-post-training group in the method of loci. For the final question, we will determine if the filters found for the athlete-control group can be used to classify the newly trained group pre-post-training.

Answering these questions will confirm the underlying neural connections associated with the difference in memory performance between the athletes and their controls, shown previously by Dresler et al. [1]. Furthermore, by analysing the change in functional networks of the novice training group, insight could be given into the underlying changing brain mechanisms when engaging in superior memory training.

Methods

Dataset

For the first part of the experiment, the fMRI data of 23 memory athletes (age 28 ± 8.6 years, 14 males) of the top-50 of the 2010-2013 World Memory Championships were analysed [1]. The fMRI data from a control group, matched in age, sex handedness, smoking, and IQ, were used to compare to the athletes. From these 23 athletes and controls, 17 completed an encoding task in the fMRI. They performed a word memorisation assignment of 72 concrete nouns of which the details can be found in [1]. Behaviourally, they have shown to possess better memorisation skills: 70.8 ± 0.6 vs 39.9 ± 3.6 words recalled after 20 minutes of encoding with a significance of $p<0.001$ using the Wilcoxon signed-rank test.

For the second part of the analysis, the fMRI task data of 51 participants (age 24 ± 3.0 years, all men) were used. The participants were assigned to one of the following three groups: loci memory training group (LOC), active-control working memory training group (WMN), or passive-control group (PAS). The groups were matched in age, sex, handedness, smoking and IQ. The participants of the LOC group got a 2-hour introductory course into the method of loci, ensuring they had an active grasp of this approach. Every day the participants in the LOC group were asked to train in the method of loci for 30 minutes on a web-based platform. In total, they prepared for over 20 hours during a six weeks time-frame. The WMN group was asked to do an n-back working memory training during the same time-frame, using no specific memorisation technique. The PAS group received no training during this time-frame. One fMRI session was conducted pre-training, and a second fMRI session was performed post-training. During the fMRI sessions, 72 concrete nouns were encoded, with different lists of words being given pre and post-training.

All the fMRI data were acquired in the Max Plank Institute of Psychiatry using a 3T scanner and a 12-channel head coil. During the encoding task, 292 $T2^*$-weighed blood oxygenation level-dependent (BOLD) images were made. The EPI sequence used was: repetition time (TR) 2.5 s, echo time (TE) 30 ms, flip angle 90 degrees, and a slice thickness of 2 mm with 42 ascending axial slices [1].

Preprocessing

All the data acquired was prepossessed utilising SPM8. The following preprocessing steps were performed on the data: T1-equilibration, realignment to the mean image, co-registration, spatial normalisation, and smoothing with an 8mm full width at half maximum (FWHM) Gaussian. Afterwards, a general linear model (GLM) was used to determine the functional connectivity during the encoding task. The GLM included six nuisance regressors capturing the translational and rotational displacement. If the frame-wise movement proved to be higher than 0.3 mm, the scan was excluded. Finally, a high-pass filter was applied to the data with a cut-off of 128 s. For more details on the preprocessing steps, see [1].

SPADE algorithm

The preprocessed athlete and control datasets were used to find the most informative brain regions in terms of covariance using the SPADE algorithm. The following steps were taken while applying the SPADE algorithm [11]:

1. Spatial dimensionality reduction

2. Computing the covariance matrices
3. Simultaneous diagonalisation
4. Model order selection
5. Classification
6. Visualisation

An overview of all the steps is presented in figure 1.

Spatial dimensionality reduction

Before applying SPADE, a dimensionality reduction was performed on each subjects' data. In total, 70 regions of interest (ROIs) were defined that are related to the six main networks of memory and visuospatial processing [1], [14]. We wanted to compare the results of SPADE to the paper of Dresler et al. and therefore chose to apply the same ROIs selection. The ROIs were located in the dorsal and ventral default mode networks, the visuospatial and higher visual networks, and the left and right medial temporal lobes. These networks are hypothesised to be related to general memory processes and therefore deemed essential when using the method of loci [14]. Next, the BOLD time courses were extracted for each ROI. Afterwards, a z-transformation was applied to ensure a mean of zero and a standard deviation of one.

Computing the covariance matrices

Subsequently, the covariance between the ROIs was calculated using the BOLD time courses, giving a 70x70 covariance matrix per participant. These covariance matrices were used as a proxy for the functional connectivity present between the ROIs during the encoding task.

Simultaneous diagonalisation

The athletes' and controls' covariance matrices were given to the SPADE algorithm. The SPADE algorithm used the two covariance matrices for simultaneous diagonalisation, which renders a set of discriminative spatial filters. For more details, see the supplementary material or refer to [13].

Model order selection

Afterwards, model order selection was used to select only the relevant spatial filters that optimally maximise the covariance for one group while minimising it for the other. One option for model order selection is a procedure based on permutation testing. When permutation testing is used, filters are selected that describe significantly more covariance for the original groups than when the groups are randomly permuted [11]. Typically, the filters are at the opposite sides of the Eigen spectrum and by definition maximise the covariance between the two groups [11].

Classification

A linear discriminant function was applied with a leave one out cross-validation scheme to test if the filters can be used to classify the two groups significantly. Typically, a leave one out cross-validation is very expensive, but as the groups' sizes were small, this remained within bounds. The number of folds is equal to the total group size for a leave one out cross-validation. At each fold, the SPADE filters were made using all the groups' data except one participant's. These filters were then used to transform the data and compute the logarithmic variance of the time-series (LVTS). The LVTS was used as training data for a Regularized Linear Discriminant Analysis (RLDA) classifier to distinguish between the two groups. Afterwards, a classification was made for the LVTS of the test data to which group it belongs. The final classification accuracy was decided by the number of correctly classified samples divided by the number of folds.

Visualization

Finally, the top most discriminative filters were transformed into spatial maps that were projected onto the brain, to understand with which brain areas the spatial filters correspond. The data were filtered by selecting all the data between the 5th percentile and the 95th percentile. The first filter indicates the areas that synchronise together to explain most of the covariance of the control group while minimising it for the athlete group and vice versa for the last filter. Functional connectivity can be understood as the covariation of brain regions during a task [15]. Therefore, the filter's projections can be interpreted as the most informative connectivity patterns present for the groups during encoding.

SPADE out of sample

Finally, the filters found from the athlete and control datasets were tested on the LOC, CON and WMN groups to see if the filters could successfully discriminate the LOC pre-post-training, as compared to the control groups. The discrimination procedure was done by using the same classification scheme as described above, but replacing the testing data with the pre-post-training data of the three groups.

Results

SPADE filters athletes and controls

We gave the athletes and controls covariance matrices to SPADE and selected permutation testing for model or-

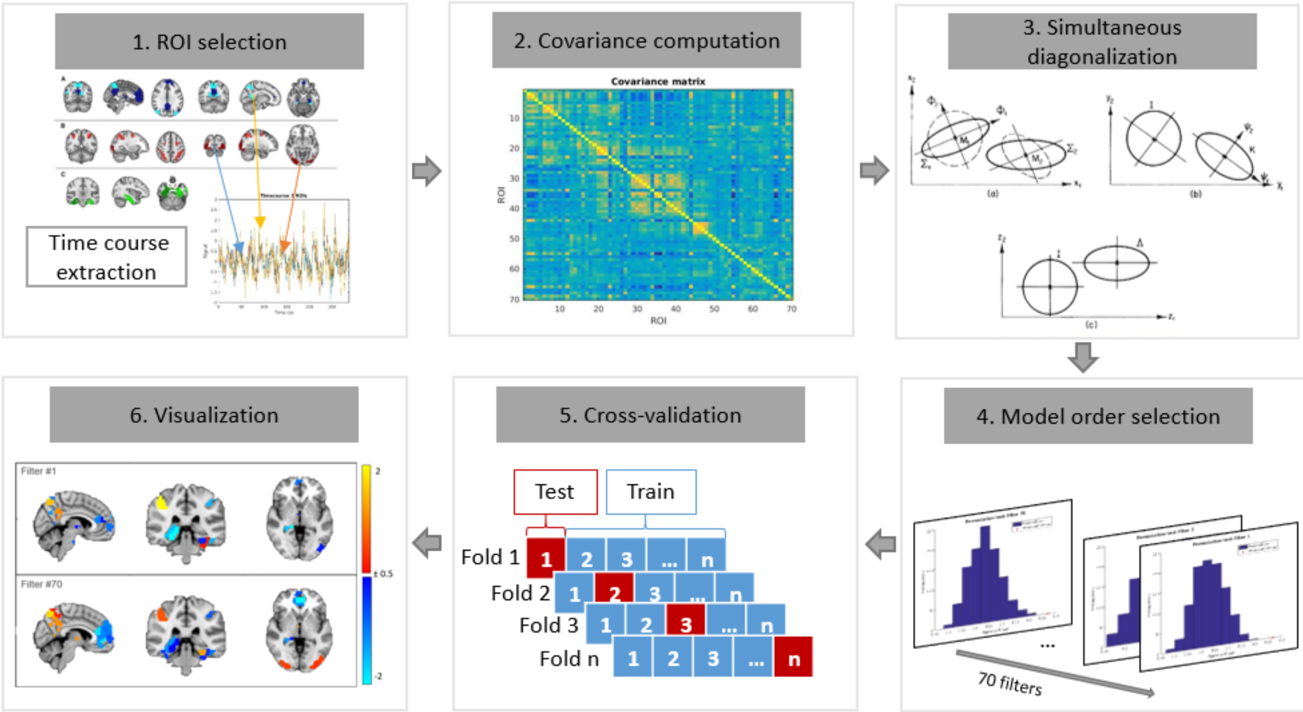

Figure 1: Overview of the Spatial Patterns for Discriminative Estimation (SPADE) algorithm applied to the memory athletes and their controls. 1) The regions of interest (ROIs) were selected, related to memory and visuospatial processing, and the BOLD time series extracted. 2) The covariances between the ROIs were calculated, giving 70x70 covariance matrices. 3) Simultaneous diagonalisation was performed, providing spatial filters [13]. 4) The most explanatory filters for the two groups were decided upon in terms of covariance, using model order selection based on permutation testing. 5) A classifier accuracy value of the found filters was calculated, using cross-validation with a Linear Discriminant Classifier. 6) The top two discriminative spatial filters were visualised by projecting them back onto the brain.

der selection. In total, 1000 permutations were performed. Two filters (#1, #70) were determined, as maximising the covariance for one group while minimising it for the other. Afterwards, a two-dimensional projection of the data onto the filters was made to illustrate that the filters produced by SPADE separated the two groups visually, see figure 2. The first and the last filter were multiplied with the time-courses of the original data. Then, the log of the variance of the transformed time-series was plotted according to:

$$W = filter$$
$$X = timecourse$$
$$\hat{X} = W^T * X$$
$$Y = log(var(\hat{X}^T))$$

In figure 2, a clear separation between the two groups in the SPADE filter space is shown, which gives an indication that the classification algorithm should provide a satisfactory classification accuracy.

Classification athletes and controls

The SPADE classification accuracy using the first and the last filter is 91%. A permutation test was constructed, to test if the resulting accuracies were significant. First, the indices of the data signifying if a participant belonged to the athletes or the controls were randomly shuffled. Second, the SPADE algorithm was applied to the shuffled groups, and the shuffled-accuracies were recorded. Third, it was checked how many times the shuffled accuracies were higher than the original accuracy or lower than one minus the original accuracy, giving a two-tailed permutation test, see figure 3. The final count was divided by the number of permutations, in this case, 10000, presenting us with a p-value for the classification accuracy. The final results of the classification are displayed in table 1 showing that the p-value of the accuracy is $0.0043 < 0.05$ and therefore significant.

Brain maps athletes and controls

The projection of the filters onto the MNI152 brain map was made, to see the spatial connectivity patterns that were

Comparison	Selected filters	Accuracy	P-value
ATH-CON	#1, #70	0.91 (0.28)	0.0043

Table 1: Overview of the results produced by the SPADE algorithm. The two datasets compared are the athletes and controls task fMRI data. The SPADE accuracy gives the classification results when using an RLDA classifier with a one leave out cross-validation scheme. The p-value is determined by a two tailed permutation test for the SPADE accuracy.

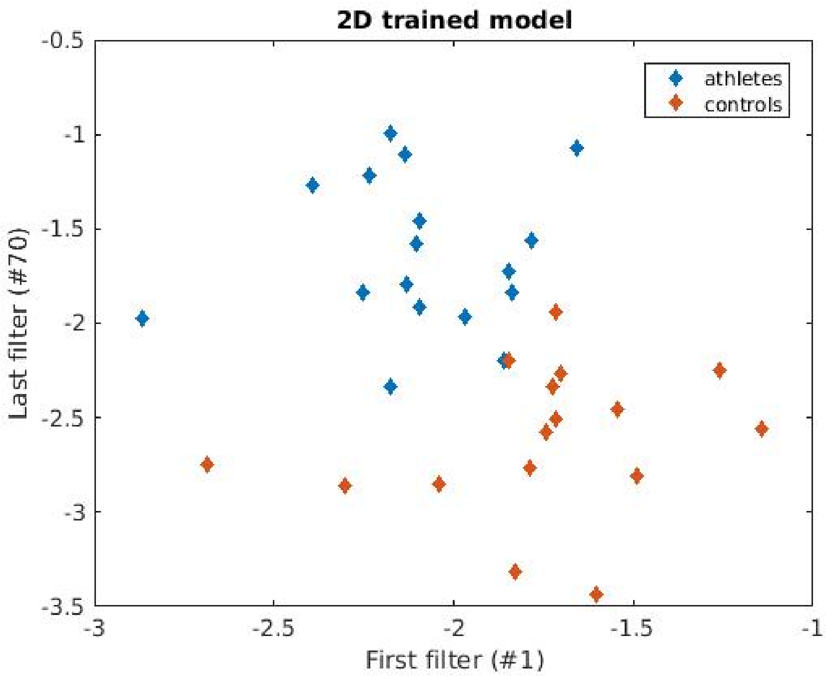

Figure 2: Showing the 2D representation of the fMRI data in the SPADE filter space. The data used is the athletes task data (blue) vs. the CON task data (red). The transformed data set is visually separable into two distinct clouds.

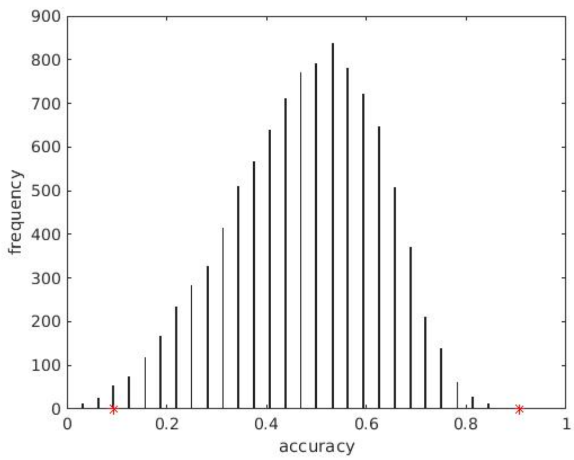

Figure 3: Two-tailed permutation test of the classification accuracy of the athletes and controls obtained with the SPADE algorithm. The red stars indicate the original classification accuracy.

learned with the SPADE filters, see figure 4. The filter explaining most of the covariance of the control group (#1), shows the bilateral hippocampus, thalamus, parahippocampal gyrus, supramarginal gyrus, cingulate gyrus, precuneus cortex and the brainstem. Most of these brain areas have been noted in previous papers to be related to memory processing and working memory tasks [11], [16]. On the other hand of the Eigen spectrum, brain regions that together explain most of the covariance for the athletes (#70), are similar to the controls with extension to the occipital pole and prefrontal cortex. These two areas have been established to be relevant during visual mental imagery [17]. One of the critical elements of the method of loci is to use visual imagery to link the to-be-remembered information to the loci. Therefore, it could be that the connectivity between these areas is relevant for the athletes during encoding, but not for the controls.

Classification pre-post training

The SPADE algorithm was also tested on the three groups (LOC, WMN and PAS) pre-post-training. Model order selection with permutation testing was used to find the most significant filters. However, using permutation testing gave zero significant filters for the three groups. The inseparability was expected for the CON and WMN group, as their technique pre-post training did not vary. For the LOC group, previous connectivity analysis performed by Dresler et al. could also not separate them pre-post-training [1]. Nevertheless, it was anticipated that the new SPADE analysis could separate the pre-post-training LOC group, as SPADE has proven to be highly sensitive to small network changes [11]. It could be that the difference pre-post-training in the covariance matrices were too small compared to the noise for SPADE to effectively separate.

SPADE out of sample results

Lastly, we tested if the filters that were learned from the SPADE algorithm with the athletes and controls could also be used to classify the LOC trained group pre-post-training, as opposed to their controls (WMN and PAS). The algo-

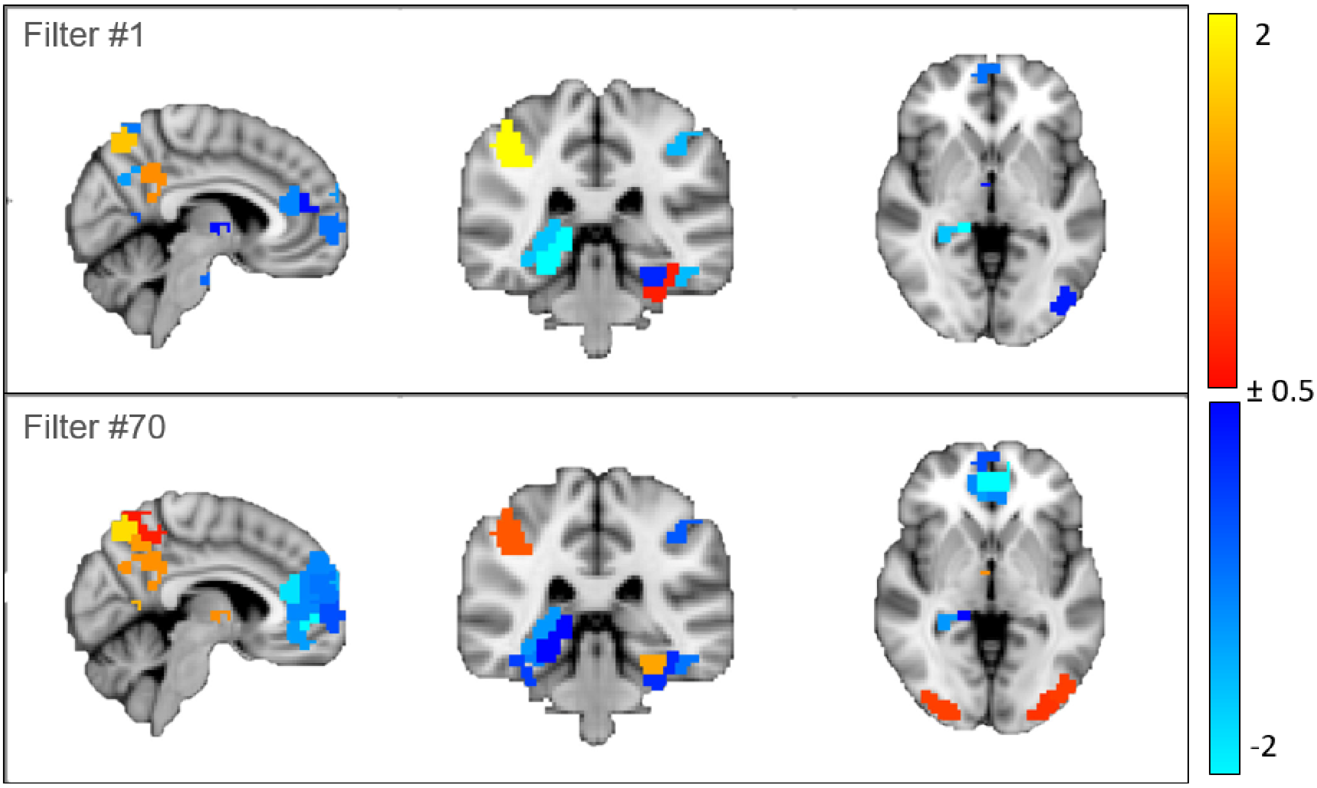

Figure 4: Projection of the discriminative filters found with the SPADE algorithm onto the MNI152 brain map. The #1 filter explains most of the covariance for the CON group. The #70 filter explains most of the covariance for the athletes' group. The covariance being a direct proxy for the connectivity of these groups during encoding. It can be noted that the athletes' group demonstrates more connectivity in the frontal, occipital and parietal brain regions, as compared to controls.

rithm SPADE out of sample was used to analyse this. To the algorithm, we gave the covariance matrices of athletes and controls to train and learn the filters. The filters selected by permutation testing remained the same (#1, #70). The classification was done using an RLDA classifier, as described above, with the LOC, WMN and PAS groups as test data. In table 2 the final results are displayed. Showing the test set classification accuracy of the LOC, WMN and PAS groups. The classification accuracy for the LOC group using the athletes and controls filters proved to be 81%. The p-value was computed for the accuracy, using a two-tailed permutation test, according to the steps explained above. The results show that the only data set the athletes and controls filters can significantly classify is the LOC pre-post-training group (p-value = 0.0036<0.05). The LOC group was the only group that was trained in the method of loci, and it was demonstrated before that the distributed functional connectivity patterns of the athletes-controls are similar to the LOC pre-post-training group [1]. Therefore, it was expected that the LOC group contained the participants that could be separated pre-post-training, using the athletes and controls filters. In conclusion, the filters that signify the brain areas that explain most of the covariance differences between athletes and controls were also discriminative for the LOC group pre-post-training.

Discussion

In this paper, a new method is applied to the datasets previously used and published by Dresler and Müller et al. to confirm and uncover the distributed networks responsible for the superior memory capabilities, in memory athletes and a newly trained group [1], [10]. The datasets used, encompassed fMRI encoding task data of participants trained in the method of loci, and the fMRI data of memory athletes of the 2010-2013 World Memory Championships. The algorithm employed is called SPADE, which created spatial

Comparison	Test accuracy	P-value
LOC pre vs. LOC post	0.82 (0.35)	0.0036
CON pre vs. CON post	0.55 (0.5)	0.24
WMN pre vs. WMN post	0.5 (0.5)	0.81

Table 2: Summary of the results of the SPADE out of sample analysis. The filters are learned from the athletes and controls. These filters are then used for classification of the three groups (LOC, WMN, PAS) pre-post-training using an RLDA classifier. The column 'test accuracy' gives the RLDA classification accuracy of the athletes and controls filters to classify the pre-post-training state of the groups.

filters that correlate with the brain regions containing the most information in terms of covariance for the groups during encoding.

Our results confirmed the outcomes found by Dresler et al. that the athletes could be distinguished from their controls based on their functional connectivity profiles [1]. The brain regions that were shown to be essential for superior memory performance by Dresler et al. were also confirmed to be present in the connectivity profile of the athletes in this paper, including the DLPFC, MPFC and the MTL. In the connectivity networks of both the athletes and controls during encoding, the following areas were determined to be present: the bilateral hippocampus, thalamus, parahippocampal gyrus, supramarginal gyrus, cingulate gyrus, precuneus cortex and the brainstem. The athlete group showed additional brain regions that covariate, located in the occipital pole and the prefrontal cortex.

A complicated issue with multivariate pattern analysis (MVPA) methods such as SPADE, is that they are generally not well suited to test a hypothesis regarding the specific involvement of certain brain regions during tasks [18]. It could be due to various reasons that covariance occurs between different brain regions — for example, certain brain areas and processes covariate naturally due to the organisation of the brain [19]. Furthermore, a multitude of brain processes could be induced by external factors, not of interest to researched behavioural mechanisms. In general, covariance patterns are difficult to localise and susceptible to a mixture of signals that covary with the attended stimulus [20]. Therefore, the filters provided by SPADE give limited information about the exact role of a particular ROI, and the patterns of weights can only be interpreted in correspondence to each other. To further understand the results demonstrated by the filters, they should be compared to earlier literature on these networks.

In previous research, the brain areas mentioned above, have been associated with working memory, visual imagination, and spatial navigation, among others. Frontal brain regions in combination with the hippocampus have been linked to attention and the maintenance of active memory representations during working memory tasks [21], [22], [23]. The mediodorsal thalamic-prefrontal cortical network has been shown to activate during successful encoding tasks [24], [25], [26]. The precuneus and frontal regions are present in spatially guided actions, mental imagery and episodic memory [27]. Extending these observations to our results implies that for athletes and controls, most of the aforementioned brain areas covariate to support extensive encoding during a working memory task.

We suggest that the additional prefrontal, parietal and occipital areas that showed to covariate for the athletes can be understood in terms of the networks activated when performing the method of loci, related to visual imagination and scheme-like-operations. The hippocampus, parahippocampal, retrosplenial, prefrontal, and parietal cortices have been pinpointed as essential during actual and imagined spatial navigation [28], [29], [30]. Furthermore, the hippocampal-prefrontal cortex connection has proven essential in assimilating new information into existing knowledge schemas [31], [32]. For visual imagination, the frontal regions direct the type of image to be formed and orchestrate the brain areas corresponding to the imagined senses [33]. The parietal cortex provides the sensory representations of the imagined image [34]. Lastly, the occipital cortex renders the visual component of the imagined scene [35]. The role of these areas have also been juxtaposed with general functions needed in memory tasks [36]. However, the only obvious behavioural difference between the athletes and controls is the use of the method of loci and therefore we hypothesise that these areas become more connected when applying this method.

Our results demonstrated that the SPADE filters could be applied to correctly decode and classify the athletes from their controls using an RLDA classifier. One of the problems with using MVPA to train classifiers is that it is hard to ultimately dictate what information the classifier used to make its predictions [37]. When a classifier is being applied on small samples, overfitting will always remain a problem. For example, when one or two participants demonstrate a lot of movement or other artefacts, it will skew the entire dataset, and the classifiers could be trained on noise [38]. In this paper, there were two methods tested to ensure that the found classification accuracy corresponded to a stable connectivity pattern. First, a leave-one-out cross-validation was performed in combination with a permutation test that determined that the classification accuracy for the athletes and controls was statistically significant. Second, the found filters were tested on an independent testing set LOC pre-post-training, which also gave a significant classification accuracy.

The results presented in this paper confirmed that the connectivity profile established in the novice group pre-post-training could be classified using the athletes and controls' connectivity profile. This classification reinforces the results earlier found by Dresler et al. that the connectivity patterns between the athletes-controls are comparable to the pre-post-training group [1]. The trained group used the same techniques to accomplish the encoding assignment as the athletes. Hence, we suspected this group could be classified using the connectivity patterns of the athletes-controls.

One fundamental limitation of our study is that to apply SPADE an ROI selection needs to be made beforehand due to memory constraints [11]. Therefore the conclusions made in this study will always be limited to the 70 brain regions chosen. For this paper, we selected brain regions located in networks related to memory and visuospatial processing. However, some results previously found for the athletes using the method of loci could not be demonstrated due to this constraint. One of them being the usage of the caudate nucleus by the memory athletes, as this was not an ROI in our selection [10]. Therefore, for future studies, it would be informative to test different ROI selections.

Conclusion

In conclusion, we demonstrated that we could decode based on connectivity patterns, if a person belongs to a memory athlete or control group using SPADE. Moreover, we can visualize the unique spatial patterns of brain activity connected with these groups. Furthermore, this classification can be extended to a newly trained group in the method of loci, separating their pre-post-training stage. Accordingly, these results confirm earlier work by Dresler et al. that the athletes and controls can be separated based on distributed changes in their functional connectivity networks and that these distributed network changes are also present in a newly trained group.

Supplementary

Simultaneous diagonalization

The SPADE algorithm stands for Spatial Patterns for Discriminative Estimation. It is a combination of dimensionality reduction, simultaneous diagonalisation, model order selection, and the visualization of the associated spatial maps [11]. If there are two covariance matrices C_1 and C_2, which are by definition symmetric, then they can be simultaneously diagonalised as follows:

1. The covariance matrix C_1 is whitened by:

$$Y = \Theta^{-1/2}\phi^T X \tag{1}$$
$$C_1\phi = \phi\Theta \tag{2}$$
$$\phi^T\phi = I \tag{3}$$

With Θ the eigenvalues and ϕ the eigenvector matrix.

2. After, the matrices C_1 and C_2 are transformed:

$$\Theta^{-1/2}\phi^T C_1\phi\Theta^{-1/2} = I \tag{4}$$
$$\Theta^{-1/2}\phi^T C_2\phi\Theta^{-1/2} = K \tag{5}$$

3. Finally, the orthonormal transformation is applied to diagonalise K.

$$Z = \Psi^T Y \tag{6}$$
$$K\Psi = \Psi\Lambda \tag{7}$$
$$\Psi^T\Psi = I \tag{8}$$

With Λ the eigenvalues and Ψ the eigenvector matrix

Therefore, the two matrices are then simultaneously diagnolised by the transformation matrix $\phi\Theta^{-1/2}\Psi$. For more details refer to [11], [13].

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