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# Identifying Cognitive Processes and Neural Substrates of Spatial Transformation in a Mental Folding Task with Cognitive Modeling

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## Abstract

The cognitive processes underlying mental folding have been investigated for decades, while the neural correlates associated with this spatial transformation are barely understood. This study combines cognitive modeling with EEG recordings from 41 subjects to investigate the general mechanisms of mental spatial transformation. By linking model-based simulation and electrocortical activity, we identified brain areas involved during mental folding. Our novel approach showed active central parietal and left parietal, as well as occipital areas during spatial storage, while the right parietal cortex was associated with spatial transformation. The left occipital and parietal regions were active especially during visual baseline trials, while the right parietal region exhibited stronger activity for more difficult folding trials, replicating previous results. The varying activation patterns imply different cognitive loads for storage and for transformation depending on task difficulty.

**Keywords:** mental folding; spatial transformation; ACT-R; electroencephalography; independent component analysis

## Introduction

Mental spatial transformation concerns ubiquitous cognitive processes that help us understand and interact with the world around us. It is implicated with general intelligence (Lohman, 2013), and aptitude in mathematics, STEM fields and reasoning ability (Uttal & Cohen, 2012; Newcombe, Booth, & Gunderson, 2019). Yet, most research focuses on a single paradigm, requiring mental rotation to identify objects (Shepard & Metzler, 1971). While general core processes underlying mental spatial transformation might exist, their exact nature seems obscured by the lack of research into other experimental paradigms of spatial transformation. A lesser presented modality of spatial transformation relates to the mental folding of a figure to allow for judgments on its shape or surfaces (Shepard & Feng, 1972). While both mental rotation and mental folding are categorized as being object-based instead of perspective-based, and featuring intrinsic instead of extrinsic transformations, mental folding is distinguished by its necessity of non-rigid transformations, meaning that the shape of the object itself is required to be changed (J. Harris, Hirsh-Pasek, & Newcombe, 2013; Atit, Shipley, & Tikoff, 2013).

Few electroencephalography (EEG) studies have been conducted on the mental folding paradigm. Milivojevic, Johnson, Hamm, and Corballis (2003) conducted a study on mental letter rotation and mental folding. For mental folding, active

areas have been found in both parietal hemispheres, in contrast to only right parietal activation for mental rotation. They interpreted the folding results as an involvement of the right parietal cortex for easy tasks, while more challenging tasks additionally invoke the left parietal cortex. Glass, Krueger, Solomon, Raymont, and Grafman (2013) analyzed the influence of brain lesions on mental folding performance, and also identified right parietal areas important to folding processes.

While EEG is able to find areas involved in mental folding and other tasks, identifying their exact functional contribution to the dynamics of cognition can be difficult. A possible remedy is cognitive modeling, which allows for the simulation of cognitive processes during specific tasks. ACT-R (Anderson, Qin, Jung, & Carter, 2007) is a cognitive architecture enabling the streamlined creation of such cognitive models. Here, cognition is modeled by the interplay of so-called modules, dedicated units of cognition for e.g. visual, declarative or motoric processing, effectively producing intra-trial predictions of cognitive processes (Anderson & Lebiere, 2014). While modules do not directly represent specific neural substrates, their activity has been mapped to brain regions before (e.g., Anderson et al., 2007; Anderson, Fincham, Qin, & Stocco, 2008; Borst & Anderson, 2015).

Activity predictions by ACT-R have been successfully used in conjunction to EEG data. Griffiths, West, and D'Anguilli (2011) were able to reproduce the timing and firing pattern of event-related potentials (ERPs) by simulating dipole generation at proposed sites related to ACT-R modules. ACT-R module activity was also found to correlate with specific cortical topographies, EEG frequency bands, and EEG oscillation patterns (van Vugt, 2012, 2013), and cognitive processing stages derived from EEG (Heimisch, Preuss, & Russwinkel, 2023). Anderson, Carter, et al. (2008) outlined several methodological obstacles for reliable model-brain comparisons, namely temporal variability between datasets and the difficulty of adequate model-fit assessment, which they suggest can be mitigated by using time-locked data such as ERPs, controlling for autocorrelation of errors, and minimizing squared deviations between observed and predicted data.

ACT-R has already been used to model data of spatial tasks. Spatial modeling frameworks for the architecture have been proposed before by Gunzelmann and Lyon (2007) and

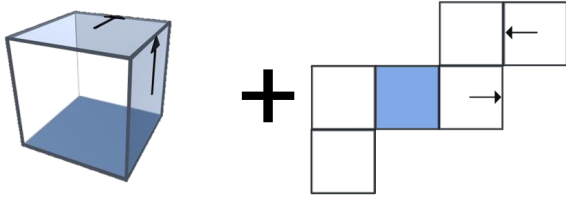


Figure 1: Example of a “match” trial with difficulty level H, with 6 SSC necessary for comparing both patterns.

Harrison and Schunn (2019), with both emphasizing separate spatial representation and transformation processes, but so far lacking available implementations. Peebles (2019) extended the visual module by rudimentary spatial processing features to simulate solving of a two-dimensional mental rotation task. Finally, earlier versions of a spatial module used in this paper were used to create cognitive models for a mental rotation (Preuss & Russwinkel, 2021; Heimisch et al., 2023) and a mental folding task (Preuss, Raddatz, & Russwinkel, 2019).

In this paper, we will analyze EEG data from a mental folding experiment, and identify relevant brain areas for distinct cognitive functions by way of a cognitive model, supported by the addition of a spatial module to the ACT-R architecture. We will show that individual ACT-R module output will be matched with clusters of EEG activity that comprise sensible regions for their respective functions on the one hand, and that spatial representational and transformational activity are differentiable on the other hand. Finally, we argue that a better understanding of cognitive processes during mental folding will provide further insight into mental spatial transformation.

## Methods

*Experiment, EEG recording and pre-processing are described in more detail in Hilton, Raddatz, and Gramann (2022).*

### Experiment

**Participants** 41 participants (29-38yrs, mean 28.8yrs, *SD* 5.1yrs; 20 female) took part in the experiment, compensated by 10€ per hour or course credits. All participants were right-handed, had normal or corrected-to-normal vision, and reported no neurological conditions. They took 60 min to complete all trials on average. Informed consent was provided prior to the beginning of the experiment, and ethical approval was granted by the Institute of Psychology and Ergonomics, TU Berlin ethics board. A short mental rotation task was performed as an online pretest to collect response time (RT) data for correlation with the main task.

**Procedure** The experiment consisted of a mental folding task based on Shepard and Feng (1972) and Wright, Thompson, Ganis, Newcombe, and Kosslyn (2008). After a fixation-cross, a reference figure appeared on screen, consisting of semi-transparent cube shapes, with a blue bottom square and an arrow each on two of the six cube surfaces. A second later, a target stimulus was presented, resembling a paper-folding

pattern of six connected squares, also with one blue bottom square and one arrow each on two of the squares. We tasked the participants with mentally folding the target stimulus to decide if the two arrows on the target figure would match the arrows on the reference figure, if folded up. “Match” or “mismatch” responses were entered into a response pad (Cedrus RB-540). The figures were grouped into 4 conditions, determined by the sum of squares carried (SSC, Shepard & Feng, 1972) necessary to fully fold each arrow square into its final position: 0 SSC (*A* or *baseline*, as spatial transformation is not required), 4 SSC (*F*), 5 SSC (*G*) and 6 SSC (*H*). 120 trials<sup>1</sup> were presented in 5 blocks each, totaling 600 trials. We presented participants with 10 practice trials before the actual task. Figure 1 displays an example of an H difficulty trial (6 foldings necessary).

**EEG recording and pre-processing** We continuously recorded 64-channel, 500 Hz EEG (BrainAmps, Brain Products) arranged according to the 10% system (Chatrjian, Lettich, & Nelson, 1985) during the experiment, referenced to FCz. We then preprocessed the resulting data using the BeMoBIL pipeline (Klug et al., 2022) for the EEGLAB toolbox (Delorme & Makeig, 2004), with the data being low-pass filtered at 124 Hz and downsampled to 250 Hz. Then, time domain cleaning (Gramann, Hohlefeld, Gehrke, & Klug, 2021) identified noisy data segments, leading to ~15% rejected data per participant. We identified Independent components (ICs) through an adaptive mixture independent component analysis (Palmer, Makeig, Kreutz-Delgado, & Rao, 2008). Afterwards, we fitted the resulting ICs with an equivalent dipole model (Oostenveld & Oostendorp, 2002) and classified brain and non-brain processes by applying ICLabel (Pion-Tonachini, Kreutz-Delgado, & Makeig, 2019), before further low-pass filtering at 75 Hz. Epochs were defined from 200 ms before reference onset to 2000 ms after target onset, and baseline correction was applied using the 200 ms pre-reference time window. We rejected the 10% noisiest trials, as well as trials with RTs deviating more than 3 median absolute deviations from the mean. The ICs thus produced were clustered over participants using a repetitive k-means algorithm (Gramann et al., 2021), allowing for prior selection of a region of interest (ROI) for cluster generation. We chose a parietal ROI (Talairach:  $x = 0$ ,  $y = -66.7$ ,  $z = 41.1$ ), based on a mental rotation meta-analysis (Zacks, 2008), and set the desired number of clusters to 16.

**Additional EEG data treatment** The cluster data was further prepared to facilitate comparison to module activity data. We included all 4 difficulty conditions and “match” and “mismatch” trials, partitioning the data into 8 conditions. A Hilbert transform was then applied to all cluster ERPs each to produce the analytical signal for each, reflecting the strength of an oscillating signal (Kozma, Aghazarian, Huntsberger, Tunstel, & Freeman, 2007). The resulting activity strength signals of each cluster will subsequently be referred to as cluster activity.

<sup>1</sup>We omitted 24 mismatch trials per block to shorten experiment duration.

## Spatial module

To facilitate model-based research on mental spatial transformation, we hypothesized and implemented a generalized framework, in the form of a spatial module for ACT-R. It extends ACT-R by the ability to perceive and process three-dimensional structures (e.g., 3D point clouds) and relies heavily on the default ACT-R architecture, adding two dedicated buffers for spatial representation and spatial transformation each. Its main function is to produce a time delay for the requested storage and transformation actions, based on mental spatial transformation literature, e.g. RT increase (Shepard & Metzler, 1971; Shepard & Feng, 1972; Just & Carpenter, 1976), memory capacity limits (Pylyshyn, 1989; Gunzelmann & Lyon, 2007), transformation complexity (Neely & Heath, 2010; Gunzelmann & Lyon, 2007), separation of representation and transformation (Baddeley & Lieberman, 2017; Gunzelmann & Lyon, 2007), and interference between the two (Sims & Hegarty, 1997). Based on simpler formulae reported in earlier studies (Preuss et al., 2019; Preuss & Russwinkel, 2021; Heimisch et al., 2023), the delay is now computed as follows:

$$\text{Transformation delay} = b + F * (1 + C * N^2) * x, \text{ for } N \leq L$$

We model transformation delay as equal to the base cost ( $b$ ) for spatially transforming objects<sup>2</sup>, plus the product of three terms: a delay factor ( $F$ ), a term representing a penalty for the currently applied number of transformations ( $N$ ) mediated by a complexity factor ( $C$ ), and the raw degree value of the transformation request ( $x$ ). If the current sum of transformations  $N$  exceeds the maximum number of applicable transformations ( $L$ ), the transformation is not applied.

## Cognitive model and activity simulation

We created a cognitive model solving a simulated replication of the experiment, based on cognitive processes theorized by Shepard and Feng (1972) and Just and Carpenter (1976), comprising visual encoding, transformation and comparison, and motor response stages. The model tried to complete both necessary transformations (one for each arrow), and initiate a comparison process of the resulting structure with the reference figure. Using instance-based learning (Gonzalez, Lerch, & Lebiere, 2003), the model was able to retrieve prior trial outcomes to bypass the need for spatial transformation. Possible non-spatial shortcuts were scanned for concurrently, with certain patterns (e.g., certain geometric relations between squares) allowing the model to skip spatial transformation. The probability of shortcut use was mediated by a reinforcement learning algorithm included in ACT-R (Fu & Anderson, 2004).

At reference figure onset, the stimulus was encoded as a spatial structure, including features possibly affording non-spatial shortcuts (e.g., an arrow on the bottom square). This process was repeated until target figure appearance to strengthen base-level activation of the reference stimulus, facilitating memory

<sup>2</sup>Set to 0 for mental folding model, instead using a fixed delay of 200 ms at time of chunk creation.

retrieval later in the trial. Target stimulus onset triggered both a separate spatial structure encoding, clearing the reference figure from active mental representation, and a background memory retrieval process to try and retrieve an associated solution to the stimulus completed in the past. After encoding, the actual transformation process was initialized, identifying “paths” from the bottom square to squares containing arrows. These paths were then consecutively folded upwards, starting at the bottom square and applying a 90° transformation at the respective next “fold” to the remaining path, until the arrow square was folded into its final position. A static transformation then rotated the folded spatial structure into the same position as the reference cube. If the background memory retrieval successfully found a representation at any time during the transformation loop, the transformation was aborted and the retrieved structure adopted from memory instead. Subsequently, the reference figure encoded at the beginning of the trial was retrieved from memory, or if faster, visually encoded again. A final comparison between the reference cube and folded target representation<sup>3</sup> subsequently selected an appropriate response. During the motor process, the folded target structure was associated with the unfolded target stimulus and saved into declarative memory, thereby creating or strengthening a solution as instance-based memory.

We fit the cognitive model as close as possible to the experimental data by adjusting ACT-R parameters, measured in correlation and root mean square error (RMSE). A grid search over a reasonable range of parameter values using 6 parameters resulted in a *latency factor* of 0.2 (default: 1), *retrieval threshold* of -1.8 (default: 0), *activation noise* of 0.5 (default: n/a, but 0.5 is recommended), *expected gain* of 1 (default: 0), *spatial delay* ( $F$ ) of 0.001 (default: n/a), and *spatial complexity* ( $C$ ) of 0.5 (default: n/a). Then, we simulated individual participants by presenting a new model instance with the same pseudo-randomized order of trials as each single participant to control for sequence effects. Binary activity was produced by each module during each trial, referred to as module activity. Subsequent aggregation over participants and trials produced a gradient output in the form of a percentage of a particular module being active across all trials during a single time sample. Only trials answered correctly by both human and modeled solver were included. Module activity was produced with a 250 Hz sample rate, and trimmed to 2000 ms after target onset to match the available EEG data. We performed no time warping, as to not falsify intra-trial modular and temporal dynamics.

## Statistical analysis

For final analysis, we selected ACT-R modules meaningful to the mental folding task, including the visual, retrieval, imaginal, and spatial modules. As the spatial module produces separate storage and transformation output, both components were included, resulting in 5 simulated cognitive structures.

<sup>3</sup>Using the Euclidean distance between folded target arrows and reference cube arrows.

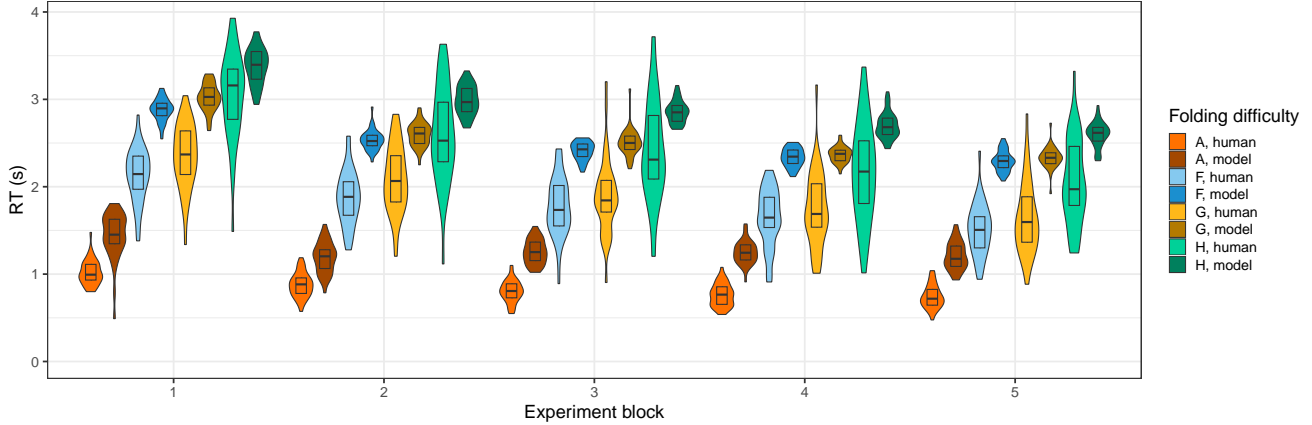


Figure 2: RTs of experiment participants (light colors) and participant-matched model instances (dark colors), grouped by folding difficulty and experiment block.

We then applied linear regression models utilizing generalized least squares (GLS) to provide statistical inference. We chose GLS as it is robust against autocorrelation of errors and unequal variances in conditions. For each cognitive activity prediction, its activity was to be predicted by each cluster’s activity. First-order autocorrelation was controlled for per condition, as was variance. Finally, we considered significant clusters for each module meaningful predictors, consequently inferring a module-cluster match.

## Results

### Experiment results

Participants showed an average correctness rate of 95.8%. We analyzed the effect of folding difficulty (factor: 0/A, 4/F, 5/G, 6/H), experiment block (factor: 1-6), and their interaction on RT by multiple linear regression, with subject as random intercept factor. The linear model explained 88% of variance (corrected  $R^2 = .88$ ). Difficulty was significant in all levels ( $\beta_{\text{folding F}} = 1.11$ ,  $\beta_{\text{folding G}} = 1.34$ ,  $\beta_{\text{folding H}} = 2.03$ , all  $p < .001$ ), as was block ( $\beta_{\text{block 2}} = -.145$ ,  $p < .05$ ;  $\beta_{\text{block 3}} = -.218$ ,  $p < .001$ ;  $\beta_{\text{block 4}} = -.260$ ,  $p < .001$ ;  $\beta_{\text{block 5}} = -.277$ ,  $p < .001$ ). Interaction of folding difficulty and block was significant for blocks 4 and 5 with level F ( $\beta_{\text{block 4 \& folding F}} = -.226$ ,  $p < .01$ ;  $\beta_{\text{block 5 \& folding F}} = -.341$ ,  $p < .001$ ), blocks 3 to 5 with level G ( $\beta_{\text{block 3 \& folding G}} = -.253$ ,  $p < .005$ ;  $\beta_{\text{block 4 \& folding G}} = -.362$ ,  $p < .001$ ;  $\beta_{\text{block 5 \& folding G}} = -.448$ ,  $p < .001$ ), and all blocks with level H ( $\beta_{\text{block 2 \& folding H}} = -.306$ ,  $\beta_{\text{block 3 \& folding H}} = -.43$ ,  $\beta_{\text{block 4 \& folding H}} = -.620$ ,  $\beta_{\text{block 5 \& folding H}} = -.724$ , all  $p < .001$ ). These results showed significantly lower RTs for all experiment blocks compared to the first, and higher RTs for more difficult conditions, with a stronger decrease in RTs for higher difficulty levels in later experiment blocks.

We calculated individual participant regression slopes for the effect of difficulty on RT for both the mental rotation pretest and the mental folding task. No significant relationship

Table 1: Cerebral areas of module-matched clusters for mental folding, sorted by coefficient strength. X, y, z refer to Talairach coordinates. ROI cluster in bold.

Module	Area	x	y	z
Visual	Right superior parietal	43	-16	48
Retrieval	Left parietal	-32	-36	44
	Right inferior temporal	50	-48	2
	Left superior frontal	-40	-5	49
	Right parietal	63	-24	20
Imaginal	-	-	-	-
Spatial (repr.)	Left occipital	-36	-67	-17
	<b>Central parietal</b>	<b>7</b>	<b>-39</b>	<b>39</b>
Spatial (transf.)	Left parietal	-32	-36	44
	Right posterior parietal	36	-69	32
	Left parietal	-32	-36	44
	Right parietal	63	-24	20

between both RT slopes was produced ( $r = .28$ ,  $p = .073$ ).

### Model fit

The cognitive model achieved a correctness rate of 100%. Participant and model RTs showed a high correlation and moderate deviation ( $r(796) = .82$ ,  $p < .001$ ,  $RMSE = .7$  on subject level;  $r(18) = .98$ ,  $p < .001$ ,  $RMSE = .62$  on group level). The cognitive model replicated individual subjects reasonably well, but yielded slower averaged RTs than human responders ( $M_{\text{human}} = 1.75$ ,  $SD_{\text{human}} = .73$ ,  $M_{\text{model}} = 2.3$ ,  $SD_{\text{model}} = .67$ ). See figure 2 for group-level results.

We performed an ANOVA on a combined simulation and experiment dataset to analyze the effect of data source (factor: human or model) and its interactions with folding difficulty and experiment block on RT, with subject as an added error term. All factors except subject reached significance ( $F_{\text{source}}(1, 1541) = 1696.3$ ,  $F_{\text{source \& rotation}}(6, 1541) = 1348.2$ ,  $F_{\text{source \& block}}(10, 1763) = 129.2$ , all  $p < .001$ ;

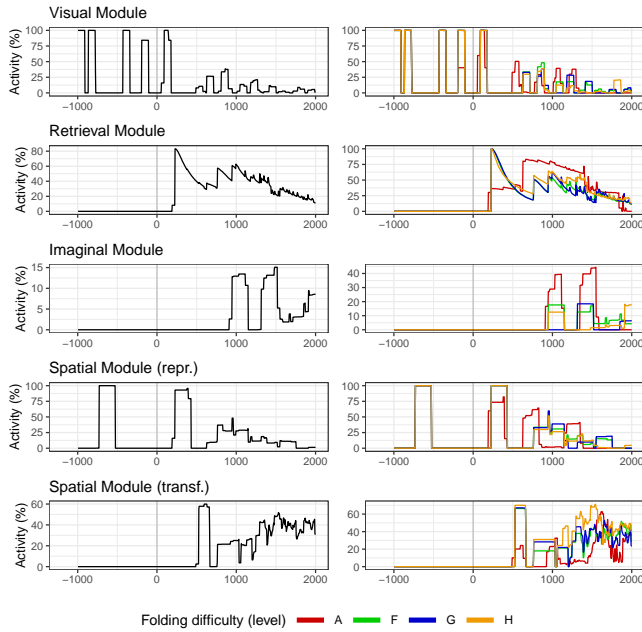


Figure 3: Activity of selected ACT-R modules during mental folding task solving, aggregated over participant-matched instances of the cognitive model, aggregated over (*left*) and separated by conditions (*right*).

$F_{\text{subject}}(2, 37) = 1.657, p = .205$ ). RT predictions from the cognitive model differ significantly from RTs observed in the experiment, with varying influence per folding difficulty and experiment block but no significant influence of subject intercepts.

### IC clustering

16 clusters were generated, composed of an average of 35 ICs ( $SD = 9.0$ , range 21-58) from 21 participants on average ( $SD = 7.5$ , range 12-40). The ROI parietal cluster contains 58 ICs from 40 participants. Additionally, a left parietal cluster of 45 ICs by 33 participants was produced.

### Module-cluster fit

Figure 3 shows the simulated activity of the visual, retrieval, imaginal, and spatial modules of ACT-R.

**Visual module** The visual module is used by the model to identify and encode the virtually displayed figures. Its GLS regression showed no improvement of fit over its null model ( $\chi^2(16, 6000) = 18.86, p = .276$ ). Nevertheless, it received significant contribution from a right superior parietal cluster ( $\beta = -.31, t(5998) = -2.17, p < .05$ ).

**Retrieval module** The cognitive model assumed short-term memory retrieval processes for handling of the multiple spatial structures necessary for a comparison. The retrieval GLS yielded high predictivity of cluster activity on module activity compared to its null model ( $\chi^2(16, 3624) = 41.16, p < .001$ ). It also held the highest amount of significant clus-

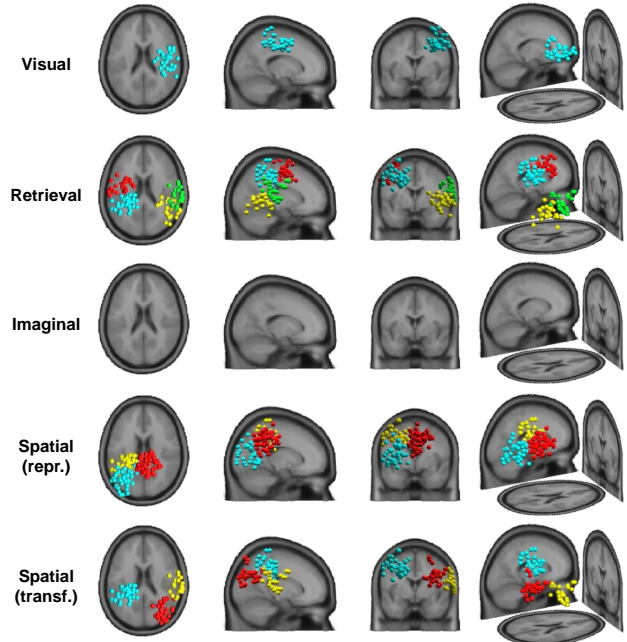


Figure 4: Mental folding IC clusters with a significant ( $p < 0.05$ ) influence on the respective module according to GLS linear models. Colors reflect ranking of clusters by coefficient strength (from most to least significant: light blue, red, yellow, green). The imaginal module identified no significant clusters.

ters among the selected modules: a left parietal ( $\beta = .293, t(3622) = 4.01, p < .001$ ), a right inferior temporal ( $\beta = -.137, t(3622) = -2.29, p < .05$ ), a left superior temporal ( $\beta = .184, t(3622) = 2.04, p < .05$ ), and a right parietal cluster ( $\beta = .105, t(3622) = 1.97, p < .05$ ).

**Imaginal module** The mental folding model used the imaginal module to associate a target stimulus with its fully transformed outcome, effectively to create a mental representation as instance memory. No significant difference between null and full model was reached for the imaginal GLS linear model ( $\chi^2(16, 2184) = 9.4, p = .9$ ), and it showed no significant clusters.

**Spatial module** The spatial module was used to handle storing of mental spatial representations, and transform these representations according to the presented task. It outputs its activity in two separate streams, as representative and transformative activity, respectively.

*Representation activity* – The spatial representation GLS linear model had a significantly better fit compared to the null model ( $\chi^2(16, 5536) = 35.91, p < .01$ ). Significance was reached by a left occipital cluster ( $\beta = -.272, t(5534) = -3.01, p < .01$ ), a central parietal (ROI cluster,  $\beta = .203, t(5534) = 2.5, p < .05$ ), and a left parietal cluster ( $\beta = .198, t(5534) = 2.12, p < .05$ ).

*Transformation activity* – The GLS model for spatial transformation reached a significant improvement of fit over the



null model ( $\chi^2(16, 3024) = 30.39, p < .05$ ). A right posterior parietal cluster ( $\beta = -.188, t(3022) = -2.26, p < .05$ ), a left parietal cluster ( $\beta = -.195, t(3022) = -2.23, p < .05$ ), and a right parietal cluster ( $\beta = .124, t(3022) = 2, p < .05$ ) reached significance.

**Identified cluster structures** Figure 4 shows Talairach brain renderings with IC clusters identified as significantly matching module activity produced by the mental folding cognitive model, which are listed in table 1. The mental folding task showed a right temporal area for visual activity; retrieval activity was associated with lateralised parietal, temporal, and frontal areas. Spatial storage activity was shown in central parietal, and left parietal and occipital areas, whereas spatial transformation activity was lateralized in parietal regions.

## Discussion

**Results discussion** The model produced a high goodness-of-fit, but still carries a non-trivial mismatch to the behavioral data, leading to lower reliability of module activity output. This comes down to the complexity of the task, requiring multiple solving steps. However, as modules are independent units and interpretable on their own, the module-cluster comparisons should be considered as a valid outcome, regardless of an imperfect model fit.

Module-cluster matches are mostly in line with expected brain areas as reported in literature (e.g., Borst & Anderson, 2015), with spatial activity found in parietal clusters. No clusters were found to match with imaginal module activity, which implies that its function in the model as an instance-forming mechanism does not hold true. As its activity was produced comparatively late in each trial however, it might have been not reflected well by the available cluster data. Retrieval module activity mirrored its associated clusters well, validating the model assumption of intra-trial retrieval processes.

**General discussion** As hypothesized in the beginning, we produced module-cluster matches in regions that have been established in literature to be functionally associated, although presenting more varied patterns than suggested by e.g. Borst and Anderson (2015). In addition, representative and transformative spatial activity was shown to be differentiable by the module, identifying a representation cluster in the proposed ROI region as well as lateralized clusters with cognitive loads shifting with increasing trial difficulty. The spatial module and cognitive model were able to predict activity, timing and variability of task conditions well.

Spatial representations were associated with central and left hemispheric areas, as were spatial transformations in low difficulty conditions. Trials with higher difficulty showed more transformation activity in the right hemisphere. The lateralization contrasts Milivojevic et al. (2003) who reported lateralization only for rotation. While visuospatial processing is usually reported to be predominantly right-hemispheric (Milivojevic, Hamm, & Corballis, 2009; I. M. Harris et al., 2000; Zacks, 2008), our results suggest lateralization to be

primarily dependent on task difficulty.

Some of the clusters matched with spatial processes are usually associated with vision, and vice versa, implying a joined visuospatial process guiding mental spatial transformation, rather than purely visual or spatial processes. With growing experience, solvers of spatial tasks might create an internal “spatial structure vocabulary”, recalling more complex spatial structures and their relation to the task outcome by sight of the stimuli alone. This is in line with (Bethell-Fox & Shepard, 1988), who found stimulus complexity to decrease in its effect on RT over the course of a 2D mental rotation experiment, and perhaps similar to an increase in domain-specific visuospatial working memory efficiency reported for, e.g., chess board states (Smith, Bartlett, Krawczyk, & Basak, 2021).

**Limitations** We found no neural correlates for simulated activity of the imaginal module, and while a parietal cluster structure was found to match visual module activity, we would have expected to find an occipital substrate. Furthermore, GLS models for both modules were not significantly better than their respective null models. This is potentially caused by the spatial focus of the task introducing a bias in neural visuospatial and working memory activity, further exacerbated by the cognitive model explicitly using the spatial module in part for visuospatial encoding and representation processes. Additionally, our use of GLS regression relied heavily on autocorrelation of predictor errors. Although this has proven effective in filtering out weak or unlikely predictors, it assumes “time” as a predictor to have high explanatory power. This generalization might effectively conceal a number of confounding variables, and may indeed be counterproductive in the analysis of experiments with shorter trials, or with a higher number of time-fixed events (see Friston (2005) for a similar argument). Both issues warrant a careful interpretation of our results, and will be examined more closely in future studies.

**Future research** We will apply the method presented in this paper to a mental rotation study in an upcoming paper, and juxtapose the resulting clusters with those presented herein (Preuss, Hilton, Gramann, & Russwinkel, 2023). As some authors theorized different cognitive loads on spatial representation and transformation between mental rotation and folding, this model-based approach might illuminate the differences and similarities of the two paradigms. Furthermore, our upcoming research will focus on a novel combined mental rotation and folding experiment, allowing analyses of mental spatial transformation in a unified manner.

## Data and Software

EEG IC cluster ERPs and statistics from mental rotation and mental folding experiments:

<https://doi.org/10.14279/depositonce-19702>

Spatial module:

<https://doi.org/10.14279/depositonce-17795>

Mental folding model:

<https://doi.org/10.14279/depositonce-19515>

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