Temporally delayed representations in alpha and beta rhythms in higher-order cortical networks track increasing relational integration demands

Conor Robinson[1,2*], Luca Cocchi[1,2], Takuya Ito[3], Luke Hearne[1*]

[1]Clinical Brain Networks Group, QIMR Berghofer Medical Research Institute, Brisbane, QLD, Australia
[2]Faculty of Medicine, University of Queensland, Brisbane, QLD, Australia
[3]T.J. Watson Research Center, IBM Research Yorktown Heights, NY, USA

Abbreviated title

Neural rhythms track integration demands

*Corresponding authors

conor.robinson@qimrberghofer.edu.au, luke.hearne@qimrberghofer.edu.au

Number of pages: 31
Number of figures: 5
Number of words: abstract: 225; introduction: 638; discussion: 1320

Conflict of interest statement

C.R., L.C., and L.J.H. are involved in a not-for-profit clinical neuromodulation centre (Queensland Neurostimulation Centre). This centre had no role in the present study.

Abstract

Relational reasoning is the ability to infer and understand the relations between multiple elements. In humans, this ability supports higher cognitive functions and is linked to fluid intelligence. Relational complexity (RC) is a cognitive framework that offers a generalisable method for classifying the complexity of reasoning problems. To date, increased RC has been linked to static patterns of brain activity supported by the frontoparietal system, but limited work has assessed the multivariate spatiotemporal dynamics that code for RC. To address this, we conducted representational similarity analysis in two independent neuroimaging datasets (Dataset 1 fMRI, n=40; Dataset 2 EEG, n=45), where brain activity was recorded while participants completed a visuospatial reasoning task that included different levels of RC (Latin Square Task). Our findings revealed that, spatially, RC representations were widespread, peaking in brain networks associated with higher-order cognition (frontoparietal, dorsal-attention, and cingulo-opercular). Temporally, RC was represented in the 2.5 - 4.1 seconds post-stimuli window and emerged in the alpha and beta frequency range. Finally, multimodal fusion analysis revealed the information carried in the representation is concordant with the theorised RC model relative to a model of cognitive effort in higher-order cortical networks. Altogether, the results further our understanding of what information is held during relational processing, highlight the spatially distributed nature of RC representations, and emphasise the importance of late frequency-resolved neural processes to resolve RC.

Significance statement

Assessing cognitive abilities in human reasoning requires a cognitive framework that can define a problem’s complexity. Relational complexity (RC) theory has emerged as a robust framework, parameterising complexity based on the number of relations that must be processed in parallel to solve a problem's underlying relational representation. To investigate ‘where’ or ‘when’ the brain codes for this cognitive abstraction, our study examined multimodal whole-brain activity during short reasoning problems at various complexity levels. We found that higher-cortical networks coded a representation tracking the transition between complexity demands, emerging during late-stage cognitive processing. Our findings provide neuroscientific evidence for a neural coding of relational complexity, pinpointing the frequency-resolved dynamics associated with these mechanisms.

Introduction

Relational reasoning, the ability to mentally manipulate and integrate relationships between interacting elements, is a core component of higher-order cognition and a hallmark of human intelligence (Waltz et al., 1998; Halford et al., 2010). Studies on relational reasoning reveal fundamental capacity limitations in the number of relations that can be processed simultaneously (Halford et al., 2005). This constraint is formalised within relational complexity (RC) theory, a framework that has uncovered performance boundaries in everyday problem-solving (Boag et al., 2006), neurodevelopment (Halford et al., 1998; Eslinger et al., 2009; Todd et al., 2019), and clinical populations (Goel and Grafman, 1995; Hearne et al., 2019). While numerous studies have demonstrated the broad utility of RC theory, a key open question remains: where and when does the brain represent RC?

Functional magnetic resonance imaging (fMRI) work has provided a map of the brain *spatial* correlates of relational reasoning (Wertheim and Ragni, 2018). This body of work has led to the perspective that a frontoparietal network (FPN), also known as the multiple-demand network, is essential for performing relational reasoning tasks (Duncan and Owen, 2000; Cocchi et al., 2013; Hearne et al., 2017; Holyoak and Monti, 2021; Morin et al., 2022). Further work has emphasised interactions between the FPN and other brain systems, such as the cingulo-opercular and sensory networks while performing complex reasoning tasks (Cocchi et al., 2013; Cole et al., 2013; Hearne et al., 2017). Studies have typically emphasised the univariate association between specific brain activations (or functional connections) and relational demands, rather than how a given brain region might code for reasoning complexity (Freund et al., 2021). Thus, it remains unclear how the spatial correlates described by prior work relate to neural representations underlying RC.

Despite significant advances in the spatial mapping, the temporal dynamics of RC have not been well documented. A handful of electroencephalography (EEG) event-related studies have investigated reasoning demands, typically reporting deviations in the amplitude of event-related potentials as a function of complexity (Cutmore et al., 2015; Xiao et al., 2022). However, these studies did not analyse the entire cognitive processing period or frequency-resolved activity, largely due to uncertainties about how relational processing unfolds in time. While distinct from RC (Halford et al., 1998; Andrews et al., 2006), research on working memory in humans and non-

human primates has demonstrated the crucial role of synchronised neural oscillatory activity in alpha and beta frequency bands (Miller et al., 2018; John et al., 2022; Fulvio et al., 2024). Combining fMRI mapping with an analysis of the oscillatory temporal dynamics underpinning RC is likely to assist in the delineation of a core temporal and spatial signature supporting the neural representation of abstract relational integration.

To explore the spatiotemporal representation of RC, we used the Latin Square Task (LST), a visuospatial reasoning task where participants solve short Sudoku-like puzzles (Birney et al., 2006; Hearne et al., 2020). Cognitive demands were modulated by changing the minimum number of relations that needed to be integrated to infer the solution. Representational Similarity Analysis (RSA) provided a means to fuse multiple datasets rich in multimodal spatial and temporal information to assess where and when RC is represented in the brain (Kriegeskorte et al., 2008). To this end, we pooled data from two independent studies assessing brain activity using fMRI and EEG while participants completed the LST at three levels of relational complexity. In line with prior studies, we predicted that RC representations would emerge in higher-order associative networks responsible for executive control in relational integration (Cocchi et al., 2013). We anticipated that the emergence of a RC representation via the integration of information across distinct brain systems would be observable in alpha and beta oscillations. Finally, we extended our analysis by employing a model-based fusion approach (Cichy et al., 2014) to quantify the unique contribution of RC to the shared spatiotemporal representation between neuroimaging datasets.

Materials and Methods

Participants

Participants were pooled across two independent datasets. In the first dataset, sixty-five healthy, right-handed participants completed the LST while undergoing fMRI (final n = 40, see exclusion criteria in the *fMRI preprocessing* section below; mean = 23 years old; age range = 18 - 33; 60% female). This dataset has been used in prior publications (Hearne et al., 2017; Shine et al., 2019). In the second dataset, forty-seven healthy participants completed the LST concurrently with EEG (final n=45, see the *EEG preprocessing* section for exclusions; mean = 25; age range = 19 - 33; 62% female). Ethics approval was granted by the University of Queensland Human Research Ethics Committee (dataset one) and the QIMR Berghofer Research Ethics Committee (dataset

two). In both experiments, participants provided written informed consent and were eligible if aged between 18 - 35 with no previous reported history of mental health or neurological disorder.

Experimental design

The LST is a nonverbal relational reasoning experimental task (Birney et al., 2006). Each LST puzzle involves the presentation of a four-by-four grid populated by shapes (squares, triangles, circles and crosses) and a target question mark. Participants are asked to solve what shape the question mark must be, given that *an item or object can only exist once in every row and column* (similar to sudoku). As shown in **Figure 1a**, puzzle complexity (Binary, Ternary and Quaternary) was modulated by modifying the number of items that needed to be interrelated in one step to solve the problem. Binary relations required linking items across a row or column, Ternary relations row and column, and Quaternary problems multiple rows and columns. In the second dataset, puzzles consisted of different coloured circles, rather than different shapes (A, B, C and D).

Each relational complexity condition comprised of twelve unique puzzle designs. Additional trials were generated by rotating each puzzle by 90 degrees (Hearne et al., 2020; Hartung et al., 2022). In the first dataset, this was performed twice to generate 36 trials at each complexity level. In the second dataset, this was performed thrice to generate 48 trials at each complexity level. Increased trial numbers were warranted in the second dataset due to EEG artefact rejection. For each dataset, the puzzle rotations were averaged to generate brain activation estimates for twelve trials per condition, thirty-six trials in total (see the *representation similarity analysis* section below for details).

Trials were presented in a pseudo randomised order, ensuring that two trials of the same complexity level were not presented sequentially. To optimise the number of trials for imaging acquisition the stimulus duration was slightly modified for each modality. In the first dataset, problems were presented for 5 seconds, with a further 2 seconds to respond via a response screen. In the second dataset, the stimulus time was 4.5 seconds puzzle onset and a 1.75 second response window.

Neuroimaging acquisition, preprocessing and activation estimation

fMRI Dataset

As reported previously (Hearne et al., 2017), fMRI data were acquired on a 7 Tesla Siemens scanner equipped with a 32-channel head coil at the Centre of Advanced Imaging, The University of Queensland, Brisbane. Whole-brain echo-planar images were collected with the following parameters: isotropic 2 mm voxels, TR = 586ms, TE = 23ms, flip angle = 40°, FOV = 208mm, 55 axial slices, multiband acceleration factor = 5. The LST was performed over three 12-minute runs (1250 volumes). Structural scans (MP2RAGE) used in the preprocessing pipeline were acquired with the following parameters: isotropic 0.75 mm voxels, TR = 4300ms, TE = 3.44 ms, and 256 slices. Stimuli were presented using PsychToolBox 3.0 (Brainard, 1997) onto a screen located at the head end of the MR scanner, and participants viewed the projected stimuli via a mirror head-mount. The grid layout of the puzzle was sized to fit within the field of view of participants, removing the need for large eye-moment to peruse the grid space.

Data were preprocessed using fMRIPrep 21.0.1 (Esteban et al., 2019) [RRID:SCR_016216], which is based on *Nipype* 1.6.1 (Gorgolewski et al., 2011) [RRID:SCR_002502]. Due to differences in signal intensity in the temporal cortex with the rest of the brain, the raw T1-weighted (T1w) images were intensity corrected using the SPM segmentation tool prior to the fMRIPrep pipeline. Based on quality control checks this step ensured that different tissues were correctly identified during the preprocessing pipeline. Following this, within the fMRIPrep pipeline, the T1w image was corrected for intensity non-uniformity (INU) with N4BiasFieldCorrection (Tustison et al., 2010), distributed with ANTs 2.3.3 (Avants et al., 2008) [RRID:SCR_004757], and used as T1w-reference throughout the workflow. The T1w-reference was then skull-stripped with a *Nipype* implementation of the antsBrainExtraction.sh workflow (from ANTs), using OASIS30ANTs as target template. Brain tissue segmentation of cerebrospinal fluid (CSF), white-matter (WM) and gray-matter (GM) was performed on the brain-extracted T1w using fast (FSL 6.0.5.1:57b01774, RRID:SCR_002823, (Zhang et al., 2001)). Brain surfaces were reconstructed using recon-all (FreeSurfer 6.0.1, RRID:SCR_001847, (Dale et al., 1999)), and the brain mask estimated previously was refined with a custom variation of the method to reconcile ANTs-derived and FreeSurfer-derived segmentations of the cortical gray-matter of Mindboggle (RRID:SCR_002438, (Klein et al., 2017)). Volume-based spatial normalization to standard space was performed through nonlinear registration with antsRegistration (ANTs 2.3.3), using brain-

extracted versions of both T1w reference and the T1w template. *FSL's MNI ICBM 152 non-linear 6th Generation Asymmetric Average Brain Stereotaxic Registration Model* was used for spatial normalisation [(Evans et al., 2012), RRID:SCR_002823; TemplateFlow ID: MNI152NLin6Asym].

For each of the three BOLD runs found per subject the following preprocessing was performed. First, a reference volume and its skull-stripped version were generated by aligning and averaging 1 single-band references (SBRefs). Head-motion parameters with respect to the BOLD reference (transformation matrices, and six corresponding rotation and translation parameters) are estimated before any spatiotemporal filtering using mcflirt (FSL 6.0.5.1:57b01774, (Jenkinson et al., 2002)). BOLD runs were slice-time corrected to 0.268s (0.5 of slice acquisition range 0s-0.535s) using 3dTshift from AFNI ((Cox and Hyde, 1997), RRID:SCR_005927). The BOLD time-series were resampled onto their original, native space by applying the transforms to correct for head-motion. These resampled BOLD time-series will be referred to as *preprocessed BOLD in original space*, or just *preprocessed BOLD*. The BOLD reference was then co-registered to the T1w reference using bbregister (FreeSurfer) which implements boundary-based registration (Greve and Fischl, 2009). Co-registration was configured with six degrees of freedom. First, a reference volume and its skull-stripped version were generated using a custom methodology of *fMRIPrep*. The three signals are extracted within the CSF, the WM, and the whole-brain masks. The BOLD time-series were resampled onto *fsaverage* surface space. *Grayordinates* files (Glasser et al., 2013) containing 91k samples were also generated using the highest-resolution fsaverage as intermediate standardized surface space. All resamplings can be performed with *a single interpolation step* by composing all the pertinent transformations. Gridded (volumetric) resamplings were performed using antsApplyTransforms (ANTs), configured with Lanczos interpolation to minimize the smoothing effects of other kernels (Lanczos, 1964). Non-gridded (surface) resamplings were performed using mri_vol2surf (FreeSurfer). Given the RSA calculates similarities between voxel / vertex activation patterns without spatial smoothing, any subjects exceeding 2 mm of head motion (six rotation and translation parameters) were excluded from further analysis (final n=40). After fMRIPrep, the functional data were further denoised by regressing fourteen nuisance signals (mean cerebrospinal fluid and white matter signals, along with the six motion parameters and their derivatives) using Nilearn (Abraham et al., 2014).

To estimate brain activations, whole-brain general linear model (GLM) analyses were conducted using Nilearn (Abraham et al., 2014) for each participant's grayordinate surface and volumetric data. Using a previously established method to estimate trial-by-trial activation patterns (Mumford et al., 2012), a separate GLM was performed for each of the 36 puzzles in the experiment. Each design matrix included two regressors; one for the three trials of interest (three rotations of the puzzle) and another for all other trials in the experiment. Each trial was modelled as a five second boxcar regressor convolved with the canonical hemodynamic response function. Three additional regressors were included to account for each run of the experiment. This procedure resulted in brain activation estimates for each of the 36 puzzles across the brain which were subsequently analysed using RSA.

EEG Dataset

EEG recordings were digitised at 2000 Hz using an ANT-neuro system with a 64 channel cap arranged in the 10-20 layout. Experimental stimuli were presented on a BenQ 24 inch computer monitor with the task paradigm implemented using PsycoPy toolbox (v2020.2.10) (Peirce et al., 2019). Similar to Dataset 1, the grid layout of the puzzle was sized to fit within the field of view of participants.

EEG recordings were preprocessed offline using EEGLAB (Delorme and Makeig, 2004). The continuous data underwent high-pass finite impulse response (FIR) filtering at 0.5 Hz to remove low-frequency drifts. Line noise centred at 50 Hz was eliminated using a notch filter spanning 47.5-52.5 Hz, followed by a 97 Hz low-pass filter to attenuate harmonic components. Bad channels, identified through visual inspection, were excluded before re-referencing to the average of all remaining channels, excluding the M1, M2, and EOG electrodes. The data were then downsampled to 250 Hz. Trial epochs were generated using the stimulus onset as a marker resulting in a -400 ms pre-stimulus and 4500 ms post-stimulus window. After independent component analysis (ICA) based artefact rejection, the excluded bad channel data were reconstructed using spherical spline interpolation. Finally, the signal underwent band-pass filtering within the EEG observable range of 1-45 Hz. Two subjects were removed from the final analysis due to excessive muscle artefacts.

EEG data was further processed and frequency decomposition performed using the MNE Python library (Gramfort et al., 2013). Epochs were baseline-corrected by subtracting the mean signal during the pre-stimulus period from the entire epoch (stimuli onset to 4500 ms). To investigate oscillatory dynamics across different frequency bands, the epoched timeseries data were decomposed into canonical frequency bands using zero-phase bandpass filtering. Specifically, the following frequency ranges were extracted: theta (4-8 Hz), alpha (8-12 Hz), beta (13-30 Hz), and gamma (30-45 Hz).

Representation similarity analysis

fMRI and EEG puzzle-induced brain activity were transformed to a common representational "puzzle space" using RSA (Kriegeskorte et al., 2008). RSA aims to model the similarity structure of brain activation patterns in response to differing tasks, conditions, or stimuli (**Figure 1**). Specifically, we estimated (dis)similarity between brain responses evoked by the 36 LST puzzles using the squared Euclidean distance. Representational dissimilarity matrices (RDMs), generated in both the fMRI and EEG datasets, were compared to a cognitive model, as well as each other (described below).

fMRI dataset

fMRI-RDMs were generated for 376 brain regions using the Glasser cortical parcellation (Glasser et al., 2016), and the Melbourne 3T S1 subcortex parcellation (Tian et al., 2020). For each participant and brain region, fMRI GLM coefficients (*z*-scored) for each of the 36 LST puzzles were organised into a puzzle-by-vertex (or voxel, in subcortex) activity pattern matrix. The RDM was then calculated as the puzzle-by-puzzle (36 x 36) squared Euclidean distance. Additionally, the resulting RDMs were averaged into thirteen previously established functional brain networks (Ji et al., 2019): auditory, cingulo-opercular, default, dorsal-Attention, frontoparietal, language, orbito-Affective, posterior-multimodal, somatomotor, subcortical, ventral-multimodal, and visual brain networks.

EEG dataset

For each participant and time point (1225 time points sampled at 250 Hz), preprocessed sensor-level EEG responses were organised into a puzzle-by-sensor activity pattern matrix. The RDM was then calculated as the puzzle-by-puzzle (36 x 36) squared Euclidean distance. This was performed for broadband signals and specific frequency ranges (theta, alpha, beta, and gamma, described previously). Following this, the RDMs were down-sampled into 50 sequential time segments of 100 ms each.

Relational complexity model

The RDM coding for the cognitive construct of relational complexity (Halford et al., 1998) is shown in **Figure 1B**. According to this model, puzzles within the same complexity condition (Binary, Ternary, or Quaternary) evoke *similar* brain activation patterns, regardless of the specific visual configuration of stimuli within the puzzle (e.g., squares, triangles, circles and crosses). This model also predicts that puzzles from different complexity conditions will elicit *dissimilar* activation patterns in a graded fashion, with Binary (easy puzzles) and Quaternary (difficult puzzles) conditions being maximally distant. Therefore, brain regions or time periods exhibiting high correspondence to this cognitive model would provide evidence that the underlying neural representations are tracking relational complexity demand rather than other factors (e.g., stimulus arrangement).

Cognitive effort model

In a similar approach to Chiou et al. (2024), we defined a data-driven ‘cognitive effort’ model. The model was generated using behavioural performance from both datasets. Specifically, the Euclidian distance was calculated between each puzzle’s accuracy and response time (averaged across participants). In this model, problems that participants found easier or harder are clustered together regardless of complexity level.

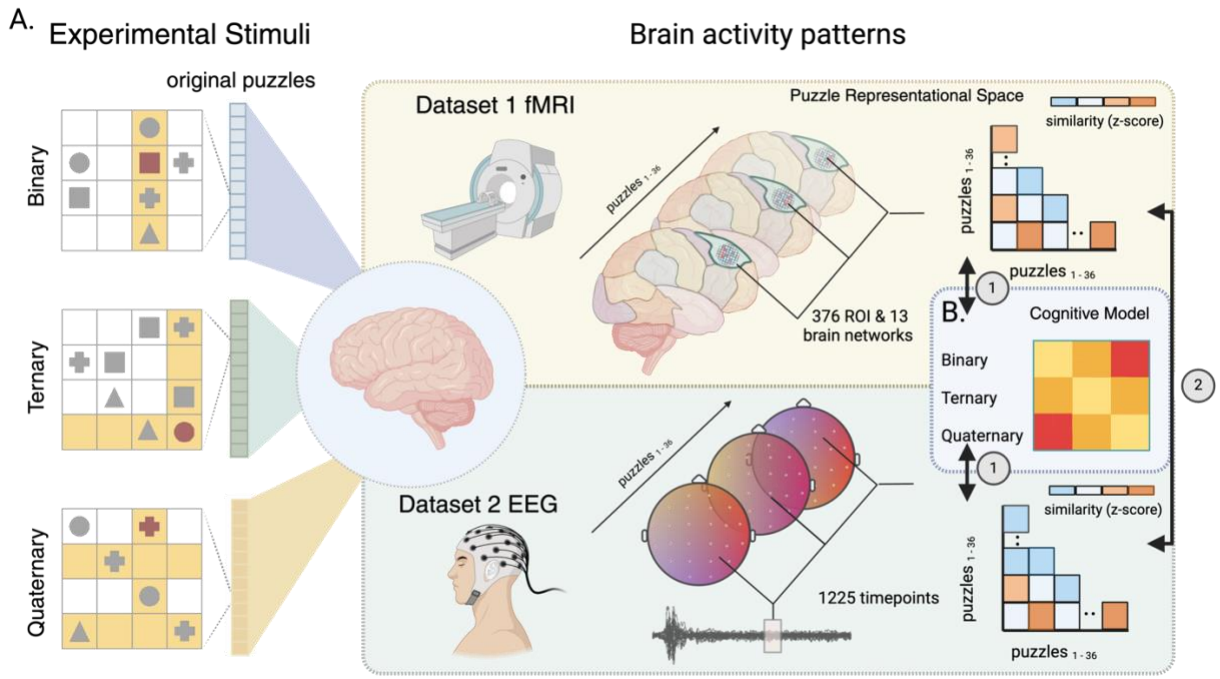

Figure 1: *Stimulus design and multivariate analysis approach*. Latin Square problems shown on the left required participants solve for the target square (solution highlighted in red) adhering to the rule that each item could only appear once in each row and column. Relational complexity was manipulated by varying the minimum number of interrelating rows and columns (highlighted in yellow) to solve for the missing item. The three puzzles illustrate example Binary, Ternary, and Quaternary complexity levels. Each cell in the corresponding-coloured vector represents one of the 36 original puzzle designs, with 12 puzzles per complexity level. While completing the task, brain activity was recorded using fMRI (dataset 1, top, gold) and EEG (dataset 2, bottom, light green). Neurophysiological responses were converted into puzzle representational dissimilarity matrices (RDMs) based on the distances between activation patterns evoked by different puzzles. Spatial fMRI RDMs were derived by correlating vertex or voxel activity patterns within parcellated brain regions for each puzzle. Temporal EEG RDMs were generated by correlating sensor-level activity patterns at each timepoint across puzzles. These spatial and temporal RDMs were (1) compared to the theoretical relational complexity model (B) and (2) assessed for spatial-temporal co-occurrence.

fMRI-EEG fusion analysis

We used commonality analysis (Hebart et al., 2018) to determine how much of the shared variance between EEG and fMRI RDMs could be explained by our RC and cognitive effort models. The commonality coefficient compares two semi-partial correlation coefficients (Spearman correlation). The first specifies the proportion of variance shared between EEG and fMRI when partialling out all model variables except the model of interest (e.g., the RC model) from fMRI. The second reflects the proportion of shared variance between EEG and fMRI after partialling out

all model variables (including the variable of interest). The commonality coefficient is the difference between both coefficients of determination (R^2). We performed this analysis for each brain network and time point, tracking the unique contributions of each model across space and time. Formally, for time *t* and network *j* the commonality coefficient is defined as:

$$C_{X_t,(Y_j,A)} = R^2_{X_t,(Y_j.B)} - R^2_{X_t,(Y_j.A,B)}$$

where *X* indicates EEG, *Y* indicates fMRI, *A* reflects the RC model, and *B* reflects the cognitive effort model.

Follow-up fMRI frontoparietal and EEG whole-brain sensor activity

As a supplementary analysis, we examined how activity in the FPN varied across the three complexity conditions. To do so, we averaged the GLM beta coefficients across each condition for each participant within each FPN region. These values were averaged across regions to generate a single value per participant, per condition.

For the spectral characteristics of the EEG data, we computed the power spectral density (PSD) using Welch's method within the data-driven beta RSA time window of interest, spanning 2.1 to 4.2 seconds post-stimulus onset. The PSD was calculated using segments of 500 samples with a 50% overlap. We applied a frequency range of interest from 2 to 45 Hz. Each participant's PSD were averaged over trials and channels to obtain a whole-brain sensor level measure of power for each complexity condition.

The periodic and aperiodic spectral parameterisation algorithm (version 2.0.0rc2) was used to parameterise neural power spectra (Donoghue et al., 2020). Settings for the algorithm were set as: peak width limits: (0.5, 12.0); max number of peaks: inf; minimum peak height: 0.0; peak threshold: 2.0; and aperiodic mode: 'fixed'. Power spectra were parameterized across the frequency range 2.0 to 45.0 Hz. High model fits of the parametrised spectrum were consistent across complexity conditions: $R^2_{\text{Binary}} = 0.975 \pm 0.014, R^2_{\text{Ternary}} = 0.973 \pm 0.013,\ R^2_{\text{Quaternary}} = 0.973 \pm 0.014,\ \text{F}(2, 88) = 0.318, p = 0.729.$ Using the previously defined fixed beta (13-30 Hz) frequency range we extracted the periodic peak frequency for each subject across conditions from the modelled spectrum. Five subjects were excluded as a peak could not be defined across all conditions.

Statistical analysis

Task performance (accuracy and response time) in each dataset was assessed using a one-way repeated measures ANOVA. To compare performance between the datasets, Spearman correlations were conducted on the participant-averaged puzzle level performance (accuracy and response time) between the two datasets.

The spatial (fMRI) and temporal (EEG) RDMs were compared with the relational complexity model RDM (**Figure 1B**) using Spearman rank correlation without tie correction (Nili et al., 2014). For each participant and each brain region, network, or epoch, the vectorized upper triangle of each empirical RDM was correlated with the vectorized upper triangle of the model RDM. These correlation values - or coding strengths - underwent normalisation via the Fisher z-transformation, and were entered into a one-sample *t*-test (Vallat, 2018). All three analyses were multiple comparisons corrected using the False Discovery Rate (FDR), α = 0.05 (fMRI $n_{regions}$ = 376, $n_{networks}$ = 13, EEG n_{epochs} = 50) (Benjamini and Yekutieli, 2001).

Statistical significance in the fMRI-EEG fusion analysis was assessed using a permutation test within each time bin (N=5000, (Hebart et al., 2018)). For each permutation, we randomly shuffled the rows and columns of the EEG RDMs (Kriegeskorte et al., 2008) and recomputed the commonality coefficients, generating a null distribution of coefficient time courses for each network. P-values were calculated as the proportion of permutations that exceeded the empirical commonality coefficient. These p-values were subsequently corrected for multiple comparisons using FDR.

Finally, an exploratory analysis was conducted to relate individual differences in brain representations and LST performance. Specifically, a Spearman correlation was performed between the relational complexity model coding strength and LST accuracy. For the EEG data, each individual's peak coding value was used. Given the exploratory nature of this analysis it was only performed in networks and frequency bands that demonstrated high coding strengths in the initial analyses (four networks and two frequency bands). A one-way repeated measures ANOVA

was used to assess the follow-up brain activation measures of the frontoparietal network and the beta band power.

Code and data availability

The fMRI data analysed in this study are openly available (https://espace.library.uq.edu.au/view/UQ:734743). The EEG data will be made available to researchers following the execution of a data transfer agreement with QIMR Berghofer. Code to perform the analyses is available on Github (released upon publication).

Results

Effect of relational complexity on accuracy and response time

Participants completed relational reasoning problems at three complexity levels (**Figure 2**). As shown in **Figure 2A** (top), results from both fMRI and EEG datasets demonstrated the characteristic degradation in performance accuracy as complexity increased: Binary ($Mean_{fMRI}$ = 96.66%, $Mean_{EEG}$ = 95.00%), Ternary ($Mean_{fMRI}$ = 87.02%, $Mean_{EEG}$ = 80.69%), and Quaternary ($Mean_{fMRI}$ = 66.25%, $Mean_{EEG}$ = 56.30%); $F(2, 78)_{fMRI} = 80.61$, $p < 0.0001$, and $F(2, 88)_{EEG} = 101.60$, $p < 0.0001$. Correspondingly, response times **Figure 2A** (bottom), increased with complexity: Binary ($Mean_{fMRI}$ = 0.74 ms, $Mean_{EEG}$ = 0.61 ms), Ternary ($Mean_{fMRI}$ = 0.81 ms, $Mean_{EEG}$ = 0.78 ms), and Quaternary ($Mean_{fMRI}$ = 0.93 ms, $Mean_{EEG}$ = 0.87 ms); $F_{fMRI}(2, 78) = 51.09$, $p < 0.0001$ and $F(2, 88)_{EEG} = 108.00$, $p < 0.0001$. To assess consistency across datasets, puzzle performance was averaged across participants in each dataset and correlated. Both accuracy ($rs = 0.95$, $p < 0.001$) and response time ($rs = 0.83$, $p < 0.001$) demonstrated a high correspondence between datasets (**Figure 2B**).

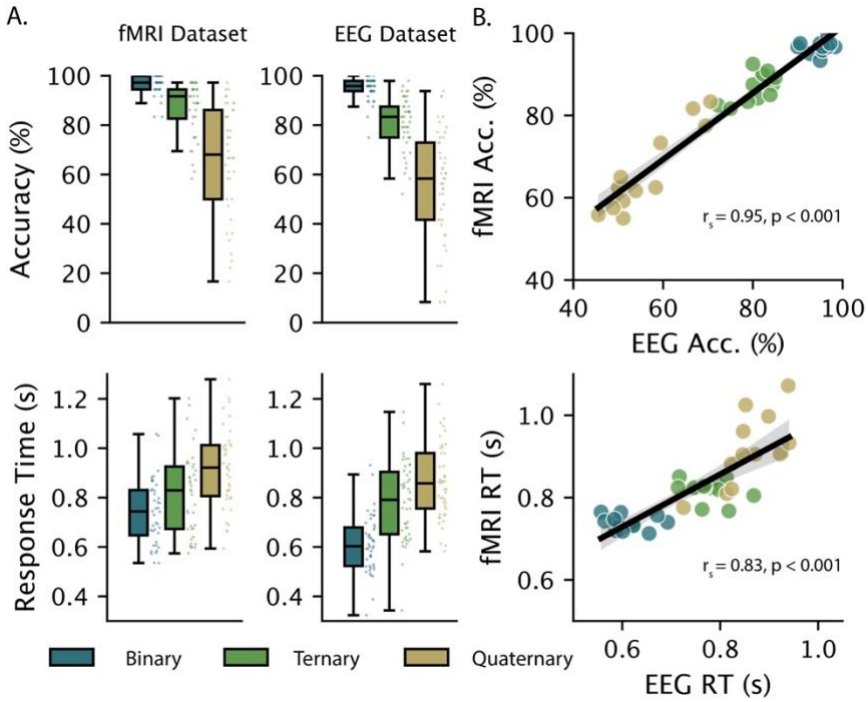

Figure 2. *Behavioural performance in the Latin Square Task*. **A.** Results replicated the expected degradation in accuracy (top panel) and delay in response time (bottom panel) associated with increased relational complexity across both fMRI (n=40) and EEG (n=45) datasets. **B.** Participant performance on the original 36 puzzles showed a positive correlation between fMRI and EEG datasets for both accuracy (top panel, rs = 0.95, p < 0.001) and reaction time (bottom panel, rs = 0.83, p < 0.001).

Spatial and temporal emergence of relational complexity

We conducted an RSA comparing the relational complexity model (**Figure 1b**) to representations derived from puzzle-evoked fMRI and EEG data. In the fMRI data, analyses were conducted at the region (**Figure 2a**) and network level (**Figure 2b**). Surprisingly, we observed strong relational complexity coding expressed across the whole brain. Of the 376 possible brain regions tested, 367 demonstrated significant correspondence to the model ($p_{FDR} < 0.05$). However, as expected, peak representational values were observed in prefrontal and parietal cortices: the superior premotor subdivision (6a), superior parietal cortex (7PL, 7Pm, 7Am, VIP, AIP, MIP), inferior parietal cortex (IP2, PGp), dorsal visual transitional area (DVT), anterior ventral insular area (AVI), medial prefrontal cortex (8bm) and dorsolateral prefrontal cortex (8C, i6-8). Accordingly, transmodal brain networks associated with goal-directed behaviour and higher-order cognition (Cole and Schneider, 2007; Duncan, 2010; Assem et al., 2020) demonstrated the strongest similarity to the

relational complexity model. Similar to the findings of the region-wise analysis, all networks showed statistical similarity to the model (all networks survived $p_{FDR} < 0.05$).

To identify when the relational complexity construct emerged in time, the model was correlated across the RDMs derived from the EEG broadband timeseries. The similarity timeseries (**Figure 2c**) revealed that relational complexity representations emerged during the 2.5 – 4.1 seconds puzzle-stimuli window ($p_{FDR} < 0.05$). At the group level, the temporal trend of the representation built over time, peaking at 4.1 s (peak correlation z = 0.037).

As a follow up analysis, we repeated the analysis in four canonical frequency bands (**Figure 3d**). Interestingly, we only found significant RC model coding in alpha and beta frequencies (alpha 2.3 – 4.2 s, beta 2.1 – 4.2 s, $p_{FDR} < 0.05$). Both frequencies mirrored the temporal trend of the broadband signal, peaking at 4.1 s (peak correlation, z = 0.049) and 3.2 s (peak correlation z = 0.052) for alpha and beta, respectively. Together, our results suggest that RC is i) most strongly represented in brain networks supporting goal-directed external behaviour (e.g., dorsal attention and frontoparietal networks), ii) emerges late in the trial period, and iii) is specifically related to alpha and beta frequency bands.

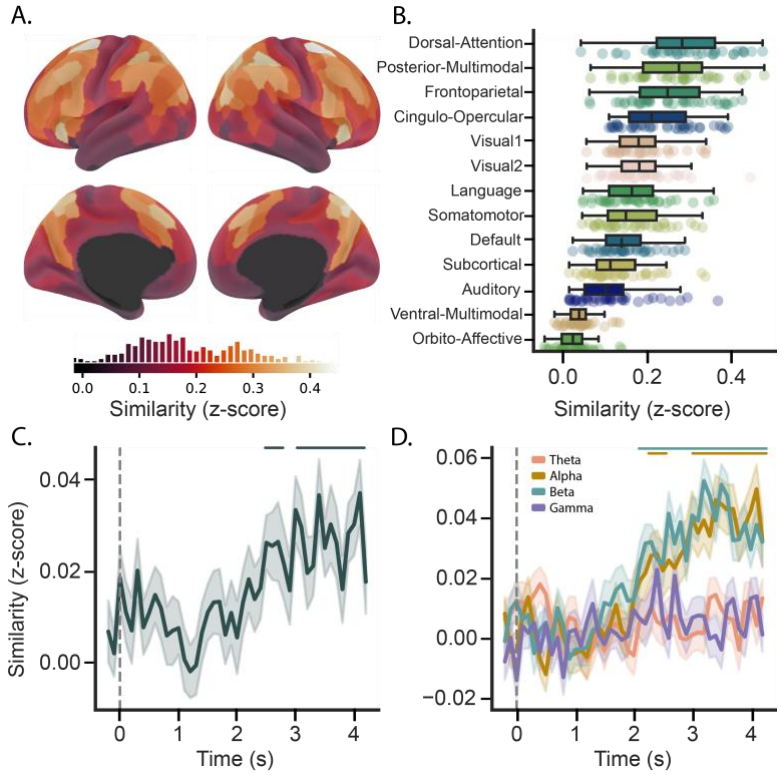

Figure 3. *Spatial and temporal signatures of relational complexity derived from fMRI and EEG data*. **A.** Group averaged brain-wide correlations between fMRI-informed representations and the relational complexity model, colour bar indicates a transition from low (blue) to high (red) correspondence. Underneath a histogram displays the frequency ROI correlations mapped onto brain surface renderings (Glasser et al., 2016; Tian et al., 2020). **B.** fMRI results when down sampled into canonical brain networks (Ji et al., 2019), ordered by effect size. **C.** Group averaged correlation between EEG-informed representations and the RC model across time. Confidence intervals indicate standard error of the mean. Black line above indicates statistically significant time bins ($p_{FDR} < 0.05$). **D.** Frequency band derived EEG representations and the RC model across time, theta (4-8 Hz, pink), alpha (8-12 Hz, gold), beta (13-30 Hz, teal), and gamma (30-45 Hz, purple). Confidence intervals indicate standard error of the mean. Highlighted segments represent time periods where the EEG signal significantly correlated with the relational complexity model ($p_{FDR} < 0.05$).

Cross-modal fusion analysis of time and frequency-resolved patterns of network representations

Next, we asked when the representational structure in a given brain network (determined from fMRI) corresponds with the representations from the time-resolved EEG signal. Using the shared representation between modalities, we further wanted to determine how much RC accounted for the explained variance in the representation. To do so, we performed a model-based fMRI-EEG

fusion commonality analysis (**Figure 4a**) (Cichy et al., 2014; Hebart et al., 2018). This approach also allowed us to compare a complementary cognitive effort model derived using participant performance (details in Methods). In contrast to RC, the cognitive effort model proposes that the information content coded in the representation can be retrospectively explained by the challenge in mapping the underlying abstraction due to a confluence of puzzle-specific properties (such as the number or configuration of items). Conversely, RC ignores puzzle-specific properties and proposes that the information in the signal codes for the dimensionality of the abstraction. Although both models aimed to capture different theoretical constructs (effort vs. complexity), they showed a high correlation (rs = 0.81, $p < 0.001$). Based on the prior results (**Figure 3d**), we narrowed our focus to the alpha and beta frequency bands.

The peak commonality coefficients from the fMRI-EEG fusion results in alpha and beta frequency bands are shown in **Figure 4b**. Most networks exhibit a similar peak onset time at 3.8 s in the alpha, while beta appeared to emerge 200 ms earlier at 3.6 s. Higher-order dorsal attention (peak alpha $R^2 = 0.35$, beta $R^2 = 0.33$), cingulo-opercular (peak alpha $R^2 = 0.36$, beta $R^2 = 0.32$) and frontoparietal (peak alpha $R^2 = 0.34$, beta $R^2 = 0.34$) networks shared the highest peak similarity between imaging modalities. The top networks showing the highest peak representation were consistent across both frequency-resolved timeseries. To further analyse the variance explained by our proposed cognitive models (**Figure 4a**), we selected the dorsal-attention (top) and frontoparietal (middle) networks, shown in Figure 4c, since they shared the highest cross-modal commonality. We also selected the default mode network (bottom), a transmodal network known to be anti-correlated in response to RC demands (Hearne et al., 2015) that showed relatively low peak fusion similarity (**Figure 4b**). The variance captured between modalities, Figure 4c, alpha (left) and beta (right) is shown by the shaded area. A shared representation in the beta band for both dorsal attention (alpha 2.3 – 4.2 s, beta 2.1 – 4.2 s, $p_{FDR} < 0.05$) and frontoparietal networks (alpha 2.3 – 4.2 s, beta 2.1 – 4.2 s, $p_{FDR} < 0.05$) preceded and maintained longer representation than the alpha band. The default mode network did not show any period with a significant commonality coefficient.

The commonality coefficients of the RC and cognitive effort models showed a similar trend to the overall correlation between the two imaging modalities over time. After 2.5 seconds post stimuli

onsets both models exhibited higher commonality coefficients than would be expected by chance. Of note, between both models, RC accounts for most of the variance of the shared representational structure. The cognitive effort model was not present in the default mode network. However, the RC model was detected in the signal despite the low shared variance between EEG and fMRI.

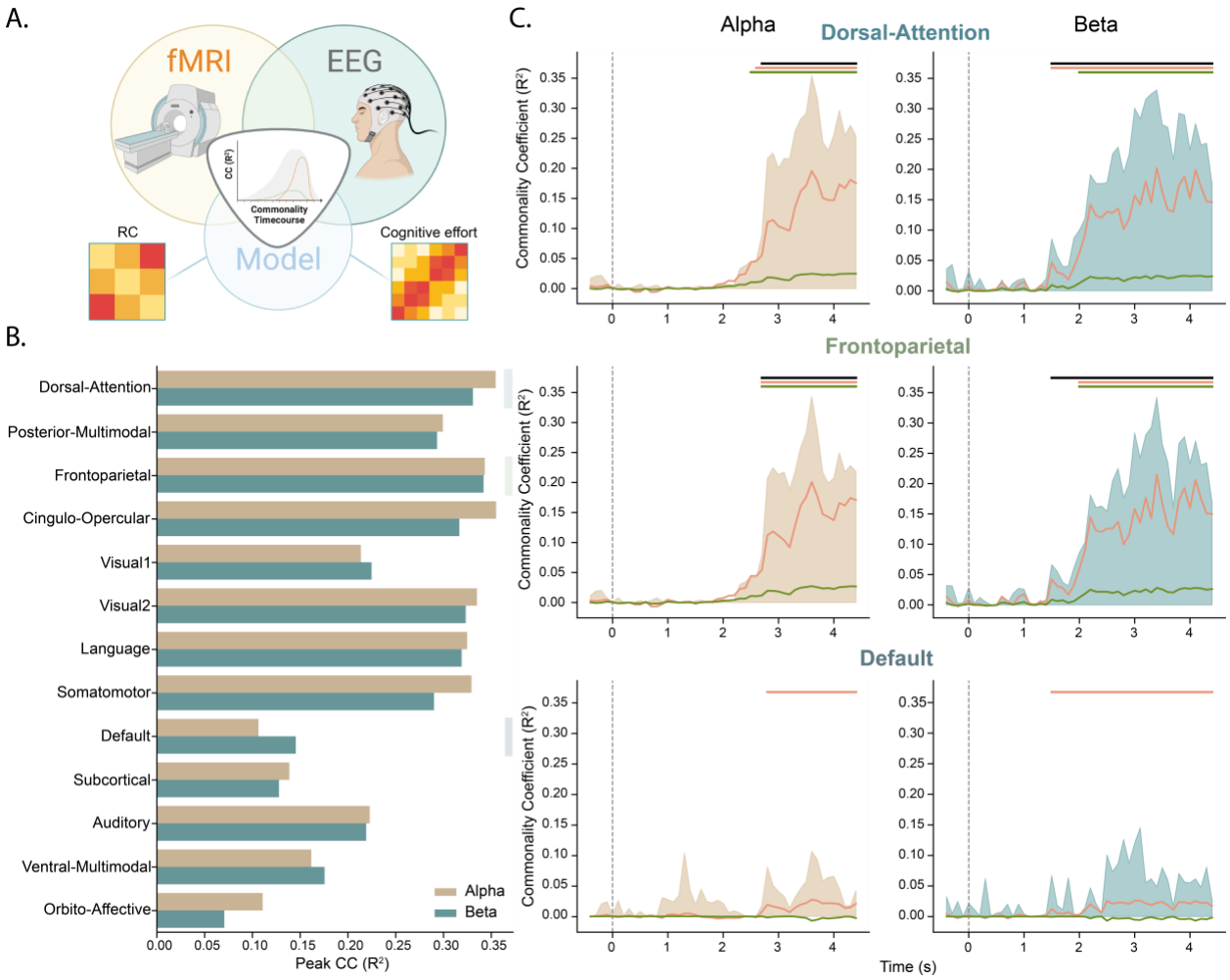

Figure 4. *Model based EEG-fMRI fusion-analysis*. **A.** Commonality analysis schematic. The commonality coefficient (CC) reflects the variance shared between the fMRI and EEG signal that can be attributed to specific task models (RC and Cognitive effort). **B.** Peak correlations between averaged fMRI and EEG data for each network within the alpha (gold) and beta frequencies (teal). **C.** Commonality coefficient timecourses for the RC model (orange line) and cognitive effort model (green line) in three exemplar brain networks (dorsal-Attention; top, frontoparietal; middle, default mode; bottom) in both the alpha (right) and beta (left) frequency bands. The shaded area indicates the proportion of variance shared between EEG and fMRI data over time.

Peak representation of RC and individual task performance

In a final exploratory analysis, we correlated individual participant task accuracy with: i) RC model coding strength across brain networks and ii) peak oscillatory RC model coding strength in the alpha and beta frequency. We observed a negative correlation between task accuracy and RC model coding strength in the frontoparietal (rs = -0.32, p = 0.045) and cingulo-opercular networks (rs = -0.33, p = 0.038, **Figure 5A**). Focusing on the Frontoparietal network (**Figure 5C**), we observed an increase in network activation as RC increased: Binary (Mean = -0.027), Ternary (Mean = 0.547) and Quaternary (Mean = 0.786); F(2, 78) = 117.00, p < 0.001.

In the EEG dataset, task accuracy also had a negative correlation with the temporal peak representation in the beta oscillatory band (rs = -0.33, p = 0.026), while no relationship was found in the alpha band (rs = 0.00, p = 0.982, **Figure 5B**). Further exploration of sensor-level activity during the RC coding window of the beta band (**Figure 2D,** 2.1 s to 4.2 s) showed a decrease in peak beta power with RC: Binary (Mean = 0.437), Ternary (Mean = 0.380) and Quaternary (Mean = 0.388); F(2, 80) = 9.68, p < 0.001. While the reported correlations do not survive appropriate correction for multiple comparisons, the reliable pattern of results across key cognitive control networks and modalities supports the genuine association between task-accuracy and the strength of RC brain representations.

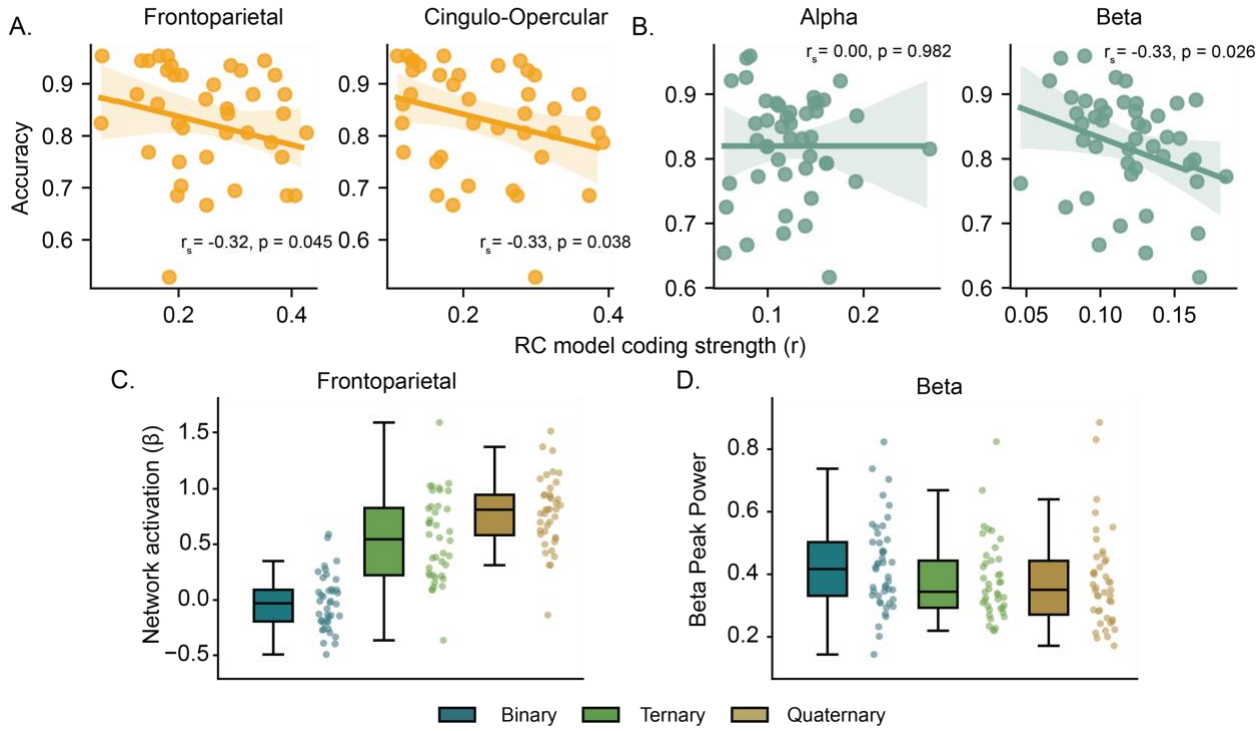

Figure 5. *Correlation between participant accuracy (y-axis) and RC model coding strength (x-axis) with corresponding brain activation across complexity levels*. **A.** fMRI RC model coding strengths for the frontoparietal (left) and cingulo-opercular (right) networks. **B.** EEG frequency derived peak RC model coding strengths in the alpha (8 – 12 Hz, left) and beta (13 – 30 Hz, right) bands. rs represents Spearman's rank correlation coefficient; p-values are uncorrected. **C.** Frontoparietal activation (β coefficients) across complexity levels. **D.** Periodic peak beta power calculated across all EEG electrodes in each complexity condition during the 2.1s to 4.2 s time window.

Discussion

In this multimodal study, we assessed the brain basis of RC representations in the context of a visuospatial reasoning task. Using representational similarity analysis, we showed that RC is supported by a widespread network of regions, with core contributions from functional brain networks associated with external goal-directed control. Results from the analysis of macroscale temporal dynamics showed that trial-based RC representations are supported by alpha and beta brain rhythms and emerged gradually, with peak correspondence in the 2.5 – 4.1 second post-stimuli onset window. The RC model showed stronger links with the shared representational structure of brain activity compared to a cognitive effort model, with individual RC model coding strength linked to variations in task performance. This set of results advances our understanding of the spatiotemporal dynamics underpinning complex reasoning, importantly unveiling that RC is coded in the representation of problems. Considering the strong association between RC and intelligence (Hansell et al., 2015), our findings showcase how distributed neural processes progressively integrate information to orient intelligent behaviour.

Our fMRI findings build on previous knowledge to show that RC is distributed throughout the brain. Previous lesion and neuroimaging work have demonstrated a key role of frontal (Christoff et al., 2001; Bunge et al., 2005; Wendelken et al., 2008) and frontoparietal circuits (Vendetti and Bunge, 2014; Wendelken et al., 2016) in supporting relational processes. However, several studies have expanded this view by showing that changes in task complexity are supported by local modulations in brain activity and connectivity in brain network regions beyond the frontal and parietal cortices (Hearne et al., 2017). For example, Cocchi et al. (Cocchi et al., 2014) demonstrated that progressively increasing problem complexity also resulted in a proportional modulation of brain activity and task-based connectivity between core nodes of the cingulo-

opercular network. These observations are in line with network-centric views of cognition and relational integration (Cole and Schneider, 2007; Morin et al., 2022), positioning frontoparietal hubs and brain-wide connectivity as central to orchestrating goal-directed cognitive control (Cole et al., 2013). Our findings extend this work by demonstrating, for the first time, that relational complexity is mapped in the information representation of frontoparietal, dorsal-attention, and cingulo-opercular networks. Visual networks also had high model correspondence, likely reflecting the interaction between the sensory cortex involved in the task and the transmodal 'multiple demand' cortex (Cocchi et al., 2014; Hearne et al., 2017). On the other hand, the default mode network did not show a strong association with the RC model, suggesting that previously observed complexity-driven changes in DMN activity and connectivity (Hearne et al., 2015) may be more related to the engagement of task-positive networks rather than the coding of RC. Consistent with previous findings we were also able to demonstrate that part of the information stored in higher-order regions reflected the behavioural effort taken to solve the problems (Chiou et al., 2024). Despite the high correlation between RC and cognitive effort models, the information content in the higher-order networks predominantly coded for the dimensionality of the abstraction as proposed to RC theory, rather than trial-specific puzzle factors associated with cognitive effort.

Coherent oscillatory activity is a fundamental element in computational theories of relational integration (Knowlton et al., 2012; Fries, 2015). Our results suggest that the widespread neural representations of RC are supported by alpha and beta oscillatory brain rhythms, which emerge after the first two seconds of stimulus onset. These results complement our fMRI findings by showing the temporal dynamics supporting the establishment of RC representation in task-relevant dorsal attention, frontoparietal, and cingulo-opercular networks. RC representation emerged following the initial computation of the perceived properties of a stimulus (shape, colour; (Cichy et al., 2014)) and mirrors the timeframe observed to implement task-relevant rules (Hebart et al., 2018). The involvement of neural activity in the alpha frequency range is consistent with findings suggesting that frontal and parietal alpha activity support logical reasoning (Brzezicka et al., 2011; Brzezicka et al., 2017; Heldmann et al., 2024). Accordingly, frontoparietal alpha and beta-rhythms have been associated with performance on matrix reasoning tasks (Ociepka et al., 2023; Penhale et al., 2024). Speculatively, within the RC representation alpha-band activity may serve to suppress irrelevant sensory inputs (Foxe and Snyder, 2011; Gray et al., 2015) or competing relational

mappings (Benedek et al., 2014), thereby facilitating the focus on task-relevant information. In contrast, beta-band oscillations are likely to support the sustained activation of task-specific neural activity (Buschman et al., 2012), facilitating the maintenance of relational representations as they are progressively integrated. Other cognitive experiments in particular working memory, attention and rule-switching tasks indicate these high-order cognitive operations decrease alpha and beta power in response to increased demands (Scharinger et al., 2017; Williams et al., 2019; Kaiser et al., 2023). However, this attenuated activity appears to facilitate an increase in frequency-specific synchronisation between brain regions (Sauseng et al., 2005; Palva et al., 2010; Buschman et al., 2012). While our study cannot disentangle the exact contribution of network-specific alpha and beta rhythms to support RC representations, it provides a solid rationale to further investigate these neural correlates.

In a final exploratory analysis, we found that individual differences in task performance were inversely related to RC model coding within the beta oscillatory band (EEG dataset) and the frontoparietal and cingulo-opercular networks (fMRI dataset). In other words, better performers produced brain representations that corresponded less to the RC model. The mechanism behind this unintuitive result is unclear, but it would suggest high performers tend to have less clear boundaries between the brain representations of different complexity levels (Binary, Ternary, Quaternary). This result may be related to the idea of neural efficiency (Neubauer and Fink, 2009), suggesting that better performers tend to expend less energy on more difficult tasks. Previous E/MEG studies have also demonstrated a similar trend where reduced beta oscillations are associated with improved spatial working memory performance (Proskovec et al., 2018). Likewise, reduced beta oscillations over the frontal and parietal areas while participants solved reasoning problems were found to be negatively correlated with general intelligence (Ociepka et al., 2023). Overall, these findings are consistent with the proposition that frontoparietal beta rhythms play a key role in establishing stable RC representations necessary to solve the problems ahead.

Given the existence of theoretical accounts of relational reasoning (Knowlton et al., 2012), as well as neural network LST solvers (Ito et al., 2024), a key future research direction is to leverage the RSA framework to test specific model-based hypotheses regarding RC. In the version of the LST

we implemented in this study, the puzzles were designed to minimise the loading of working memory demands across complexity levels, reducing multiple processing steps to isolate RC. However, other variations of RC tasks may allow for alternative processing strategies, such as segmentation or chunking, that can overcome trial-specific complexity based on problem attributes (Hartung et al., 2022). This opens up opportunities to explore more nuanced questions of relational integration by examining the trade-offs involved in building complex representations across a diverse range of visuospatial, semantic, and analogical tasks (Halford et al., 1998), and addressing the broader question of whether RC is represented across a domain-general set of problems. A model comparison approach (Schutt et al., 2023), as demonstrated in recent studies (Daws et al., 2020; Chiou et al., 2024), would help to directly contrast different models of reasoning. One insight we gained from this method – when combined with a fusion analysis (Hebart et al., 2018) – was that RC captured the majority of variance shared between EEG and fMRI when contrasted with a cognitive effort model.

In conclusion, our study provides a novel characterisation of the spatial and temporal brain processes underpinning representations of complexity during a relational reasoning task. Our results highlight the role of domain-general functional networks and suggest a key role of alpha and beta oscillatory patterns in the service of human relational reasoning. The current results advance our understanding of the neural mechanisms of reasoning and facilitate the establishment of formal generative models of RC.

Acknowledgments

C.R is supported by an Australian Government Research Training Program Scholarship and a Living Stipend through the penurious administration of the University of Queensland. C.R is also supported by a QIMR administered Living Stipend extension funded by L.J.H. Figure 1 and Figure 4a was created with BioRender.com. This work was supported by the Australian NHMRC (LC: GN2001283 and GNT2027597, LJH: APP1194070).

Author contributions

L.J.H. and C.R conceptualised the research goals; L.J.H. supervised the investigation, collected and pre-processed dataset 1 and assisted with the formal data analysis. C.R collected and pre-

processed dataset 2 formally analysed the data and wrote the first draft. All authors reviewed and edited the manuscript.

References

Abraham A, Pedregosa F, Eickenberg M, Gervais P, Mueller A, Kossaifi J, Gramfort A, Thirion B, Varoquaux G (2014) Machine learning for neuroimaging with scikit-learn. Frontiers in Neuroinformatics 8.

Andrews G, Birney D, Halford GS (2006) Relational processing and working memory capacity in comprehension of relative clause sentences. Mem Cognit 34:1325-1340.

Assem M, Glasser MF, Van Essen DC, Duncan J (2020) A Domain-General Cognitive Core Defined in Multimodally Parcellated Human Cortex. Cereb Cortex 30:4361-4380.

Avants BB, Epstein CL, Grossman M, Gee JC (2008) Symmetric diffeomorphic image registration with cross-correlation: evaluating automated labeling of elderly and neurodegenerative brain. Med Image Anal 12:26-41.

Benedek M, Schickel RJ, Jauk E, Fink A, Neubauer AC (2014) Alpha power increases in right parietal cortex reflects focused internal attention. Neuropsychologia 56:393-400.

Birney DP, Halford GS, Andrews G (2006) Measuring the Influence of Complexity on Relational Reasoning: The Development of the Latin Square Task. Educational and Psychological Measurement 66:146-171.

Boag C, Neal A, Loft S, Halford GS (2006) An analysis of relational complexity in an air traffic control conflict detection task. Ergonomics 49:1508-1526.

Brainard DH (1997) The Psychophysics Toolbox. Spat Vis 10:433-436.

Brzezicka A, Kaminski M, Kaminski J, Blinowska K (2011) Information transfer during a transitive reasoning task. Brain Topogr 24:1-8.

Brzezicka A, Kamiński J, Kamińska OK, Wołyńczyk-Gmaj D, Sedek G (2017) Frontal EEG alpha band asymmetry as a predictor of reasoning deficiency in depressed people. Cogn Emot 31:868-878.

Bunge SA, Wendelken C, Badre D, Wagner AD (2005) Analogical reasoning and prefrontal cortex: evidence for separable retrieval and integration mechanisms. Cereb Cortex 15:239-249.

Buschman TJ, Denovellis EL, Diogo C, Bullock D, Miller EK (2012) Synchronous oscillatory neural ensembles for rules in the prefrontal cortex. Neuron 76:838-846.

Chiou R, Duncan J, Jefferies E, Lambon Ralph MA (2024) The dimensionality of neural coding for cognitive control is gradually transformed within the lateral prefrontal cortex. bioRxiv:2024.2002.2005.578918.

Christoff K, Prabhakaran V, Dorfman J, Zhao Z, Kroger JK, Holyoak KJ, Gabrieli JD (2001) Rostrolateral prefrontal cortex involvement in relational integration during reasoning. Neuroimage 14:1136-1149.

Cichy RM, Pantazis D, Oliva A (2014) Resolving human object recognition in space and time. Nat Neurosci 17:455-462.

Cocchi L, Zalesky A, Fornito A, Mattingley JB (2013) Dynamic cooperation and competition between brain systems during cognitive control. Trends in Cognitive Sciences 17:493-501.

Cocchi L, Halford GS, Zalesky A, Harding IH, Ramm BJ, Cutmore T, Shum DH, Mattingley JB (2014) Complexity in relational processing predicts changes in functional brain network dynamics. Cereb Cortex 24:2283-2296.

Cole MW, Schneider W (2007) The cognitive control network: Integrated cortical regions with dissociable functions. Neuroimage 37:343-360.

Cole MW, Reynolds JR, Power JD, Repovs G, Anticevic A, Braver TS (2013) Multi-task connectivity reveals flexible hubs for adaptive task control. Nat Neurosci 16:1348-1355.

Cox RW, Hyde JS (1997) Software tools for analysis and visualization of fMRI data. NMR in Biomedicine 10:171-178.

Cutmore TRH, Halford GS, Wang Y, Ramm BJ, Spokes T, Shum DHK (2015) Neural correlates of deductive reasoning: An ERP study with the Wason Selection Task. International Journal of Psychophysiology 98:381-388.

Dale AM, Fischl B, Sereno MI (1999) Cortical Surface-Based Analysis: I. Segmentation and Surface Reconstruction. NeuroImage 9:179-194.

Daws RE, Soreq E, Li Y, Sandrone S, Hampshire A (2020) Contrasting hierarchical and multiple-demand accounts of frontal lobe functional organisation during task-switching. bioRxiv:2020.2006.2027.175133.

Delorme A, Makeig S (2004) EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. J Neurosci Methods 134:9-21.

Donoghue T, Haller M, Peterson EJ, Varma P, Sebastian P, Gao R, Noto T, Lara AH, Wallis JD, Knight RT, Shestyuk A, Voytek B (2020) Parameterizing neural power spectra into periodic and aperiodic components. Nature Neuroscience 23:1655-1665.

Duncan J (2010) The multiple-demand (MD) system of the primate brain: mental programs for intelligent behaviour. Trends Cogn Sci 14:172-179.

Duncan J, Owen AM (2000) Common regions of the human frontal lobe recruited by diverse cognitive demands. Trends Neurosci 23:475-483.

Eslinger PJ, Blair C, Wang J, Lipovsky B, Realmuto J, Baker D, Thorne S, Gamson D, Zimmerman E, Rohrer L, Yang QX (2009) Developmental shifts in fMRI activations during visuospatial relational reasoning. Brain Cogn 69:1-10.

Esteban O, Markiewicz CJ, Blair RW, Moodie CA, Isik AI, Erramuzpe A, Kent JD, Goncalves M, DuPre E, Snyder M, Oya H, Ghosh SS, Wright J, Durnez J, Poldrack RA, Gorgolewski KJ (2019) fMRIPrep: a robust preprocessing pipeline for functional MRI. Nat Methods 16:111-116.

Evans AC, Janke AL, Collins DL, Baillet S (2012) Brain templates and atlases. NeuroImage 62:911-922.

Foxe JJ, Snyder AC (2011) The Role of Alpha-Band Brain Oscillations as a Sensory Suppression Mechanism during Selective Attention. Frontiers in Psychology 2.

Freund MC, Etzel JA, Braver TS (2021) Neural Coding of Cognitive Control: The Representational Similarity Analysis Approach. Trends Cogn Sci 25:622-638.

Fries P (2015) Rhythms for Cognition: Communication through Coherence. Neuron 88:220-235.

Fulvio JM, Haegens S, Postle BR (2024) Single-pulse Transcranial-magnetic Stimulation Affects Working-memory Performance via Posterior Beta-band Oscillations. Journal of Cognitive Neuroscience:1-20.

Glasser MF, Sotiropoulos SN, Wilson JA, Coalson TS, Fischl B, Andersson JL, Xu J, Jbabdi S, Webster M, Polimeni JR, Van Essen DC, Jenkinson M (2013) The minimal preprocessing pipelines for the Human Connectome Project. NeuroImage 80:105-124.

Glasser MF, Coalson TS, Robinson EC, Hacker CD, Harwell J, Yacoub E, Ugurbil K, Andersson J, Beckmann CF, Jenkinson M, Smith SM, Van Essen DC (2016) A multi-modal parcellation of human cerebral cortex. Nature 536:171-178.

Goel V, Grafman J (1995) Are the frontal lobes implicated in "planning" functions? Interpreting data from the Tower of Hanoi. Neuropsychologia 33:623-642.

Gorgolewski K, Burns CD, Madison C, Clark D, Halchenko YO, Waskom ML, Ghosh SS (2011) Nipype: a flexible, lightweight and extensible neuroimaging data processing framework in python. Front Neuroinform 5:13.

Gramfort A, Luessi M, Larson E, Engemann DA, Strohmeier D, Brodbeck C, Goj R, Jas M, Brooks T, Parkkonen L, Hamalainen M (2013) MEG and EEG data analysis with MNE-Python. Front Neurosci 7:267.

Gray MJ, Frey HP, Wilson TJ, Foxe JJ (2015) Oscillatory recruitment of bilateral visual cortex during spatial attention to competing rhythmic inputs. J Neurosci 35:5489-5503.

Greve DN, Fischl B (2009) Accurate and robust brain image alignment using boundary-based registration. Neuroimage 48:63-72.

Halford GS, Wilson WH, Phillips S (1998) Processing capacity defined by relational complexity: implications for comparative, developmental, and cognitive psychology. Behav Brain Sci 21:803-831; discussion 831-864.

Halford GS, Wilson WH, Phillips S (2010) Relational knowledge: the foundation of higher cognition. Trends Cogn Sci 14:497-505.

Halford GS, Baker R, McCredden JE, Bain JD (2005) How many variables can humans process? Psychol Sci 16:70-76.

Hansell NK et al. (2015) Genetic basis of a cognitive complexity metric. PLoS One 10:e0123886.

Hartung J, Goecke B, Schroeders U, Schmitz F, Wilhelm O (2022) Latin square tasks: A multi-study evaluation. Intelligence 94:101683.

Hearne L, Cocchi L, Zalesky A, Mattingley JB (2015) Interactions between default mode and control networks as a function of increasing cognitive reasoning complexity. Human Brain Mapping 36:2719-2731.

Hearne LJ, Cocchi L, Zalesky A, Mattingley JB (2017) Reconfiguration of Brain Network Architectures between Resting-State and Complexity-Dependent Cognitive Reasoning. J Neurosci 37:8399-8411.

Hearne LJ, Birney DP, Cocchi L, Mattingley JB (2020) The Latin Square Task as a measure of relational reasoning: A replication and assessment of reliability. European Journal of Psychological Assessment 36:296-302.

Hearne LJ, Dean RJ, Robinson GA, Richards LJ, Mattingley JB, Cocchi L (2019) Increased cognitive complexity reveals abnormal brain network activity in individuals with corpus callosum dysgenesis. Neuroimage Clin 21:101595.

Hebart MN, Bankson BB, Harel A, Baker CI, Cichy RM (2018) The representational dynamics of task and object processing in humans. Elife 7.

Heldmann M, Rohde LS, Munte TF, Ye Z (2024) Cross-frequency and inter-regional phase synchronization in explicit transitive inference. Cereb Cortex 34.

Holyoak KJ, Monti MM (2021) Relational Integration in the Human Brain: A Review and Synthesis. J Cogn Neurosci 33:341-356.

Ito T, Cocchi L, Klinger T, Ram P, Campbell M, Hearne L (2024) The Importance of Positional Encoding Initialization in Transformers for Relational Reasoning. arXiv preprint arXiv:240608272.

Jenkinson M, Bannister P, Brady M, Smith S (2002) Improved Optimization for the Robust and Accurate Linear Registration and Motion Correction of Brain Images. NeuroImage 17:825-841.

Ji JL, Spronk M, Kulkarni K, Repovs G, Anticevic A, Cole MW (2019) Mapping the human brain's cortical-subcortical functional network organization. Neuroimage 185:35-57.

John AR, Singh AK, Do TTN, Eidels A, Nalivaiko E, Gavgani AM, Brown S, Bennett M, Lal S, Simpson AM, Gustin SM, Double K, Walker FR, Kleitman S, Morley J, Lin CT (2022) Unraveling the Physiological Correlates of Mental Workload Variations in Tracking and Collision Prediction Tasks. IEEE Transactions on Neural Systems and Rehabilitation Engineering 30:770-781.

Kaiser J, Oberschulte JM, Heckmann M, Schutz-Bosbach S (2023) Flexible Changes in Attentional Focus and Task Rules Rely on A Shared Set of Frontoparietal Oscillatory Dynamics. J Cogn Neurosci 35:1075-1091.

Klein A, Ghosh SS, Bao FS, Giard J, Hame Y, Stavsky E, Lee N, Rossa B, Reuter M, Chaibub Neto E, Keshavan A (2017) Mindboggling morphometry of human brains. PLoS Comput Biol 13:e1005350.

Knowlton BJ, Morrison RG, Hummel JE, Holyoak KJ (2012) A neurocomputational system for relational reasoning. Trends Cogn Sci 16:373-381.

Kriegeskorte N, Mur M, Bandettini P (2008) Representational similarity analysis - connecting the branches of systems neuroscience. Frontiers in Systems Neuroscience 2.

Lanczos C (1964) Evaluation of Noisy Data. Journal of the Society for Industrial and Applied Mathematics Series B Numerical Analysis 1:76-85.

Miller EK, Lundqvist M, Bastos AM (2018) Working Memory 2.0. Neuron 100:463-475.

Morin TM, Moore KN, Isenburg K, Ma W, Stern CE (2022) Functional reconfiguration of task-active frontoparietal control network facilitates abstract reasoning. Cerebral Cortex 33:5761-5773.

Mumford JA, Turner BO, Ashby FG, Poldrack RA (2012) Deconvolving BOLD activation in event-related designs for multivoxel pattern classification analyses. Neuroimage 59:2636-2643.

Neubauer AC, Fink A (2009) Intelligence and neural efficiency. Neuroscience & Biobehavioral Reviews 33:1004-1023.

Ociepka M, Kałamała P, Chuderski A (2023) Take your time: Slow brain rhythms predict fluid intelligence. Intelligence 100:101780.

Palva JM, Monto S, Kulashekhar S, Palva S (2010) Neuronal synchrony reveals working memory networks and predicts individual memory capacity. Proc Natl Acad Sci U S A 107:7580-7585.

Peirce J, Gray JR, Simpson S, MacAskill M, Höchenberger R, Sogo H, Kastman E, Lindeløv JK (2019) PsychoPy2: Experiments in behavior made easy. Behavior Research Methods 51:195-203.

Penhale SH, Arif Y, Schantell M, Johnson HJ, Willett MP, Okelberry HJ, Meehan CE, Heinrichs-Graham E, Wilson TW (2024) Healthy aging alters the oscillatory dynamics and fronto-parietal connectivity serving fluid intelligence. Hum Brain Mapp 45:e26591.

Proskovec AL, Wiesman AI, Heinrichs-Graham E, Wilson TW (2018) Beta Oscillatory Dynamics in the Prefrontal and Superior Temporal Cortices Predict Spatial Working Memory Performance. Sci Rep 8:8488.

Sauseng P, Klimesch W, Doppelmayr M, Pecherstorfer T, Freunberger R, Hanslmayr S (2005) EEG alpha synchronization and functional coupling during top-down processing in a working memory task. Hum Brain Mapp 26:148-155.

Scharinger C, Soutschek A, Schubert T, Gerjets P (2017) Comparison of the Working Memory Load in N-Back and Working Memory Span Tasks by Means of EEG Frequency Band Power and P300 Amplitude. Front Hum Neurosci 11:6.

Schutt HH, Kipnis AD, Diedrichsen J, Kriegeskorte N (2023) Statistical inference on representational geometries. Elife 12.

Shine JM, Hearne LJ, Breakspear M, Hwang K, Müller EJ, Sporns O, Poldrack RA, Mattingley JB, Cocchi L (2019) The Low-Dimensional Neural Architecture of Cognitive Complexity Is Related to Activity in Medial Thalamic Nuclei. Neuron 104:849-855.e843.

Tian Y, Margulies DS, Breakspear M, Zalesky A (2020) Topographic organization of the human subcortex unveiled with functional connectivity gradients. Nat Neurosci 23:1421-1432.

Todd JM, Andrews G, Conlon EG (2019) Relational thinking in later adulthood. Psychol Aging 34:486-501.

Tustison NJ, Avants BB, Cook PA, Zheng Y, Egan A, Yushkevich PA, Gee JC (2010) N4ITK: improved N3 bias correction. IEEE Trans Med Imaging 29:1310-1320.

Vendetti MS, Bunge SA (2014) Evolutionary and developmental changes in the lateral frontoparietal network: a little goes a long way for higher-level cognition. Neuron 84:906-917.

Waltz JA, Knowlton BJ, Holyoak KJ (1998) Relational complexity, the central executive, and prefrontal cortex. Behavioral and Brain Sciences 21:846-847.

Wendelken C, Ferrer E, Whitaker KJ, Bunge SA (2016) Fronto-Parietal Network Reconfiguration Supports the Development of Reasoning Ability. Cereb Cortex 26:2178-2190.

Wendelken C, Nakhabenko D, Donohue SE, Carter CS, Bunge SA (2008) “Brain Is to Thought as Stomach Is to ??”: Investigating the Role of Rostrolateral Prefrontal Cortex in Relational Reasoning. Journal of Cognitive Neuroscience 20:682-693.

Wertheim J, Ragni M (2018) The Neural Correlates of Relational Reasoning: A Meta-analysis of 47 Functional Magnetic Resonance Studies. J Cogn Neurosci 30:1734-1748.

Williams CC, Kappen M, Hassall CD, Wright B, Krigolson OE (2019) Thinking theta and alpha: Mechanisms of intuitive and analytical reasoning. Neuroimage 189:574-580.

Xiao F, Wang ZD, Yuan SQ, Liang K, Chen Q (2022) Relational integration predicted numerical inductive reasoning: ERP Evidence from the N400 and LNC. Psychophysiology 59:e14046.

Zhang Y, Brady M, Smith S (2001) Segmentation of brain MR images through a hidden Markov random field model and the expectation-maximization algorithm. IEEE Transactions on Medical Imaging 20:45-57.