Mapping patterns of thought onto brain activity during movie-watching

Raven S. Wallace[1], Brontë Mckeown[1], Ian Goodall-Halliwell[1], Louis Chitiz[1], Philippe Forest[13], Theodoros Karapanagiotidis[2], Bridget Mulholland[1], Adam G Turnbull[3], Tamera Vanderwal[4], Samyogita Hardikar[5], Tirso Gonzalez Alam[10], Boris Bernhardt[6], Hao-Ting Wang[7], Will Strawson[2], Michael Milham[8], Ting Xu[8], Daniel Margulies[9], Giulia L. Poerio[2], Elizabeth S. Jefferies[10], Jeremy I. Skipper[11], Jeffery Wammes[1], Robert Leech[12] & Jonathan Smallwood[1]

[1] Department of Psychology, Queens University

[2] School of Psychology, University of Sussex

[3] Department of Psychology, Stanford University

[4] Faculty of Medicine, University of British Columbia

[5] Department of Neurology, Max Planck School of Cognition

[6] Montreal Neurological Institute-Hospital, McGill University

[7] Centre de Recherche de l'Institut Universitaire de Geriatrie de Montreal

[8] Child Mind Institute, New York

[9] Integrative Neuroscience and Cognition Center, University of Paris

[10] Department of Psychology, University of York

[11] Division of Psychology & Language Sciences, University College London

[12] Institute of Psychiatry, Psychology & Neuroscience, King's College London

[13] Mathematical and Electrical Engineering Department, IMT Atlantique

Corresponding author:

Raven S. Wallace,

Department of Psychology,

Queen's University,

Kingston, Ontario.

Canada.

Email: raven.wallace@queensu.ca

Abstract

Movie watching is a central aspect of our lives and an important paradigm for understanding the brain mechanisms behind cognition as it occurs in daily life. Contemporary cognitive neuroscience has made important strides in understanding how brain activity emerges during movies and determining how the dynamics of brain regions during movies can be mapped across individuals. However, we currently lack an understanding of how patterns of ongoing thoughts map onto the brain signals that occur when we watch a film, partly because methods of sampling experience disrupt the dynamics of brain activity and the experience of movie watching. Our study established a novel method for mapping thought patterns onto the brain activity that occur at different moments of a film, which does not disrupt the time course of brain activity or the movie-watching experience. We found that in moments when experience sampling highlighted engagement with multi-sensory features of the film, or highlighted thought with episodic features, regions of sensory cortex were more active and subsequent memory for events in the movie is better. These results highlight the critical role that sensory systems play in the multi-modal experience of movie-watching and place important constraints on the contribution of systems in association cortex, like the default network.

Significance statement

Naturalistic states like movie-watching provide an important window into the brain mechanisms behind cognition in daily life. However, we know relatively little about the mapping between brain activity during movies and associated thought patterns because of difficulties in measuring cognition without disrupting how brain activity naturally unfolds. We establish a novel method to link different experiential states to brain activity during movie-watching with minimal interruptions to viewers or disruptions to brain dynamics. We found patterns indicative of engaged movie-watching occur when visual and auditory cortex are active and predict better memory for information from the films. Our study, therefore, establishes multi-modal brain activity within sensory systems as an integral feature of the movie-watching experience.

Introduction

A core goal of cognitive neuroscience is to understand how sensory input describing events in the external world is translated into the patterns of thoughts we experience in our lives. Complex naturalistic states, such as movie watching, are important paradigms to understand this process because they allow cognition and brain dynamics to be understood in a situation that maps directly onto experiences in the real world [1-5]. Developments in cognitive neuroscience, leveraging state-of-the-art brain imaging techniques such as functional magnetic resonance imaging (fMRI), have established core features of neural patterns that emerge across participants during movie-watching tasks [2], highlighting their similarity across individuals [6] and their links to memory for information in the films [7]. However, it is more difficult to reliably map ongoing thought patterns in this context since experiential sampling, the gold-standard for tracking thought patterns [8], has the potential to disrupt the natural unfolding of brain activity during movie watching. The goal of our study was to minimize the disruptive impact of sampling ongoing experience by using a novel approach that, for the first time, explicitly links patterns of ongoing thought to brain activity during movie-watching paradigms across genres of film.

Contemporary theories of ongoing thought suggest that a primary dimension to differentiate subjective experiences is the extent to which they depend on immediate sensory input [8, 9]. Cognitive states that are 'coupled' to events in the immediate environment are assumed to be linked to greater cortical processing of sensory input [10], better task performance, and better memory for events in narrative comprehension tasks like reading [11-13]. In contrast, perceptually 'decoupled' states from sensory input, such as the experience of mind-wandering [14, 15], provide an opportunity to pursue thoughts derived from memory [13, 16] but can be linked to compromised task performance and worse memory for events that

occurred [17]. Given dynamic changes in visual and auditory input drive the experience of movie-watching, it is likely that a critical feature of the movie-watching experience is a focus on the neural mapping of incoming sensory input.

Consistent with this perspective, recent work in cognitive neuroscience suggest an important role for primary systems, such as visual and auditory cortices during movie watching; however, they also hypothesize a role for regions of association cortex linked to higher-order thought, such as the default mode network (DMN) or the frontoparietal network (FPN) [2, 4, 18]. The sensory mapping of the visual and auditory features of the multi-modal movie experience is argued to be one of the theoretically important reasons for studying movies in the first place [19]. On the other hand, higher-order systems like the DMN or FPN are argued to play a complementary role in movie watching. For example, the DMN is hypothesised to be important in social cognition, episodic memory, and conceptual knowledge — all of which are likely important for understanding the narrative of the film (for a review of the broad role the DMN plays in cognition, see [20]). However, the DMN has also been implicated in perceptually decoupled states likely to be antagonistic to movie watching, such as mind-wandering [13, 21-23]. Similarly, the FPN is important for multiple types of tasks, including those superficially different from movies, such as working memory maintenance, reflecting this networks hypothesized role in goal maintenance [24, 25]. The broad role that systems in association cortex, like the DMN and FPN, play in cognition suggests that any role in movie watching may be linked to a more general role they play in cognition and behaviour. Although studies have highlighted the role of both primary sensory and higher-order systems, such as the DMN and the FPN [4, 26] in movie watching, our lack of a formal understanding of the mapping between thought patterns when we watch films and associated patterns of brain activity means the specific

role that different brain systems play in the conscious experience of movie watching remains largely a matter of speculation [27].

Our experiment was designed to better understand how patterns of brain activity at different moments during a film map onto the ongoing thoughts accompanying them. We used multi-dimensional experience sampling (mDES) to describe ongoing thought patterns during the movie-watching experience [8]. mDES is an experience sampling method that identifies different features of thought by probing participants about multiple different dimensions of their experiences. mDES can provide a description of a person's thoughts, generating reliable thought patterns across laboratory cognitive tasks [20, 28, 29] and in daily life [30, 31] and is sensitive to accompanying changes in brain activity [22, 32]. One challenge that arises when attempting to map the dynamics of thought onto brain activity during movie watching is accounting for the inherently disruptive nature of experience sampling: To measure experience with sufficient frequency to map the dynamics of thoughts during movies would disrupt the natural dynamics of the brain and would also alter the viewer's experience. To overcome this, we developed a novel methodological approach in which participants are probed five times in a ten-minute movie clip (11 minutes total, no sampling in the first minute) using a jittered technique — such that probes are delivered at different intervals across the film for different people depending on the condition they're assigned to. Probe orders were counterbalanced to minimize the systematic impact of prior and later probes at any given sampling moment. We leveraged this technique to construct a precise description of the dynamics of experience for every 15 seconds of three ten-minute movie clips for which existing fMRI data were available [33]. We then mapped the time series of experience measured by mDES in our laboratory onto the time series of brain activity. In this way, we can explicitly understand how the patterns of thoughts that dominate at different

moments in a film relate to the brain activity at these time points and gain a better understanding of how different neural systems contribute to the movie-watching experience.

Results

Analytic Goal

The goal of our study, therefore, was to understand the association between patterns of brain activity over time during movie clips and the patterns of thought that participants reported at the corresponding moment (see Figure 1). This can be conceptualized as identifying the mapping between two multi-dimensional spaces, one reflecting the time series of brain activity and the other describing the time series of ongoing experience (see Figure 1). In our study, we selected three 11-minute clips from movies for which recordings of brain data in fMRI already existed (Figure 1, Sample 1). A second set of participants viewed the same movie clips, providing intermittent reports on their thought patterns using mDES (Figure 1, Sample 2). Our goal was to understand the mapping between the patterns of brain activity at each moment of the film and the reports of ongoing thought recorded at the same point in the movie. We applied Principal Components Analysis (PCA) to the mDES data to reduce these data in a set of four simple dimensions that explained the thought patterns reported during the movies. These are represented as word clouds in Figure 1. We performed two analyses to understand the associations between the mDES reports and brain activity at each point in the film. Our first analysis computed the mean time series of experience for each of the four thought pattern components (averaged across participants in Sample 2) and used this as a regressor of interest in a model predicting brain activity recorded from each participant from Sample 1. We refer to this as a *voxel-space* analysis, and we used it to perform a whole brain analysis, mapping activity in

each region to each dimension of ongoing thought. In our second analysis, we projected the grand mean of brain activity for each volume of each film against the first five dimensions of brain activity from a decomposition of the Human Connectome Project (HCP) resting state date to form a 5D "brain-space" that describes the trajectory of the brain during each movie (Figure 1, note only the first four dimensions are shown) [34]. We used the results of this analysis to produce coordinates for each TR of each movie, which were used as explanatory variables in a linear mixed model in which the location of each mDES probe in the "thought space" described by the PCA dimensions were the dependent variables. We refer to this second analysis as a *state-space* analysis (see [35-37] for prior examples of this approach).

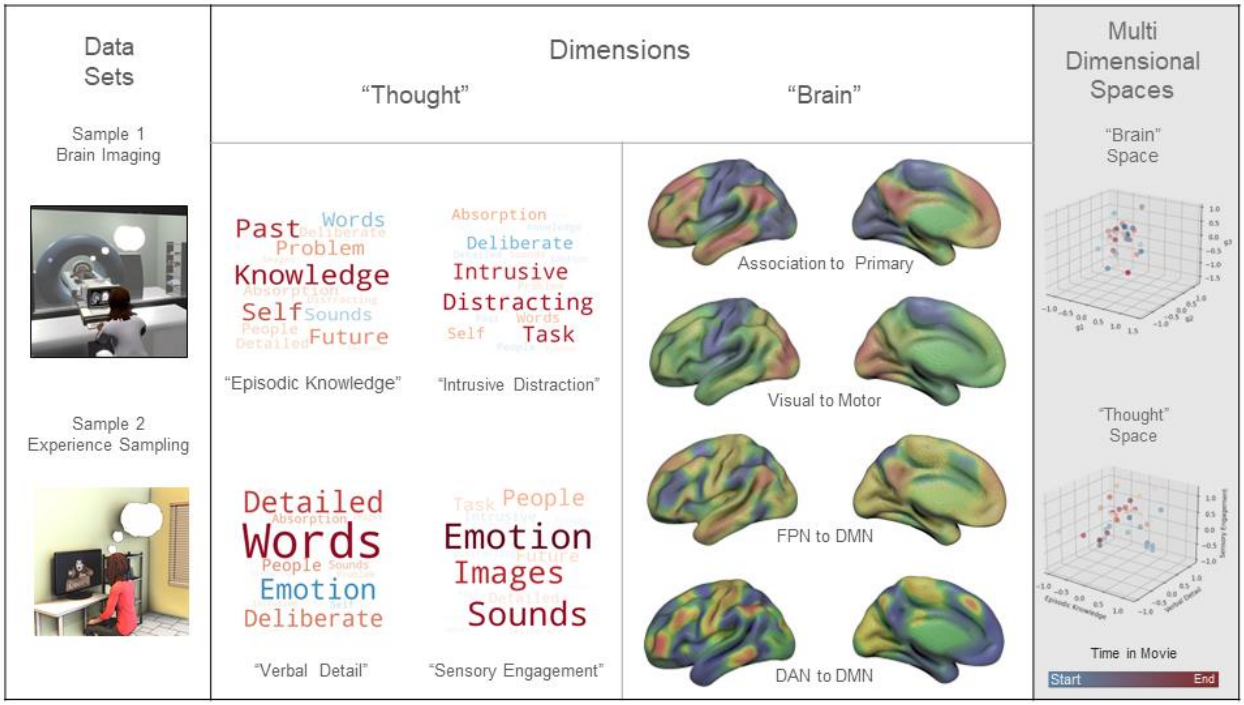

Figure 1. Using fMRI data and experience sampling data to map patterns of ongoing thought onto brain activity during movie-watching. *Left to Right* - One sample of participants was scanned while watching movies (Sample 1), and a different set of participants responded to experience sampling probes (Sample 2) while watching the same movies. Decomposition of

mDES data into low-dimension experiential patterns using principal component analysis (PCA) produced a set of dimensions that describe experience during movie watching (a "thought-space" of the movie watching experience). Word clouds illustrate how the question map onto each dimension that describes this space with the font size describing their importance (bigger = more important) and the colour describing their polarity (red = positive, blue = negative). Similarly, we created a brain space to describe the movie-watching experience by comparing each moment in the film to validated dimensions of brain variation. For this purpose we used the dimensions defined from the resting states of the HCP conducted by Margulies [34] (often referred to as gradients): Gradient 1 (Association to Primary cortex), Gradient 2 (Visual to Motor cortex), Gradient 3 (Frontoparietal to Default Mode Networks) and Gradient 4 (Dorsal Attention Network (DAN)/Visual to Default Mode Networks) of brain variation dimensions illustrated by colour to map activity in state space analysis (purple = low, yellow = high) (not shown: Gradient 5 (Lateral Default Mode to Primary sensory cortex)) [34]. Two 3D scatter plots illustrating two examples from our data of how the movie watching can be seen as two complimentary trajectories through a "Brain Space" (focusing on Gradients 1, 2 and 3, shown at the top) and a "Thought Space" (focusing on"Episodic Knowledge", "Verbal Detail", and "Sensory Engagement", shown at the bottom). In these plots, the cooler points (blue) occur earlier in the movie clip, and the warmer (red) points occur later.

Generation of the thought-space

The first step in our analysis was to decompose the mDES data using PCA to produce the dimensions that make up the "thought-space" we will use for our subsequent analysis (Figure 1, see Methods). Based on the scree plot (see Supplementary Figure 1), the data best fit a four component solution, and these are displayed as word clouds (see Methods for further details). In

these words clouds, items with a similar colour are related, and the font size highlights their importance. Component 1 contributed 26.1% of the variance explained and loaded highly on terms “past,” “self,” and “knowledge,” and negatively on “words” and “sounds” and will be referred to as “Episodic Knowledge.” Component 2 explained 10.5% of the variance and loaded positively on the items “intrusive” and “distracting” and negatively on “deliberateness” and will be referred to as “Intrusive Distraction”. Component 3 loaded positively on “words,” “detail,” and “deliberateness”, explained 7.7% of the variance, and was called “Verbal Detail.” Finally, Component 4 contributed 6.8% of the explained variance, loaded positively on emotion, images, sounds and people and was named “Sensory Engagement”. See Supplementary Table 1 for a description of mDES questionnaire, see Supplementary Table 2 for percentage of variance explained by principal components overall and in each movie.

Split-half reliability results

A bootstrapped split-half reliability analysis was conducted to confirm that the four-component solution provided a reasonable description of our data. This analysis repeatedly divided the mDES data into two random samples and evaluated the correlation between the two halves’ components. The reliability analysis supported the 4-component solution was reproducible because it had a strong homologue similarity score (r = .96, 95% CI [.93, 1.00], see Methods for further details).

Variation in thought patterns

Next, we examined how these dimensions describe experience within each movie (see Figure 2). We performed four linear mixed models (LMM), one for each thought component (Episodic Knowledge, Intrusive Distraction, Verbal Detail, and Sensory Engagement), in which the movie was the explanatory variable of interest and participants was included as a random

effect. The significance threshold was adjusted using the False Discovery Rate (FDR) to control for family-wise error (FWE) within the model (one for each movie). The four-model analyses found significant differences in overall thought pattern scores across the three movies, including reported thoughts resembling "Episodic Knowledge", $F(2, 2015.3) = 5.41$, $p = .005$, "Intrusive Distraction", $F(2, 2015.3) = 77.84$, $p < .001$, "Verbal Detail", $F(2, 2015.4) = 13.90$, $p < .001$, and "Sensory Engagement", $F(2, 2015.7) = 82.69$, $p < .001$. This suggests that within each model, there was a significantly different score for the reported thought pattern in at least one of the movies. To investigate how the movies differ from each other in each thought component score, post-hoc pairwise comparisons were conducted for each model. Post hoc pairwise comparisons using the least-squares means (lsmeans) were conducted to investigate the effect of memory performance across the different films and significance thresholds were adjusted using the Tukey method for controlling FWE within the model. The first model suggests patterns of answers in Little Miss Sunshine showed lower similarity to "Episodic Knowledge" ($M = -0.12$, $SE = .10$) than patterns of thoughts reported in 500 Days of Summer ($M = 0.11$, $SE = .10$), $t(2016) = -3.27$, $p = .003$. However, there were no significant differences for "Episodic Knowledge" scores during Citizenfour ($M = -0.02$, $SE = .10$) compared to Little Miss Sunshine, $t(2015) = 1.31$, $p = .392$, or 500 Days of Summer, $t(2016) = -1.97$, $p = .121$. The second model found reported thoughts were more similar to the pattern of "Intrusive Distraction" during Citizenfour ($M = 0.41$, $SE = .09$) than during Little Miss Sunshine ($M = -0.15$, $SE = .09$), $t(2015) = 9.66$, $p < .001$, and 500 Days of Summer ($M = -0.27$, $SE = .09$), $t(2015) = 11.66$, $p < .001$. There were no differences in how similar reported thoughts were to "Intrusive Distraction" scores between Little Miss Sunshine and 500 Days of Summer, $t(2016) = 2.03$, $p = .106$. Model three found reported thoughts resembeled patterns of "Verbal Detail" more for Citizenfour ($M = 0.17$, $SE =$

.09) than for Little Miss Sunshine (M = -0.14, SE = .09), t(2015) = 5.14, p <.001 or 500 Days of Summer (M = -0.04, SE = .09), t(2016) = 3.58, p = .001. Again, there were no significant differences in "Verbal Detail" scores between Little Miss Sunshine and 500 Days of Summer, t(2016) = -1.54, p = .271. Lastly, model four found reported thoughts during Citizenfour resembled patterns of "Sensory Engagement" (M = -0.32, SE = .07) less than for either Little Miss Sunshine (M = -0.01, SE = .07), t(2015) = -6.07, p <.001, or 500 Days of Summer (M = 0.33, SE = .07), t(2016) = -12.85, p <.001. Additionally, reported thoughts during Little Miss Sunshine resembled patterns of "Sensory Engagement" less than during 500 Days of Summer, t(2016) = -6.81, p <.001. The results are presented visually in Figure 2, to see details of the LMM output see Supplementary Table 3.

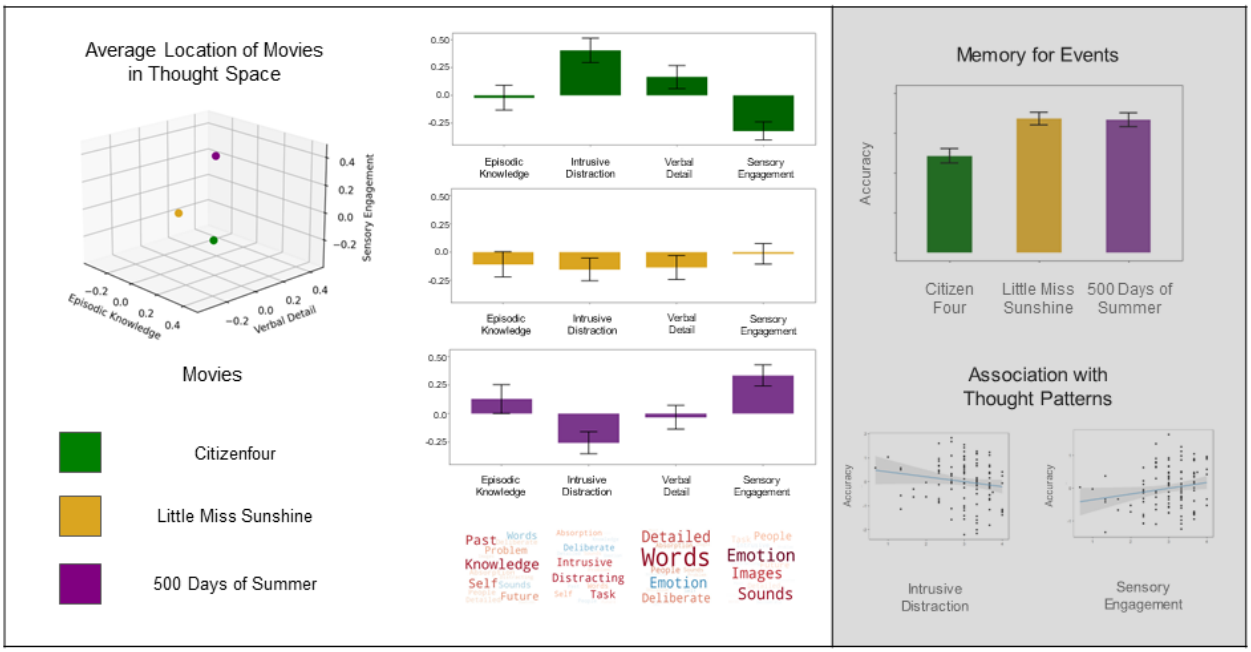

Figure 2. How thought patterns differ across genres of movies and relate to comprehension. *Left to Right* – The 3D scatterplot shows the average location of each film on three of the four PCA dimensions, "Episodic Knowledge", "Verbal Detail" and "Sensory Engagement". The bar graphs

show the average loading on each dimension, with the error bars showing the 95% Confidence Intervals. The plots on the right illustrate the relationship between the mDES dimensions and memory for information in the film. The top barplot shows the average comprehension score on each film with 95% Confidence Intervals error bars. The scatter plots below show the association between mDES components and comprehension. The scatter plot on the left shows the negative linear relationship between the "Intrusive Distraction" thought and memory and the plot on the right show a positive association with "Sensory Engagement." The blue line represents the best fit line and the shaded area shows the 95% Confidence Intervals.

Comprehension

Next, we examined how the thought patterns relate to the participants' memory of the information from the movie (Figure 2). Participants answered four comprehension questions for each film (12 total) which were related to relevant information in the film clip they just watched (see Supplementary Table 4 for comprehension questionnaire). We performed a LMM for which movie and each thought pattern were explanatory variables of interest, included both as main effects and their interaction with the Movie. Comprehension score was the dependent variable and participant was included as a random effect. FDR was used to control for FWE consisting of a total of nine comparisons. The analysis revealed three significant main effects and an interaction. First, there was a significant main effect of movie genre on memory, $F(2, 254.12) = 49.33$, $p < .001$. Post hoc pairwise comparisons using the least-squares means (lsmeans) were conducted to investigate the effect of memory performance across the different films. Significance thresholds for the post-hoc comparisons were adjusted using the Tukey method for controlling FWE within the model. Comprehension scores were significantly lower for questions related to information in Citizenfour ($M = 2.42$, $SE = .09$) compared to Little Miss Sunshine (*M*

= 3.35, *SE* = .08), $t(249) = -9.16$, $p < .001$, as well as 500 Days of Summer (*M* = 3.33, *SE* = .08), $t(273) = -8.33$, $p < .001$. Notably, there was no significant difference in comprehension performance between Little Miss Sunshine and 500 Days of Summer, $t(242) = -.18$, $p = .982$. There were also two significant main effects of thought patterns — "Intrusive Distraction" significantly predicted worse overall comprehension across the three movies, $F(1, 324.41) = 9.27$, $p = .011$, whereas "Sensory Engagement" was significantly associated with better overall comprehension, $F(1, 341.44) = 8.30$, $p = .013$. Finally, there was a significant movie by thought pattern interaction for "Episodic Knowledge", $F(2, 268.96) = 4.46$, $p = .028$. To follow up on this significant interaction, a post-hoc simple slopes analysis was performed to assess the effect of "Episodic Knowledge" on comprehension performance across levels of movie, using FDR to control for multiple comparisons. The analysis found moments when thoughts were more similar "Episodic Knowledge" were associated with significantly better comprehension performance for information in 500 Days of Summer, $t(319.83) = 2.54$, $p = .030$. The interaction predicted positive comprehension performance for information in Little Miss Sunshine, $t(321.85) = 0.93$, $b = 0.07$, *SE* = .07, $p = .350$, and negative comprehension performance for information in Citizenfour, $t(317.55) = -1.39$, $b = -0.09$, *SE* = .06, $p = .240$, though these were not statistically significant. To see the full model output and the lsmeans output, see Supplementary Table 5**.**

Brain – Thought Mappings: Voxel-space Analysis

Having established the dimensions that characterize the mDES data, their prevalence in each movie and their associations to memory, we next examined how these dimensions of experience relate to the brain activity at each moment in the films. Our first analysis examined this question at the voxel level using FSL. In this analysis, the averaged time course of each PCA dimension (collapsed across all individuals in Sample 2) was included as a regressor of interest

at the first level for each of the three movies for the brain activity recorded in each subject in Sample 1. To perform a group comparison of these analyses, we used FLAME in FSL with a cluster forming threshold of $z = 3.1$ FWE and controlled for the number of regressors of interest to determine the significance of each cluster ($p < .0125$). This generated four group-level thresholded maps corresponding to regions whose activation during moments in the film where correlated with relevant thought pattern (see Figure 3 and Supplementary Table 4). "Episodic Knowledge" was significantly positively associated with activation in primary visual cortex (b = 0.62, 95% CI [0.27, 0.97]). "Intrusive Distraction" was significantly associated with deactivation in the FPN (b = -0.78, 95% CI [-1.37, -0.20]). "Verbal Detail" was significantly associated with suppression of activity in primary auditory cortex (b = -1.64, 95% CI [-2.11, -1.17]). Lastly, "Sensory Engagement" was significantly associated with activation in both primary visual and auditory cortexes (b = 1.26, 95% CI [0.81, 1.70]). We also performed a functional connectivity analysis using each set of clusters as the seed region, see Supplementary Figure 2 and Supplementary Table 6.

Our voxel-space analysis highlights two notable features of how thought patterns during movie watching were linked to brain activity. First, most of the regions whose activity that we are able to predict based on mDES scores tended to fall within sensory cortex. Notably, "Sensory Engagement", a pattern of multi-sensory thought linked to sounds and images, is associated with increased activity in both the visual and auditory systems. Interestingly these regions overlap with regions linked to "Episodic Knowledge" maps (Posterior [orange and red]) and those linked to "Verbal Detail" (Right [orange and purple]). Second, the only regions identified outside primary cortex were linked to "Intrusive Distraction" and broadly fall within regions of the FPN (See Supplementary Figure 4 for a comparison with the FPN as defined by [38]), showing

reduced activity in this system during moments when this experience was dominant. This pattern is consistent with views of the FPN as playing an active role in maintaining a state of non-distracted task focus [39]. See Supplementary Table 8 for the output of the analysis.

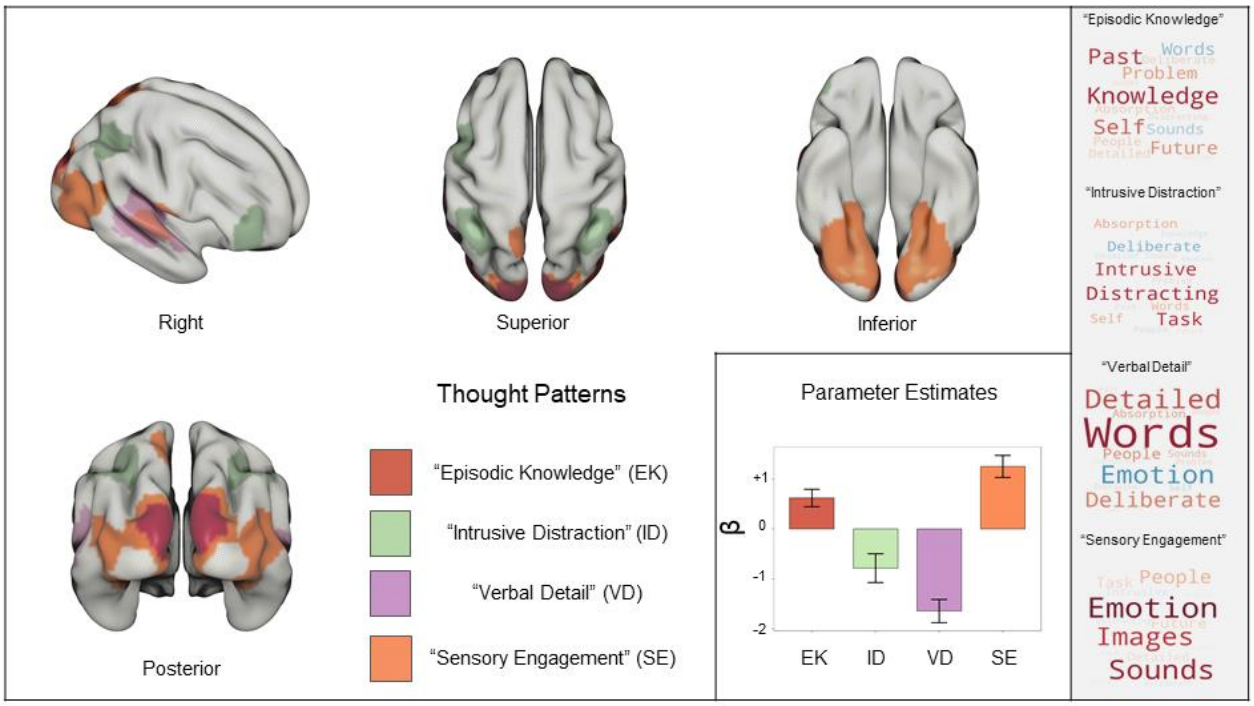

Figure 3. Group-level neural activation patterns associated with each of the dimensions of thought identified in a voxel space analysis. *Left to Right* - Regions in red are associated with activity corresponding to reports of "Episodic Knowledge," green regions are associated with "Intrusive Distraction," areas in purple are associated with "Verbal Detail," and the regions in orange represent activity associated with "Sensory Engagement". The bar plot illustrates the directionality of each parameter estimate with error bars representing 95% Confidence Intervals. Corresponding word clouds for each thought pattern (*top to bottom:* "Episodic Knowledge," "Intrusive Distraction," "Verbal Detail," and "Sensory Engagement") are on the right for reference. Regions linked to "Sensory Engagement" overlap with those linked to "Episodic Detail" in a region of visual cortex and those associated with "Verbal Detail" in temporal cortex.

Our analysis highlighted significant overlap across analyses in regions of visual and auditory cortex. To better understand these common regions, we calculated the overlap in these maps (left hand panel of Figure 4) and performed a meta-analysis using Neurosynth to identify their likely functions (See Supplementary Table 9 for term loadings). The results of this meta analysis are displayed in the form of word clouds where it can be seen that regions common to reduced "Verbal Detail" and greater "Sensory Engagement" are linked to auditory processes ("sounds", "noise" and "pitch"). In contrast, regions common to "Sensory Engagement" and "Episodic Knowledge" are most likely associated with "videos" (see Supplementary Table 5 for individual decoded term scores). Finally, we conducted a resting state functional connectivity analysis using the regions overlap as seeds (right hand panel of Figure 4). This highlighted that both regions exhibited patterns of functional connectivity that included many overlapping areas (coloured yellow) that importantly included both regions of overlap.

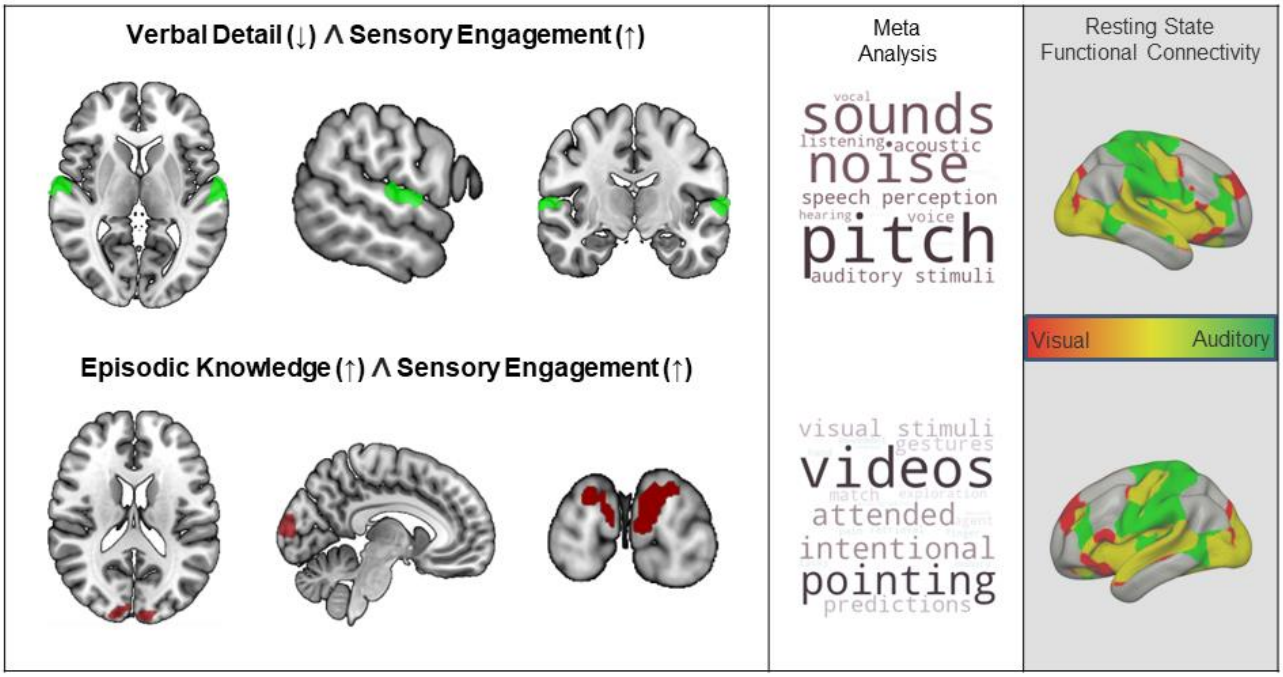

Figure 4. Regions of overlapping activation within sensory regions associated with different patterns of thought. The upper panel shows a common region of superior temporal cortex associated with positive reports of thoughts like "Sensory Engagement" and negative reports of thoughts like "Verbal Detail". The lower panel shows a common region of dorsal visual cortex associated with thoughts reported like "Sensory Engagement" and "Episodic Detail". The word clouds show the results of a Neurosynth meta-analysis of the regions highlighting the most likely functions associated with these regions. The font size describes their importance (bigger = more important) and the colour describing their polarity (darker = positive). The panel on the right show the results of a seed based functional connectivity of these regions of overlap from a resting state study. Regions in red indicate those connected to the region of visual cortex, regions in green show those linked to the region of auditory cortex and regions in yellow are common to both spatial maps.

State Space Analysis

Our final analysis used a "state-space" approach to determine how brain activity at each moment in the film predicted the patterns of thoughts reported at these moments (for prior examples in the domain of tasks, see [35, 36], See Methods). In this analysis, the coordinates of the group average of each TR in the "brain-space" are explanatory variables, and the coordinates of each experience sampling moment in the "thought-space" was the dependent variable. We ran four LMMs, one for each thought component, in each case using the location of each sampling point in the movie on Gradients 1-5 as explanatory variables and the scores for each thought pattern component ("Episodic Knowledge", "Intrusive Distraction", "Verbal Detail" and "Sensory Engagement) were the dependent variable. Participant was included as a random intercept. The significance threshold was adjusted using the FDR to control for FWE within each

model, controlling for a total of five comparisons. After correction, we found two significant main effects. First, we found a significant main effect of Gradient 4 (DAN/Visual) predicted the similarity of answers to the "Episodic Knowledge" component, $t(.01) = 2.17$, $p = .013$. This suggests that moments when thoughts were most similar to "Episodic Knowledge" were associated with increased brain activity in regions high on Gradient 4 (See Figure 6). There was also a significant main effect of Gradient 1 (Association to Primary) predicting patterns of thought related to "Sensory Engagement", $t(2046.34) = -3.26$, $p = .006$. These results show that moments when thoughts are high on "Sensory Engagement" were associated with increased brain activity in regions within the primary cortex low on Gradient 1 (See Figure 6). See Supplementary Table 7 for complete results.

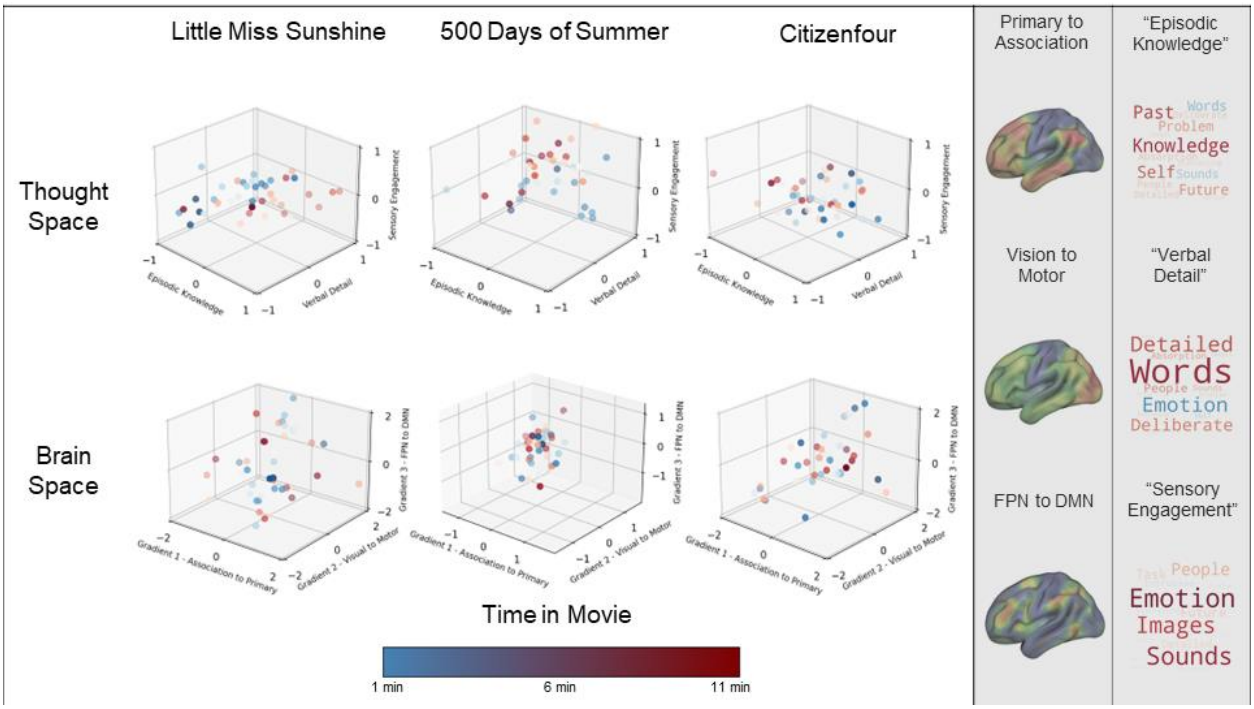

Figure 5. Comparison of the locations of each moments across the movie clip in the (top row) "Thought Space" and the "Brain Space". *Left to Right* – 3D scatterplots of the coordinate locations of each thought pattern ("Episodic Knowledge", "Verbal Detail", and "Sensory

Engagement) and gradients 1-3 (Gradient 1 (Associated – Primary), Gradient 2 (Visual – Somato-motor), Gradient 3 (Frontoparietal – Default) during Little Miss Sunshine, 500 Days of Summer and Citizenfour. Observations in blue occur earlier during the film and observations in red occur later in the film. The gradient maps (1-3) and thought pattern word clouds are on the right for reference.

Our analyses highlighted links between patterns of self reports resembling “Sensory Engagement” and “Episodic Knowledge” were associated with patterns of brain activity in both our voxel and state space analyses. In our next analysis, therefore, we conducted a series spin tests to formally understand the mapping between the voxel-based and state space analyses. To this end we sampled the location of the identified cluster in our voxel analysis on the gradient of interest (e.g. the cluster of voxels associated with “Sensory Engagement" on Gradient 1) and used the spin tests to determine the likelihood that we get a score with this magnitude by chance (based on a null distribution of 2500 permutations). This analysis identified that our voxel-based estimate of “Sensory engagement” falls within the primary cortex of Gradient 1 at a level that is unlikely to occur by chance, $p = .018$, while the location of “Episodic Knowledge” on Gradient 4 was not statistically significant, $p = .251$ (See Figure 6).

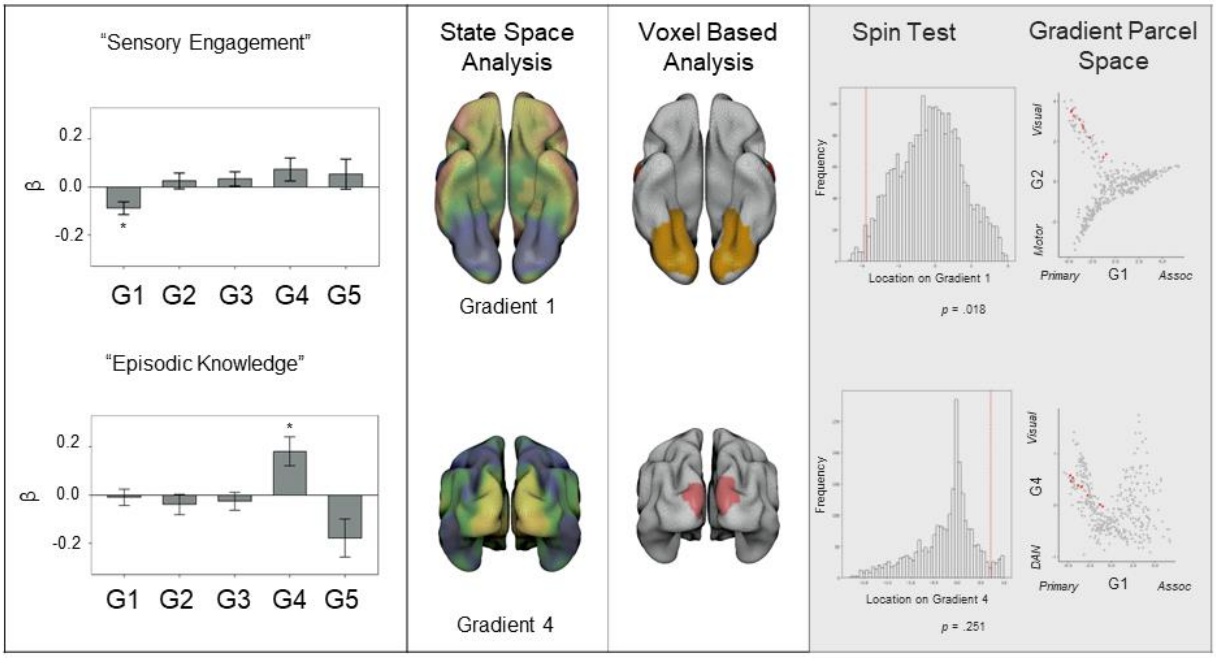

Figure 6. Comparison of State Space- and Voxel-based analyses of "Sensory Engagement" and "Episodic Knowledge" with Gradients. *Left to right* – The barplots illustrate the associations for the significant models using Gradients 1-5 as explanatory variables and the thought patterns, "Sensory Engagement" and "Episodic Knowledge" as dependent variables. To formally compare these results to those using the voxel space analysis we performed two spin tests (perm = 2500). The first spin test revealed the location of the cluster of voxels associated with "Sensory Engagement" are located within the sensory regions of Gradient 1, unlike to have have occurred by chance, $p = .018$. In contrast, the location of the cluster of voxels associated with Episodic Knowledge on Gradient 4 was within the null distribution, $p = .251$. The locations of the relevant clusters in gradient parcel space are presented on the left hand of this figure (red points indicate the location of parcels from the relevant comparison).

Discussion

Our study aimed to identify how patterns of thought during movie watching relate to brain activity during movie clips from three different genres: 500 Days of Summer (a romance), Little Miss Sunshine (a comedy) and Citizenfour (a documentary). We used open-source fMRI data from one group of participants (Sample 1) who watched these films while brain activity was recorded using fMRI and measured ongoing thought patterns using mDES in a second group of participants (Sample 2) for whom no brain activity was acquired (Figure 1). We used a novel sampling approach that allowed us to build a detailed understanding of the time series of different thought patterns every 15 seconds in the clips by only sampling individual participants a relatively small number of times per movie, minimizing disruption of the subjective experience of movie watching. Our analyses examined the overlap between the time series of brain activity in Sample 1 and reported thought patterns in Sample 2 to reveal, for the first time, the relationship between brain activity at different moments in a film and the associated experiential states.

Across the movies, we identified four thought patterns. First, "Sensory Engagement" was related to multi-modal sensory experience (loading on images, sounds, people, and with positive emotional tone). "Sensory Engagement" was highest in the romance movie, associated with better overall comprehension performance across all movies, linked to activity in primary cortex by both the voxel based analysis and the state space analysis, and which were formally linked through a spin test. Second, "Episodic knowledge" was linked to experiences related to knowledge, the past, and the self. This pattern was also highest during the romance movie, specificallt associated with better memory of information in this context, and to increased activity in medial regions of primary visual cortex by both our state space and voxel space

analysis. Unlike sensory engagement result these two results could not be formally linked via a spin test. Third, “Verbal Detail” which described experience as deliberate, detailed experiences in the form of words and with a negative emotional valance. “Verbal Detail” and was most prevalent in the documentary and associated with relative reductions in primary auditory cortex activation using our voxel space analysis. Finally, “Intrusive Distraction” was related to thoughts with intrusive, distracting features that were spontaneous in nature. This thought pattern predicted poorer overall comprehension across all the movies and emerged in moments during the movies associated with reduced activation in regions of the FPN by our voxel space analysis.

Our study suggests that “Sensory Engagement” is likely to reflect a pattern of enjoyable multi-sensory experience that is an integral aspect of movie-watching. This thought pattern was linked to better memory for information across all the movies and was related to multi-modal features of both brain and experience, implicating both auditory and visual cortex (regions at the sensory end of the principle gradient of functional brain organisation). “Sensory Engagement” was the thought pattern with the most consistent and clearest links to the brain since it was the only thought pattern that showed a brain-thought mapping across our voxel and state space analysis that were formally linked using a spin test (see Figure 2 and 6). It also had the clearest association to comprehension of information from the movies indicating that it reflects a state of attentional coupoling to the information in the movie itself [40]. Taken together, the identification of the “Sensory Engagement” state establishes the important role sensory systems play in our experience while we watch movies. It also provides important corroboration for contemporary perspectives that movie watching is a useful and important paradigm for understanding the brain basis behind naturalistic states because it links brain activity in sensory systems to ongoing thought patterns [19].

Although our study highlighted neural activity in primary sensory cortex, we found less evidence for the hypothesized role of association cortex, and in particular the DMN, in the movie watching experience. Neither our voxel or state space analyses highlighted this system (See Figure 3 and 6). Moreover, our spin test established that regions implicated in "Sensory Engagement" fall at the sensory end of Gradient 1 and is therefore related to neural activity with regions that both functionally and structurally are most distinct from the DMN regions [34]. Moreover, the pattern of "Episodic Knowledge" identified by our analysis focuses on features of cognition such as the past, knowledge, people and that self — all of which are terms that previous literature suggests could relate to the DMN [8, 18]. However, both our voxel space, and, our state space analysis highlighted this experience was related to situations when brain activity was higher within visual cortex.

Although our study did not identify a role of the DMN in movie watching, there are several possible methodological reasons why such a mapping may nonetheless exist. For example, it is possible that our choice of films (documentary, romance, and comedy) may have precluded a genre in which the DMN may play a more obvious role (for example, mystery or suspense). Another possibility is that the DMN may be relevant to an understanding aspect of experience that is only captured during longer intervals of movie watching, such as extended plot lines or unexpected events, or other features of movies that depend on the segmentation of a movie into different events [41]. We only sampled experience in short 11-minute clips, so it is possible that the DMN relates to aspects of experience that are important for movie-watching over longer time periods. It is also possible that unique features of the DMN make it difficult for our method to reveal its role in experience. The DMN is a spatially heterogeneous system, and highly variable across individuals [42]. Since our analytic approach links thought patterns in one

set of individuals to brain activity in another, it could be challenging for this method to identify its role in movie-related thought patterns in a highly idiosyncratic brain network such as the DMN [42, 43]. This possibility could be easily tested by examining mappings between thought patterns and individuals using precision scanning methods [44]. Studies have also highlighted that the DMN is heterogeneous in the functions it is involved in and, in particular, is hypothesized to shift flexibly from perpetually decoupled to coupled states [13]. So, for example, the role this network is hypothesized to play in off-task or mind-wandering states may obscure its' role in perceptually coupled states (like movie watching).

It is important to note that while our study does not establish what role DMN plays in movie-watching states, it does highlight a clear role for sensory systems in multiple ongoing thought patterns. Thus, based on our study, whatever role the DMN plays during movie-watching, it is likely to be built upon the role of sensory systems. Consistent with this possibility, contemporary views on the DMN argue that its function arises from its' topographical location in the cortex [8]. According to this perspective, the DMN is located at the maximal distance from primary systems, but also constitutes the apex of processing streams like the ventral and dorsal streams [34]. We have previously argued that whatever role the DMN plays in cognition, it may often entail interactions with primary systems, possibly through the transformation of neural signals along different processing streams [8]. In other words, it is possible based on our study that the DMN plays a role in movie watching that complements information processing taking place in sensory input, an important but less direct contribution to the movie watching experience than regions in visual or auditory cortex. Since the DMN is widely hypothesied to be important in movie watching, we performed an exploratory functional connectivity analysis to examine whether the sensory regions we identified in our study are functionally coupled to the

DMN at rest (see Supplementary Figures 3-5). This revealed that the sensory regions identified in our study shared a common set of regions within the DMN (including anterior regions of the temporal lobe and the inferior frontal gyrus, see Supplementary Figure 2). This analysis was exploratory and so any results should be treated with caution, however, it is consistent with the possibility that a more fine-grained precision mapping approach could identify the role these regions play in ongoing thought during movie watching.

In summary, our study used a novel paradigm to establish the role that primary systems play during our experiences while we watch movies. Nonetheless, important questions about other features of experience during move-watching remain unanswered. For example, "Intrusive Distraction" was the only thought pattern associated with activity outside primary sensory systems and was seen to emerge at moments in films when activity during regions within the FPN was reduced (See Supplementary Figure 4 and Supplementary Table 7 for the overlap between the regions identified linked to "Intrusive Distraction" and the FPN as defined by Yeo and colleagues [45]). Interestingly, the association between greater distraction and reduced activity within the FPN is consistent with this networks assumed role in goal maintenance [46] and psychological perspectives that argue that distraction emerges when executive control is reduced, consistent with it's links to worse performance [47]. Given that processes that drive "Intrusive Distraction" are likely to depend on individual and contextual factors, further research may be necessary to understand this brain-cognition mapping fully. Likewise, patterns of "Verbal Detail" were associated with moments in the films where auditory cortex activation was reduced. This may reflect a shift in attention away from the processing of the auditory input related to the movie towards evaluative thoughts about the people or events in the film, perhaps in the form of inner speech [39]. These thoughts may occur when participants form opinions

about movie characters, elaborate or make inferences about the information they have encoded from the film [48]. This possibility could be easily explored by examining more specific experience sampling items that directly target inner speech or comprehension questions that target inferential processing on events within the movies (See [12]). Importantly, our study provides a novel method for answering these questions and others regarding the brain basis of experiences during films that can be applied in a simple cost effective manner. In the future the ease with which our method can be applied to different groups of individuals and to different types of media means that it will be possible to build a more comprehensive and culturally inclusive understanding of the links between brain activity and the movie-watching experience.

Methods

Participant Pool – Laboratory Sample

The sample consisted of 120 participants (98 women (81.7%), 17 men (14.2%), 5 non-binary or similar gender identity (3.3%); age: M = 18.83, SD = 1.19, range of 18-23) who participated in the in-person laboratory study to watch three 11-minute movie clips, responded to mDES probes, and completed a brief comprehension assessment. All participants spoke English, with 95% of the sample primarily residing in Canada (China (1.7%), India (.8%), Nigeria (.8%), USA (1.7%)). This study was granted ethics clearance by the Queen's University General Research Ethics Board. Participants were recruited between March 2023 and April 2023 through the Queen's University Psychology Participant Pool. Participants provided written, informed consent via electronic documentation before participating in the research study. Participants were rewarded with one-course credit or $10.00 for their participation and were provided with a verbal and written debrief form upon completion of the study.

Participant Pool – Brain Data Sample

See Aliko and colleagues for description of the sample [33].

Resting-state Participant Pool

191 student volunteers (123 women (64.4%); age: M = 20.1 ± 2.25 years, range of 18 – 31) with normal or corrected-to-normal vision and no history of neurological disorders participated in this study. Written informed consent was obtained from all subjects prior to the resting-state scan. The study was approved by the ethics committees of the Department of Psychology and York Neuroimaging Centre, University of York. This data has been used in previous studies to examine the neural basis of memory and mind-wandering, including region-of-interest based connectivity analysis and cortical thickness investigations [37, 49-57].

Procedure

Participants attended an individual in-person testing session at the laboratory at Queen's University to watch movie clips after providing written informed consent and providing basic demographic information. Participants were assigned to a testing booth, a small room with a desk, a chair, a computer to present the stimuli, and a pair of headphones to listen to the audio stimuli. Participants were required to attend to the computer screen to watch and listen to three randomly presented 11-minute video clips. During each movie clip, participants were briefly interrupted five times to answer randomly assigned mDES probes about the content of their thoughts just prior to the probe. After the first minute of each clip, each probe was delivered once every two minutes, using a jittered technique, by assigning participants to a counterbalanced probe order to minimize the systematic impact of prior and later probes at any given sampling moment (see Supplementary Figure 5 for visualization). Once participants finished watching the

three clips, they completed a 12-item comprehension questionnaire on Qualtrics, with four items related to information from each of the three movie clips (see Supplementary Table 3).

Multi-dimensional experience sampling (mDES)

Participants received 15 total mDES probes across the three clips, five for each, and all responses were made with respect to their thoughts just before the probe interrupted their viewing. No probes were administered within the first minute of the clip — the first possible probe was administered at the 75-second mark to allow participants to situate themselves with the context of the movie clip. Each of the 16 mDES questions appeared in a randomized order, and participants were asked to use the directional arrow keys to move a slider across the screen to indicate, on a scale of 1(not at all) to 10 (completely), how much that particular feature characterized their thoughts. The specific items used in this experiment are presented in Supplementary Table 1.

Probe Orders

There were 16 probe orders that a participant could be assigned to for each movie, which determined the delivery time of the five mDES probes throughout each 11-minute clip. Each subject ID was assigned to three different probe orders for each of the three films, and no subject ID was given the same probe order twice. This was achieved by creating a matrix of equally distributed probe orders across subject IDs to ensure each moment in the movie was probed an equal amount of times while uniquely distributing probes to control for order effects. Probe orders were designed to sample participants at every 15-second interval of the entire movie clip but only probed a single participant five times per clip. This allowed us to sample experience as frequently as possible without interrupting participants from naturalistic viewing by oversampling or too frequent probes and to control for ordering effects from the delivery time of

the other probes. Each participant received a probe approximately every two minutes using a jittered technique. The first eight probe orders do not share any of the same probe delivery times, whereas the latter eight probe orders (9-16) have been shuffled so that they share one probe time with only one of the orders from the former eight orders. Across orders 9-16, each probe from the first eight orders is repeated in a different combination of probes so that mDES responses at each probe are derived from participants in two different orders. See Supplementary Figure 6.

Movie Clip Stimuli

Movie stimuli were presented in 11-minute scenes from movies 500 Days of Summer, Little Miss Sunshine and Citizenfour. Stimuli were selected from the Naturalistic Neuroimaging Database (NNDb) [33] and chosen based on genre and cut from the full-length movie down to 11-minute clips. Participants were informed they would watch three movie clips from varying genres but were presented randomly. Written instructions were presented on screen at the beginning of each clip. After watching the three clips and responding to the mDES probes, participants were presented with a Qualtrics questionnaire to complete a comprehension test on the content of each film clip.

Comprehension questions

Participants completed a comprehension test of 12 questions, four from each movie. The questions were collaboratively created to test general knowledge about the movie that would otherwise not be common sense, and cover events that occur during the beginning, middle and end of the clip. An example of one of the comprehension questions was “What breakfast item did Olive order a la mode?” for the movie clip Little Miss Sunshine. A table of all the questions with corresponding answers can be found in Supplementary Table 3. Participants responded using 1-2 words, and otherwise instructed to enter “?” if they had no answer.

Brain Analysis

Our analyses used brain data acquired and shared by the NNDb, an open-access database of pre-processed MNI 2mm fMRI data (TR = 1) of participants who watched one of 10 full-length movies [33]. We utilized MNI 2mm fMRI data corresponding to participants who watched 500 Days of Summer (n = 20), Citizenfour (n = 18) and Little Miss Sunshine (n = 6). The specific pre-processing steps applied to the brain data and specific details of the sample are described in [33].

Voxel-space Analysis

Our analysis used the pre-processed data from [33]. The first step in our analysis was to extract the brain activity for each individual for the 10-minute section that we sampled in experience using mDES. To map the mDES time series onto these data we created a mean time series for across each movie, which described the mDES experience, averaged across 40 observations, at every 15 second interval. Next, we interpolated this time series to generate a time series of experience that matched the TR used to sample brain activity in Sample 1 (1 second). Next, the interpolated time series for each PCA for each film were included as regressors for each individual's brain activity (*i.e*. 4 regressors for each movie). Finally, we used FLAME as implemented in FSL to perform a group level analysis across each of the three movie clips. In this analysis we set the cluster forming threshold at $z = 3.1$ and corrected for FWE by accounting for the number of voxels in the brain and the 3 movies we examined and the 4 PCAs in each movie. This resulted in the correction of the FWE p-value from FSL $p < .0025$.

Brain-space Analysis

To create the "brain space" coordinates, we first calculated a group-averaged timeseries for each movie. To do this, we first z-scored each individuals' timeseries data and then calculated the mean activity in each voxel at each TR across the whole sample, resulting in a group-averaged brain volume at each TR. Next, we applied a binarized mask to each group-averaged brain volume at each TR. This mask was generated based on the (cortical and subcortical) gradient maps openly available on Neurovault (https://identifiers.org/neurovault.collection:1598). These gradient maps were produced from the decomposition of the Human Connectome Project resting-state fMRI data [34]. Then, we calculated the (spearman rank) correlation between each group-averaged per-TR brain map and each of the first five gradient maps. Consistent with published literature, the results of these correlations constitute the coordinates of each moment of the film in the 5D Brain space [35]. An example of these coordinates is presented in the upper left panel of Figure 5. The code for this analysis is openly available at https://github.com/willstrawson/StateSpace (v1.0.0).

Cognitive Decoding

Connectivity maps were uploaded to Neurovault [58] (https://neurovault.org/collections/13821/) and decoded using Neurosynth [45]. Neurosynth is an automated meta-analysis tool that uses text-mining approaches to extract terms from neuroimaging articles that typically co-occur with specific peak coordinates of activation. It can be used to generate a set of terms frequently associated with a spatial map. The results of cognitive decoding were rendered as word clouds using in-house scripts implemented in Python. We excluded terms referring to neuroanatomy (*e.g.,* "inferior" or "sulcus"), as well as the second

occurrence of repeated terms (*e.g.,* “semantic” and “semantics”). The size of each word in the word cloud relates to the frequency of that term across studies.

Analysis of intrinsic functional connectivity using resting-state fMRI

Our analysis additionally used resting state cohort data (see below) to seed the maps created from each of the four thought pattern time series regressors from the prior analysis. We used this seed based analysis to see if different resting state networks converge with the maps we have generated from movie-watching.

Pre-processing

Pre-processing and statistical analyses of resting-state data were performed using the CONN functional connectivity toolbox V.20a (http://www.nitrc.org/projects/conn; [59] implemented through SPM (Version 12.0) and MATLAB (Version 19a). For pre-processing, functional volumes were slice-time (bottom-up, interleaved) and motion-corrected, skull-stripped and co-registered to the high-resolution structural image, spatially normalized to the Montreal Neurological Institute (MNI) space using the unified-segmentation algorithm, smoothed with a 6 mm FWHM Gaussian kernel, and band-passed filtered (.008 - .09 Hz) to reduce low-frequency drift and noise effects. A pre-processing pipeline of nuisance regression included motion (twelve parameters: the six translation and rotation parameters and their temporal derivatives), scrubbing (outlier volumes were identified through the composite artifact detection algorithm ART in CONN with conservative settings, including scan-by-scan change in global signal z-value threshold = 3; subject motion threshold = 5 mm; differential motion and composite motion exceeding 95% percentile in the normative sample) and CompCor components (the first five)

attributable to the signal from white matter and CSF [60] as well as a linear detrending term, eliminating the need for global signal normalization [61, 62]

Seed Selection and Analysis

Intrinsic connectivity seeds were binarized masks derived from voxel-space analysis using FLAME through FSL. We excluded all non-grey matter voxels that fell within these masks. We performed seed-to-voxel analyses convolved with a canonical haemodynamic response function for each of these seeds. At the group-level, analyses were carried out using CONN with cluster correction at $p < .05$ and a threshold of p-FDR = .001 (two-tailed) to define contiguous clusters.

References

1. Finn, E.S. and P.A. Bandettini, *Movie-watching outperforms rest for functional connectivity-based prediction of behavior.* Neuroimage, 2021. **235**.
2. Hasson, U., et al., *Neurocinematics: The Neuroscience of Film.* Projections, 2008. **2**: p. 1-26.
3. Haxby, J.V., M.I. Gobbini, and S.A. Nastase, *Naturalistic stimuli reveal a dominant role for agentic action in visual representation.* Neuroimage, 2020. **216**.
4. Vanderwal, T., J. Eilbott, and F.X. Castellanos, *Movies in the magnet: Naturalistic paradigms in developmental functional neuroimaging.* Dev Cogn Neurosci, 2019. **36**: p. 100600.
5. Matusz, P.J., et al., *Are we ready for real-world neuroscience?* 2019, MIT Press One Rogers Street, Cambridge, MA 02142-1209, USA journals-info …. p. 327-338.
6. Nastase, S.A., et al., *Measuring shared responses across subjects using intersubject correlation.* Soc Cogn Affect Neurosci, 2019. **14**(6): p. 667-685.
7. Hasson, U., et al., *Enhanced intersubject correlations during movie viewing correlate with successful episodic encoding.* Neuron, 2008. **57**(3): p. 452-62.
8. Smallwood, J., et al., *The neural correlates of ongoing conscious thought.* Iscience, 2021. **24**(3).
9. Smallwood, J., *Distinguishing how from why the mind wanders: a process-occurrence framework for self-generated mental activity.* Psychol Bull, 2013. **139**(3): p. 519-535.
10. Smallwood, J., et al., *Going AWOL in the brain: mind wandering reduces cortical analysis of external events.* J Cogn Neurosci, 2008. **20**(3): p. 458-69.
11. Smallwood, J. and J. Andrews-Hanna, *Not all minds that wander are lost: the importance of a balanced perspective on the mind-wandering state.* Front Psychol, 2013. **4**: p. 441.
12. Smallwood, J., M. McSpadden, and J.W. Schooler, *When attention matters: The curious incident of the wandering mind.* Memory & Cognition, 2008. **36**(6): p. 1144-1150.
13. Zhang, M., et al., *Perceptual coupling and decoupling of the default mode network during mind-wandering and reading.* eLife, 2022. **11**: p. e74011.
14. Smallwood, J. and J.W. Schooler, *The restless mind.* Psychol Bull, 2006. **132**(6): p. 946-958.
15. Smallwood, J. and J.W. Schooler, *The science of mind wandering: empirically navigating the stream of consciousness.* Annu Rev Psychol, 2015. **66**: p. 487-518.
16. Medea, B., et al., *How do we decide what to do? Resting-state connectivity patterns and components of self-generated thought linked to the development of more concrete personal goals.* Experimental Brain Research, 2018. **236**(9): p. 2469-2481.
17. Schooler, J.W., et al., *Meta-awareness, perceptual decoupling and the wandering mind.* Trends in Cognitive Sciences, 2011. **15**(7): p. 319-326.
18. Yang, E., et al., *The default network dominates neural responses to evolving movie stories.* Nature Communications, 2023. **14**(1): p. 4197.
19. Finn, E.S., *Is it time to put rest to rest?* Trends in Cognitive Sciences, 2021. **25**(12): p. 1021-1032.
20. Smallwood, J., et al., *The default mode network in cognition: a topographical perspective.* Nature Reviews Neuroscience, 2021. **22**(8): p. 503-513.

21. Christoff, K., et al., *Experience sampling during fMRI reveals default network and executive system contributions to mind wandering.* Proc Natl Acad Sci U S A, 2009. **106**(21): p. 8719-24.
22. Konu, D., et al., *A role for the ventromedial prefrontal cortex in self-generated episodic social cognition.* NeuroImage, 2020. **218**: p. 116977.
23. Zhang, M.C., et al., *Distinct individual differences in default mode network connectivity relate to off-task thought and text memory during reading.* Scientific Reports, 2019. **9**.
24. D'Esposito, M. and B.R. Postle, *The Cognitive Neuroscience of Working Memory.* Annual Review of Psychology, Vol 66, 2015. **66**: p. 115-142.
25. Chenot, Q., et al., *Functional Connectivity Within the Fronto-Parietal Network Predicts Complex Task Performance: A fNIRS Study.* Frontiers in Neuroergonomics, 2021. **2**.
26. Rohr, C.S., et al., *Functional network integration and attention skills in young children.* Developmental Cognitive Neuroscience, 2018. **30**: p. 200-211.
27. Demertzi, A., et al., *Human consciousness is supported by dynamic complex patterns of brain signal coordination.* Science advances, 2019. **5**(2): p. eaat7603.
28. Konu, D., et al., *Exploring patterns of ongoing thought under naturalistic and conventional task-based conditions.* Consciousness and Cognition, 2021. **93**.
29. Turnbull, A., et al., *Age-related changes in ongoing thought relate to external context and individual cognition.* Consciousness and Cognition, 2021. **96**: p. 103226.
30. McKeown, B., et al., *The impact of social isolation and changes in work patterns on ongoing thought during the first COVID-19 lockdown in the United Kingdom.* Proceedings of the National Academy of Sciences, 2021. **118**(40): p. e2102565118.
31. Mulholland, B., et al., *Patterns of ongoing thought in the real world.* Consciousness and Cognition, 2023. **114**: p. 103530.
32. Turnbull, A., et al., *Left dorsolateral prefrontal cortex supports context-dependent prioritisation of off-task thought.* Nature Communications, 2019. **10**.
33. Aliko, S., et al., *A naturalistic neuroimaging database for understanding the brain using ecological stimuli.* Scientific Data, 2020. **7**(1).
34. Margulies, D.S., et al., *Situating the default-mode network along a principal gradient of macroscale cortical organization.* Proc Natl Acad Sci U S A, 2016. **113**(44): p. 12574-12579.
35. McKeown, B., et al., *Experience sampling reveals the role that covert goal states play in task-relevant behavior.* Scientific Reports, 2023. **13**(1): p. 21710.
36. Turnbull, A., et al., *Reductions in task positive neural systems occur with the passage of time and are associated with changes in ongoing thought.* Scientific Reports, 2020. **10**(1): p. 9912.
37. Karapanagiotidis, T., et al., *Tracking thoughts: Exploring the neural architecture of mental time travel during mind-wandering.* NeuroImage, 2017. **147**: p. 272-281.
38. Yeo, B.T., et al., *The organization of the human cerebral cortex estimated by intrinsic functional connectivity.* J Neurophysiol, 2011. **106**(3): p. 1125-65.
39. Scolari, M., K.N. Seidl-Rathkopf, and S. Kastner, *Functions of the human frontoparietal attention network: Evidence from neuroimaging.* Current Opinion in Behavioral Sciences, 2015. **1**: p. 32-39.
40. Smallwood, J., *Penetrating the fog of the decoupled mind: The effects of visual salience in the sustained attention to response task.* Canadian Journal of Experimental Psychology / Revue canadienne de psychologie expérimentale, 2013. **67**(1): p. 32-40.

41. Geerligs, L., et al., *A partially nested cortical hierarchy of neural states underlies event segmentation in the human brain.* Elife, 2022. **11**.
42. Braga, R.M. and R.L. Buckner, *Parallel Interdigitated Distributed Networks within the Individual Estimated by Intrinsic Functional Connectivity.* Neuron, 2017. **95**(2): p. 457-471.e5.
43. Daitch, A.L. and J. Parvizi, *Spatial and temporal heterogeneity of neural responses in human posteromedial cortex.* Proceedings of the National Academy of Sciences of the United States of America, 2018. **115**(18): p. 4785-4790.
44. Gordon, E.M., et al., *Precision Functional Mapping of Individual Human Brains.* Neuron, 2017. **95**(4): p. 791-807.e7.
45. Yarkoni, T., et al., *Large-scale automated synthesis of human functional neuroimaging data.* Nature Methods, 2011. **8**(8): p. 665-670.
46. Cole, M.W. and W. Schneider, *The cognitive control network: Integrated cortical regions with dissociable functions.* Neuroimage, 2007. **37**(1): p. 343-60.
47. McVay, J.C. and M.J. Kane, *Does mind wandering reflect executive function or executive failure? Comment on Smallwood and Schooler (2006) and Watkins (2008).* Psychol Bull, 2010. **136**(2): p. 188-197.
48. Alderson-Day, B. and C. Fernyhough, *Inner Speech: Development, Cognitive Functions, Phenomenology, and Neurobiology.* Psychol Bull, 2015. **141**(5): p. 931-65.
49. Evans, M., et al., *Controlled semantic summation correlates with intrinsic connectivity between default mode and control networks.* Cortex, 2020. **129**: p. 356-375.
50. Gonzalez Alam, T., et al., *Meaningful inhibition: Exploring the role of meaning and modality in response inhibition.* NeuroImage, 2018. **181**: p. 108-119.
51. Gonzalez Alam, T.R.d.J., et al., *Degrees of lateralisation in semantic cognition: Evidence from intrinsic connectivity.* NeuroImage, 2019. **202**: p. 116089.
52. Gonzalez Alam, T.R.d.J., et al., *A tale of two gradients: differences between the left and right hemispheres predict semantic cognition.* Brain Structure and Function, 2022. **227**(2): p. 631-654.
53. Gonzalez Alam, T.R.J., et al., *Intrinsic connectivity of anterior temporal lobe relates to individual differences in semantic retrieval for landmarks.* Cortex, 2021. **134**: p. 76-91.
54. Poerio, G.L., et al., *The role of the default mode network in component processes underlying the wandering mind.* Social Cognitive and Affective Neuroscience, 2017. **12**(7): p. 1047-1062.
55. Turnbull, A., et al., *The ebb and flow of attention: Between-subject variation in intrinsic connectivity and cognition associated with the dynamics of ongoing experience.* NeuroImage, 2019. **185**: p. 286-299.
56. Vatansever, D., et al., *Varieties of semantic cognition revealed through simultaneous decomposition of intrinsic brain connectivity and behaviour.* NeuroImage, 2017. **158**: p. 1-11.
57. Wang, H.-T., et al., *Dimensions of Experience: Exploring the Heterogeneity of the Wandering Mind.* Psychological Science, 2017. **29**(1): p. 56-71.
58. Gorgolewski, K.J., et al., *NeuroVault.org: a web-based repository for collecting and sharing unthresholded statistical maps of the human brain.* Frontiers in Neuroinformatics, 2015. **9**.

59. Whitfield-Gabrieli, S. and A. Nieto-Castanon, *Conn: A Functional Connectivity Toolbox for Correlated and Anticorrelated Brain Networks.* Brain Connectivity, 2012. **2**(3): p. 125-141.
60. Behzadi, H., N.L. Hadipour, and M. Mirzaei, *A density functional study of (17)O, (14)N and (2)H electric field gradient tensors in the real crystalline structure of alpha-glycine.* Biophys Chem, 2007. **125**(1): p. 179-83.
61. Chai, X.J., et al., *Anticorrelations in resting state networks without global signal regression.* Neuroimage, 2012. **59**(2): p. 1420-8.
62. Murphy, K., et al., *The impact of global signal regression on resting state correlations: Are anti-correlated networks introduced?* NeuroImage, 2009. **44**(3): p. 893-905.