Unveiling Multi-level and Multi-modal Semantic Representations in the Human Brain using Large Language Models

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Abstract

 In recent studies, researchers have used large language models (LLMs) to explore semantic representations in the brain; however, they have typically assessed different levels of semantic content, such as speech, objects, and stories, separately. In this study, we recorded brain activity using functional magnetic resonance imaging (fMRI) while participants viewed 8.3 hours of dramas and movies. We annotated 010 these stimuli at multiple semantic levels, which enabled us to extract latent representations of 012 LLMs for this content. Our findings demon- strate that LLMs predict human brain activ- ity more accurately than traditional language 015 models, particularly for complex background stories. Furthermore, we identify distinct brain regions associated with different semantic representations, including multi-modal vision- semantic representations, which highlights the importance of modeling multi-level and multi- modal semantic representations simultaneously. We will make our fMRI dataset publicly avail- able to facilitate further research on aligning LLMs with human brain function.

⁰²⁵ 1 Introduction

 Language models, which learn the statistical struc- ture of languages from large corpora to enable ma- chines to understand semantics, have made signifi- cant advances [\(Devlin et al.,](#page-8-0) [2018;](#page-8-0) [Radford et al.,](#page-9-0) [2019;](#page-9-0) [Zhang et al.,](#page-10-0) [2022;](#page-10-0) [Touvron et al.,](#page-9-1) [2023\)](#page-9-1). Be- cause semantic comprehension is fundamental to human intelligence, the correspondence between human brain activity and the latent representations of language models has been an intriguing sub- ject of research. To examine the correspondence between human and language models, in recent studies, researchers used brain encoding mod- els [\(Naselaris et al.,](#page-9-2) [2011;](#page-9-2) [Nishimoto et al.,](#page-9-3) [2011;](#page-9-3) [Huth et al.,](#page-9-4) [2012\)](#page-9-4) to predict brain activity based on the high-dimensional latent representations of language models [\(Jain and Huth,](#page-9-5) [2018;](#page-9-5) [Jat et al.,](#page-9-6)

[2019;](#page-9-6) [Toneva and Wehbe,](#page-9-7) [2019;](#page-9-7) [Caucheteux et al.,](#page-8-1) **042** [2021;](#page-8-1) [Schrimpf et al.,](#page-9-8) [2021;](#page-9-8) [Goldstein et al.,](#page-8-2) [2022;](#page-8-2) **043** [Caucheteux et al.,](#page-8-3) [2022;](#page-8-3) [Antonello et al.,](#page-8-4) [2023\)](#page-8-4). **044** The quantitative assessment of the correspondence **045** between the two can serve as a unique benchmark **046** for modern large language models (LLMs) because **047** it potentially provides a biological benchmark for **048** the alignment between LLMs and humans. **049**

In previous studies, researchers typically focused **050** on a single aspect of semantic comprehension (e.g., **051** speech content); however, realistic scenarios are 052 inherently multifaceted. For instance, a scene in **053** which two people are speaking can be depicted 054 through multiple semantic levels in language: their **055** speech content, their identities and the visual ap- **056** pearance of their outfits, the location and time of **057** the scene, and the broader context of the conversa- **058** tion. In traditional studies, researchers often ad- **059** dress these levels of semantics separately, which **060** leads to a lack of clarity on how multiple levels of **061** semantic content are attributed to brain activity and **062** how the latent representations of language models **063** might align with the human brain processing of **064** multiple levels of content. 065

In this study, we address these issues by record- **066** ing human brain activity using functional magnetic **067** resonance imaging (fMRI) while participants view **068** 8.3 hours of videos of dramas or movies. Impor- **069** tantly, we heavily annotate these videos across mul- **070** tiple levels of semantic content related to the drama, **071** including speech dialogue, visual objects, and back- **072** ground story. We extract latent representations of **073** these annotations from LLMs, then build encoding **074** models that predict brain activity from these latent **075** representations to quantitatively compare how each **076** type of information is represented in different brain **077** regions. Furthermore, we quantitatively assess **078** how each brain region uniquely captures differ- **079** ent aspects of semantic content using different **080** types of latent representations derived from LLMs **081** and multi-modal LLMs. **082**

083 Our contributions are as follows:

- **084** 1. Unlike previous researchers, who modeled **085** various semantic modalities independently, **086** we demonstrate that different semantic modal-**087** ities uniquely account for brain activity in dis-**088** tinct brain regions.
- **089** 2. We show that the superiority of LLMs is not **090** uniform across different modalities: LLMs **091** are particularly effective in modeling story-**092** related information.
- **093** 3. We show that latent representations of multi-**094** modal vision-semantic LLMs predict brain **095** activity and uniquely capture representations **096** in the association cortex better than unimodal **097** models combined .
- **098** 4. We collect densely annotated fMRI datasets **099** acquired while the participants watch 8.3 **100** hours of videos as another benchmark for the **101** biological metric of the alignment between **102** LLMs and humans. We will publish these **103** datasets.

¹⁰⁴ 2 Related work

 In numerous previous studies, researchers exam- ined the relationship between the latent represen- tations of language models and brain activity dur- ing speech comprehension. These researchers pri- marily focused on the correspondence between la- tent representations of language models obtained [f](#page-8-5)rom speech transcriptions and brain activity [\(Huth](#page-8-5) [et al.,](#page-8-5) [2016;](#page-8-5) [Jat et al.,](#page-9-6) [2019;](#page-9-6) [Toneva and Wehbe,](#page-9-7) [2019;](#page-9-7) [Schmitt et al.,](#page-9-9) [2021;](#page-9-9) [Caucheteux et al.,](#page-8-1) [2021,](#page-8-1) [2022\)](#page-8-3). Recent findings have further demonstrated that LLMs provide a better explanation of brain ac- [t](#page-9-8)ivity than traditional language models [\(Schrimpf](#page-9-8) [et al.,](#page-9-8) [2021;](#page-9-8) [Goldstein et al.,](#page-8-2) [2022;](#page-8-2) [Antonello et al.,](#page-8-4) [2023;](#page-8-4) [Tuckute et al.,](#page-9-10) [2024\)](#page-9-10).

 Regarding the semantic content of the visual object in the scene, the correspondence between the latent representations of deep learning models related to the displayed objects and human brain [a](#page-8-6)ctivity have been studied extensively [\(Güçlü and](#page-8-6) [van Gerven,](#page-8-6) [2015;](#page-8-6) [Horikawa and Kamitani,](#page-8-7) [2017;](#page-8-7) [Groen et al.,](#page-8-8) [2018;](#page-8-8) [Wen et al.,](#page-10-1) [2018;](#page-10-1) [Khosla et al.,](#page-9-11) [2021;](#page-9-11) [Allen et al.,](#page-8-9) [2022;](#page-8-9) [Chen et al.,](#page-8-10) [2023;](#page-8-10) [Wang](#page-10-2) [et al.,](#page-10-2) [2023;](#page-10-2) [St-Yves et al.,](#page-9-12) [2023;](#page-9-12) [Takagi and Nishi-](#page-9-13) [moto,](#page-9-13) [2023;](#page-9-13) [Luo et al.,](#page-9-14) [2023\)](#page-9-14). In most of these studies, researchers used neuroimaging data while participants watched static images or short video **130 clips.** 131

Although several neuroscience studies have been conducted in which researchers explored high-level **133** story content in the brain using a naturalistic movie [w](#page-10-3)atching experiment [\(Hasson et al.,](#page-8-11) [2008;](#page-8-11) [Wehbe](#page-10-3) [et al.,](#page-10-3) [2014;](#page-10-3) [Aw and Toneva,](#page-8-12) [2022;](#page-8-12) [Chang et al.,](#page-8-13) **136** [2021;](#page-8-13) [Nastase et al.,](#page-9-15) [2021\)](#page-9-15), these researchers typi- **137** cally did not explicitly model high-level story con- **138** tent using language models. Furthermore, they have not examined the unique explanatory power story-specific semantic content exerts on brain activity compared with other types of semantic con- **142** tent. **143**

There is a growing consensus that LLMs mir- **144** ror human brain activity more accurately than traditional language models during semantic com- **146** prehension; however, in the individual studies de- **147** scribed above, the reseachers addressed discrete aspects of semantic comprehension independently. This is problematic because humans process dif- **150** ferent types of semantic content simultaneously in naturalistic scenarios, and such content may be represented differently in LLMs and the human brain. **153** Here, we address these issues by evaluating how much each level of semantic content uniquely explains brain activity compared with other semantic **156** content. 157

3 Methods **¹⁵⁸**

3.1 fMRI experiments **159**

We collect brain activity data from six healthy participants with normal and corrected-normal vision **161** (three females; age 22–40, mean = 28.7) while **162** they freely watch 8.3 hours of videos of movies **163** or drama series. All participants are right-handed, **164** native Japanese speakers. They provided written in- **165** formed consent for the study and the release of their **166** data. The ethics and safety committees approved **167** the experimental protocol. **168**

MRI data are acquired using a 3T MAGNETOM **169** Vida scanner (Siemens, Germany) with a standard **170** Siemens 64-channel volume coil. Blood oxygena- **171** tion level-dependent (BOLD) images are acquired **172** using a multiband gradient echo-planar imaging **173** sequence [\(Moeller et al.,](#page-9-16) [2010\)](#page-9-16) (TR = 1,000 ms, 174 TE = 30 ms, flip angle = 60° , voxel size = $2 \times 2 \times 2$ 175 mm³, matrix size = 96×96 , 72 slices with a thickness of 2 mm, slice gap 0 mm, $FOV = 192 \times 192$ 177 mm², bandwidth 1736Hz/pixel, partial Fourier 6/8, 178 multiband acceleration factor 6). Anatomical data **179**

Figure 1: Overview of the experiment and brain encoding models. a In the experiment, participants watch 8.3 hours of videos of dramas or movies while we measure their brain activity inside an fMRI scanner. We densely annotate the videos with multiple levels of semantic content, which are used for extracting latent representations from multiple language models. The annotations provide examples from specific scenes in the series '*Suits*'. b For each semantic feature obtained by the language models, we estimate linear weights for predicting brain activity across the cerebral cortex from the feature using ridge regression. We subsequently apply the estimated weights to the features of the test data to estimate brain activity. We calculate prediction performance using Pearson's correlation coefficient between the predicted and actual fMRI responses.

 were collected using the same 3T scanner using T1-weighted MPRAGE (TR = 2530 ms, TE = 3.26 182 ms, flip angle = 9° , voxel size = $1 \times 1 \times 1$ mm³, **FOV** = 256×256 mm²). The preprocessing of the functional data includes motion correction, coregis- tration, and detrending. See Section [A.1](#page-10-4) for details of the acquisition and preprocessing procedures.

187 3.2 Stimuli

 We use nine videos of movies or drama series as stimuli (10 episodes in total), with dense annota- tions related to those videos. The videos encom- pass various genres. Eight are international videos and one is a Japanese animation. The average play- back time of the 10 episodes is 49.98 minutes (rang- ing from 21 minutes to 125 minutes). We divide each episode into two to nine parts, each approximately 10 minutes long, for use as stimulus videos **196** during the fMRI experiment. We play all the inter- **197** national videos in Japanese dubbed versions and **198** the subjects understand them in Japanese. We will **199** make our fMRI dataset publicly available for fu- **200** ture research on acceptance. See Section [A.1.1](#page-10-5) for **201** details of data collection. **202**

The annotations include five levels of semantic **203** content from the videos: transcriptions of spoken **204** dialogue (*Speech*), objects in the scene (*Object*), **205** background story of the scene (*Story*), summary of **206** the story (*Summary*), and information about time **207** and location (*TimePlace*) (Figure [1a](#page-2-0)). The seman- **208** tic content consists of annotations that describe **209** the stimulus videos in natural language. This con- **210** tent differs in the nature of the description and the **211** timespan of the annotations. Specifically, *Speech* **212**

Table 1: Summary of the five language models.

 corresponds to the intervals of speaking, whereas *Object* is annotated every second, *Story* every 5 seconds, *Summary* approximately every 1-3 min- utes, and *TimePlace* every time the screen changes. Multiple annotators independently label each level of semantic content, except for *Speech*: five for *Object*, three each for *Summary* and *TimePlace*, and two for *Story*. For all five classes of semantic annotations, at least two researchers independently and regularly review the annotations, making cor- rections if any errors are found in the descriptions. We also quantitatively confirm that the results are robustly reproduced when the annotators or data are divided. See Sections [A.2](#page-11-0) and [A.3](#page-13-0) for details of annotations and quality control.

 We divide the data into training and test datasets, and calculate all the prediction performance re- sults presented in this paper using the test dataset. Specifically, we use the fMRI scanning sessions corresponding to the last split of each movie or drama series, 7,737 seconds in total, as test data. We use the remaining sessions, 22,262 seconds in total, as training data.

236 3.3 Feature extraction

 We obtain latent representations from five language models (Figure [1a](#page-2-0)): Word2Vec [\(Mikolov et al.,](#page-9-17) [2013\)](#page-9-17), BERT [\(Devlin et al.,](#page-8-0) [2018\)](#page-8-0), GPT2 [\(Radford](#page-9-0) [et al.,](#page-9-0) [2019\)](#page-9-0), OPT [\(Zhang et al.,](#page-10-0) [2022\)](#page-10-0), and Llama 2 [\(Touvron et al.,](#page-9-1) [2023\)](#page-9-1). We use Word2vec as a traditional language model. The summary of these language models is presented in Table [1.](#page-3-0) See Section [A.1.5](#page-11-1) for the information of the models we **245** used.

 We extract the latent representations of the lan- guage models for the annotations from each of the hidden layers, except for Word2Vec, from which we obtain word embeddings. For each latent rep- resentation from each hidden layer, we build brain encoding model (see Section [3.4\)](#page-4-0). We first extract

the latent representations of annotations, each of **252** which consists of several tokens or words, for each **253** time point. Then, we average the latent represen- **254** tations of the LLMs across tokens or average the **255** word embeddings of Word2Vec across words. Be- **256** cause multiple annotations exist for each second, **257** except for *Speech* annotations, we calculate the **258** latent representations for each annotator for each **259** language model and then average the latent rep- **260** resentations across all annotators. For OPT and **261** Llama 2, we reduce the dimensions of the flattened **262** stimulus features using principal component anal- **263** ysis (PCA) and set the number of dimensions to **264** 1280 (the same dimension as GPT2). We calculate **265** the PCA loadings based on the training data and **266** apply these loadings to the test data. In the main **267** analysis we calculate latent representations using **268** the annotation that correspond to the TR (1 sec- **269** ond). We confirm that the results do not change **270** significantly when we use longer context-lengths **271** (see Figure [A.7\)](#page-19-0). **272**

We also explore how uniquely different levels of **273** semantic content explain brain activity compared **274** with features from other modalities: vision, audio, 275 and vision-semantic. For visual features, we extract **276** latent representations from DeiT [\(Touvron et al.,](#page-9-18) **277** [2021\)](#page-9-18) and ResNet [\(He et al.,](#page-8-14) [2016\)](#page-8-14). We input the **278** first and middle frames of each second of the video **279** into the model and extract the output from each **280** hidden layer. For audio features, we extract the **281** latent representations of audio data in the video **282** [u](#page-9-19)sing AST [\(Gong et al.,](#page-8-15) [2021\)](#page-8-15) and MMS [\(Pratap](#page-9-19) **283** [et al.,](#page-9-19) [2023\)](#page-9-19). We input audio data into the model **284** in 1-second intervals. We extract the output from **285** each hidden layer in response to the input. For **286** both the vision and audio modalities, we reduce **287** the dimensions of the flattened stimulus features **288** using PCA and set the number of dimensions to **289** 1280. We calculate the PCA loadings based on the **290** training data and apply these loadings to the test **291** data. **292**

In addition to the unimodal feature, we extract **293** vision-semantic multi-modal representations from **294** GIT [\(Wang et al.,](#page-10-6) [2022\)](#page-10-6), BridgeTower [\(Xu et al.,](#page-10-7) **295** [2023\)](#page-10-7), and LLaVA-v1.5 [\(Liu et al.,](#page-9-20) [2023\)](#page-9-20). To ob- **296** tain these vision-semantic representations, we in- **297** put pairs of vision and semantic into the vision- **298** semantic models, which are the same as the in- **299** put for unimodal models. We use output from the **300** text-decoder in GIT, the cross-modal encoder in **301** BridgeTower, and the text-decoder in LLaVA-v1.5 **302** as vision-semantic features. We average the latent **303**

 representations of text and images across tokens, re- spectively. We finally reduce the dimensions of the flattened features using PCA and set the number of dimensions to 1280. In variance partitioning analy- sis used to investigate unique variance explained by multi-modal features compared with unimodal fea- [t](#page-10-8)ures (see Section [3.7\)](#page-5-0), we use Vicuna-v1.5 [\(Zheng](#page-10-8) [et al.,](#page-10-8) [2024\)](#page-10-8), which is the base model of the text decoder of LLaVA-v1.5, and CLIP [\(Radford et al.,](#page-9-21) [2021\)](#page-9-21), which is the image encoder of LLaVA-v1.5. For CLIP, we use the model in LLaVA-v1.5, and for Vicuna-v1.5, we use the model provided by **316** lmsys.

317 3.4 Brain encoding models

 To investigate how different levels of semantic con- tent are represented differently in the human brain, we first build brain encoding models to predict brain activity from the latent representations of lan- guage models for each semantic content indepen- dently (see Figure [1b](#page-2-0)). We separately construct en- coding models for each subject, feature, and layer (if applicable).

 We model the mapping between the stimulus features and brain responses using a linear model $Y = XW$, where Y denotes the brain activity of voxels from fMRI data, X denotes the correspond- ing stimulus features, and W denotes the linear weights on the features for each voxel. We esti- mate the model weights from training data using L2-regularized linear regression, which we subse- quently apply to test data. We explore regulariza- tion parameters during training for each voxel us- ing cross-validation procedure. Because the dataset contains nine dramas and movies, to tune the reg- ularization parameters during training, we select sessions from two to three dramas or movies as validation data and use the remaining videos as training data. We repeat this procedure across all dramas and movies. For the evaluation, we use Pearson's correlation coefficients between the pre- dicted and measured fMRI signals. We compute the statistical significance using blockwise permu- tation testing. Specifically, to generate a null distri- bution, we shuffle the voxel's actual response time course before calculating Pearson's correlation be- tween the predicted response time course and the permuted response time course. During this pro- cess, we shuffle the actual response time course in blocks of 10TRs to preserve the temporal correla- tion between slices. We identify voxels that have scores significantly higher than those expected by

chance in the null distribution. We set the thresh- **355** old for statistical significance to $P < 0.05$ and 356 correct for multiple comparisons using the FDR **357** procedure. We conduct all encoding analyses using **358 the** *himalaya* **library^{[2](#page-4-1)}[\(la Tour et al.,](#page-9-22) [2022\)](#page-9-22). We will** 359 make our code publicly available on acceptance. In 360 the analysis for comparing different language mod- **361** els (Figures [2](#page-5-1) and [3\)](#page-6-0), we assume hemodynamic **362** delays of 8-10 seconds from neural activity to the **363** BOLD signal. We confirm that choice of delay **364** time does not significantly affect on the results **365** (See Figure [A.6\)](#page-18-0). In the analysis for comparing **366** multi-modal features (Figure [5\)](#page-7-0), we use the delay 367 time of 6-8 seconds for the analysis of all features. **368**

3.5 Comparison of different levels of semantic **369 content** 370

To examine how uniquely each level of semantic **371** content explains brain activity, we construct a brain **372** encoding model that incorporates all the semantic **373** features and evaluate the unique variance explained **374** by each semantic feature using variance partition- **375** ing analysis [\(la Tour et al.,](#page-9-22) [2022\)](#page-9-22). In variance **376** partitioning analysis, we determine the unique vari- **377** ance explained by subtracting the prediction perfor- **378** mance of a model with a certain feature of interest **379** removed from the prediction performance of the **380** full model that includes all features. To estimate **381** the model weights, we use banded ridge regression **382** [\(la Tour et al.,](#page-9-22) [2022\)](#page-9-22), which can optimally estimate **383** the regularization parameter for different feature **384** spaces. For variance partitioning analysis, we use **385** Llama 2 as LLMs, and use the latent representa- **386** tions from the layers that demonstrate the highest **387** accuracy in cross-validation within the training data **388** for each level of semantic content in the previous **389** encoding model analysis. **390**

3.6 Principal component analysis **391**

For interpretation purposes, we apply PCA to the **392** weight matrix of the encoding model [\(Huth et al.,](#page-9-4) $\qquad \qquad$ 393 [2012\)](#page-9-4). Here, we focus on the representation of the **394** *Story* feature because the representation of such **395** high-level semantic content in the brain has not **396** been quantitatively evaluated in previous studies. **397** We use only the voxels with top 5,000 prediction 398 performance. To interpret the estimated PCs, we **399** project randomly selected 1,640 *Story* annotations **400** onto each PC, thus acquiring PC scores for the an- **401** notation. To further interpret the PC scores, we use **402**

² https://github.com/gallantlab/himalaya

Figure 2: Encoding model results. a Prediction performance (measured using Pearson's correlation coefficients) when predicting the brain activity of a single participant (DM09) from the latent representations of different language models for five distinct levels of semantic content. The figure presents the average prediction performance on the test dataset for the top 5,000 voxels, which we select within the training cross-validation folds in the layer that exhibits the highest prediction performance. We choose layers and voxels for each semantic content and each language model, respectively. The error bars indicate the standard error of the mean across voxels. **b** Prediction performance for a single subject (DM09) when all five levels of semantic content are used simultaneously using Llama 2, projected onto the inflated (top, lateral, and medial views) and flattened cortical surface (bottom, occipital areas are at the center), for both the left and right hemispheres. Brain regions with significant accuracy are colored (all colored voxels $P < 0.05$, FDR corrected).

 GPT-4 (*gpt-4-1106-preview* in the OpenAI API) to classify these annotations into five semantic at- tributes that are commonly present throughout the annotations. Finally, we interpret PC1, PC2 and PC3 as axes that represent content related to the environment, interaction and cooperation in the drama respectively. See Section [A.1.4](#page-11-2) for details.

410 3.7 Comparison of different modalities

 Taking advantage of the fact that our stimuli con- sist of visual, auditory, and semantic multi-modal elements, we compare the prediction performance of the visual, auditory, and semantic modalities of brain activity. Thus, we use not only unimodal features but also multi-modal features of the vision- semantic modality. We build the encoding model following the same procedure described previously and compare its whole-brain prediction perfor-**420** mance.

 Furthermore, we test whether the multi-modal features can predict brain activity components that unimodal features cannot. For this purpose, we use variance partitioning analysis as described earlier. The analysis procedure remains nearly identical to the procedure we use for the different levels of semantic content. We concentrate this analysis

on LLaVA-v1.5, which performs particularly well **428** among multi-modal models. As unimodal mod- **429** els, we use Vicuna-v1.5 for the semantic modality, **430** CLIP for the vision modality, and AST for the au- **431** dio modality. Here, we use *Speech* as semantic **432** features. **433**

4 Results **⁴³⁴**

4.1 Comparison of the language models **435**

We first evaluate how different levels of seman- **436** tic content explain brain activity independently. **437** Figure [2a](#page-5-1) shows that *Speech*, *Object*, and *Story* **438** content predict brain activity with higher accu- **439** racy than *Summary* and *TimePlace* content. No- **440** tably, the larger the model, the better the predic- **441** tion performance, and in particular, Llama 2 con- **442** sistently achieves higher prediction performance **443** than Word2Vec for all subjects for *Speech*, *Object*, **444** and *Story* ($P < 0.05$, paired t-test). It also shows 445 that large models achieve higher prediction per- **446** formance for high-level background *Story* content. **447** See Figure [A.1](#page-14-0) for the results for all subjects. Fig- **448** ure [2b](#page-5-1) shows the prediction performance of the **449** encoding model with all five levels of semantic **450** content simultaneously with Llama 2. It demon- **451**

Figure 3: Variance partitioning analysis. Unique variance explained by the latent representations of the semantic content of (a) *Speech*, (b) *Object*, and c *Story* for a single subject (DM09). We use Llama 2 as a language model. For illustration purposes, we color only the voxels with a unique variance above 0.03.

Figure 4: Principal component analysis. PCA on the encoding weight matrix of the latent representations of Llama 2 identifies the first three PCs for two subjects (Left, DM03; Right, DM09). Only the voxels with top 5,000 prediction performance are used for PCA.

 strates that we can predict brain activity across a wide range of brain regions involved in high-level cognition, in addition to sensory areas that include vision and audio.

456 4.2 Variance partitioning analysis

 In the previous analysis, we showed that the LLMs' latent representations of *Speech*, *Object*, and *Story* content predict brain activity well. However, the unique contribution of each level of semantic con- tent to the explanation of brain activity remains unclear. Next, we use variance partitioning anal- ysis [\(la Tour et al.,](#page-9-22) [2022\)](#page-9-22) to determine the extent to which the different types of semantic content uniquely account for brain activity.

 Figure [3](#page-6-0) shows that the latent representations of Llama 2 for the semantic content of *Speech*, *Object*, and *Story* correspond to spatially distinct brain regions. By contrast, *Summary* and *Time- Place* do not have unique variance (see Figure [A.2\)](#page-14-1). Specifically, *Speech* is associated with the auditory cortex, *Object* with the visual cortex, and *Story* with a broader brain region, including the higher visual cortex, precuneus, and frontal cortex. Fur- thermore, when we perform similar analysis using Word2Vec with *Story*, the unique variance is lower than that of Llama 2. This suggests that our encoding results obtained by LLMs reflect high-level **478** semantic information representations in the brain **479** (see Figure [A.3\)](#page-15-0). **480**

These findings are consistent with those of previ- **481** ous researchers who focused on individual modali- **482** ties (e.g. [\(Huth et al.,](#page-8-5) [2016\)](#page-8-5)). However, a critical **483** distinction from earlier work is that we focus **484** on the unique explanatory power of individual **485** modalities when compared with other modal- **486 ities**; that is, building on insights from previous 487 studies, we present the first comprehensive results **488** that integrate various semantic content into a single **489** study. Figure [A.2](#page-14-1) shows the results for all subjects **490** for all semantic content. **491**

4.3 Principal component analysis **492**

Thus far, we have demonstrated that different levels **493** of semantic content uniquely explain spatially dis- **494** tinct brain regions. Next, we analyze what specific **495** information is captured by our encoding models by **496** applying PCA to the weight of the encoding model **497** for the latent representations of Llama 2 for *Story* **498** content. **499**

The first three PCs explain the weight matrices **500** of the top 5000 voxels, based on prediction perfor- **501** mance, with explained variance ratios of 27.2 ± 502 4.5%, 13.7 ± 1.3 %, and 7.6 ± 1.6 % (mean \pm s.t.d, 503

Figure 5: Comparisons among the modalities. a Prediction performance when predicting the brain activity of a single participant (DM09) from the latent representations of the feature modalities. The results for Llama 2 are the same as those in Figure [2b](#page-5-1). b Unique variance explained by four modality features for a single subject (DM09). Here, we use *Speech* as semantic features for Vicuna-v1.5 and LLaVA-v1.5. For illustration purposes, we color only the voxels with unique variance above 0.03.

 N=6). Figure [4a](#page-6-1) presents the projection of PC scores computed for each voxel for two example participants (DM03 and DM09). While high-level semantic content within *Story* annotations is pre- sumed to vary significantly between individuals, we observe certain trends across participants, par- ticularly PC1 and PC2. See Figure [A.4](#page-16-0) for the results for all subjects.

512 4.4 Comparisons among the modalities

 Given the multi-modal nature of the stimuli in our study, we can quantitatively compare the prediction performance of latent representations of semantics with that of other modalities, such as vision and **517** audio.

 Figure [5a](#page-7-0) shows the prediction performance of each modality's latent representation. Similar to the semantic features, the visual and auditory features predict brain activity well. Interestingly, the multi- modal features (e.g. LLaVA-v1.5) predict brain activity better than all other features.

 Figure [5b](#page-7-0) demonstrates that the multi-modal fea- tures (LLaVA-v1.5) uniquely predict brain activ- ity in the association cortex, which cannot be ex-plained by the unimodal features.

 Together, these results suggest that the informa- tion processing style of state-of-the-art multi-modal deep learning models corresponds to human brain activity better and more uniquely than the unimodal models. This is intriguing because human cog- nition is inherently multi-modal and multi-modal models might capture such a computational process in their latent representations. See Figure [A.5](#page-17-0) for the results for all subjects.

5 Discussion and conclusions **⁵³⁷**

In this study, we quantitatively compared the re- **538** lationship between different latent representations **539** of LLMs and brain activity using diverse anno- **540** tations of semantic content. To achieve this, we **541** collected 8.3 hours of an fMRI dataset of brain **542** activity recorded while participants watched exten- **543** sively annotated videos. We demonstrated that the **544** LLMs' latent representations explain brain activity **545** particularly well for high-level background story **546** content compared with traditional language models. **547** Moreover, our results show that different levels of **548** semantic content are distributed differently in the **549** brain. Finally, we demonstrated that multi-modal **550** vision-semantic models explain brain activity better **551** and more uniquely than unimodal models. **552**

We reemphasize that these insights were not ap- **553** parent from the modeling of individual features, as 554 was performed in previous studies. For instance, **555** the absence of unique variance for *Summary* and **556** *TimePlace* is a significant insight, which indicates **557** that simply including these types of information **558** in encoding analysis might not be sufficient for **559** capturing high-level semantic representations in **560** the brain. Our results do not indicate that such **561** information is absent in the brain but the absence **562** could be caused by the limitations of the modeling **563** approaches or fMRI measurement. Hence, in fu- **564** ture work, we need to consider how to model these **565** types of high-level information using our data as a **566** new biological benchmark for alignment between **567** LLMs and humans. **568**

⁵⁶⁹ 6 Limitations

 Firstly, we constructed our encoding models using multiple (five) levels of semantic content. Although this approach is more comprehensive compared to previous research, which typically used only one level of semantic content, our study still does not encompass the full diversity of semantic content processed in reality. Moving forward, it will be cru- cial to use resources like LLMs to annotate stimuli and model a richer human semantic experience.

 In this study, our focus was on the individual level, which is the most typical approach in the field of brain encoding models. We did not exten- sively compare how the representations of semantic content differ among individuals. To better capture the diversity of human cognition, it is important for future studies to explore how these computations vary between individuals, requiring more data from a larger number of participants.

 In this study, we used vision-language models to examine the importance of multi-modal fea- tures. However, human perception encompasses a broader range of modalities, including not just vision and language, but also hearing and other senses. To comprehensively understand these pro- cesses, it is important for future research to utilize models that can handle a greater variety of modali-**596** ties.

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822 **A Appendix**

823 A.1 fMRI dataset and preprocessing

818 Zhuohan Li, Dacheng Li, Eric Xing, et al. 2024.

781 suppressing the human language network using large

786 els of human high-level visual cortex emerge from

824 A.1.1 Stimuli

 In our study, we used multi-modal stimuli from nine DVDs, which encompassed 10 episodes of television drama series and a feature film, as de- tailed in Table [A.2.](#page-22-0) The selection of these nine DVDs adhered to specific criteria: We chose 1) in- ternationally acclaimed dramas and films, premised on the belief that their fame ensured the compelling nature of their content. This was intended to capti-vate the participants' attention during the narratives

in our study. 2) We included a diverse range of **834** genres. Typically, a single story predominantly fea- **835** tures certain characters whose dialogue and actions **836** reflect the genre. In such limited scenarios, when **837** deploying algorithms based on machine learning **838** to analyze BOLD signals, ensuring the generaliz- **839** ability of results may prove to be challenging. To **840** cover a broad spectrum of scenarios, we included **841** films from multiple genres; The average total du- **842** ration for the 10 episodes was 49.98 minutes (Ta- **843** ble [A.2\)](#page-22-0). Each episode was segmented into two **844** to nine segments for use in our imaging sessions. **845** We chose the segmentation points to maintain seg- 846 ment lengths of approximately 10 minutes and to **847** coincide with transitions between narrative scenes, **848** thereby facilitating the participants' comprehen- **849** sion of each episode. For each segment, except **850** the initial segment, we included the concluding **851** 20 seconds of the preceding segment. The result- **852** ing segments varied in length from 512 seconds to **853** 1271 seconds, with an average of 746.8 seconds **854** (Table [A.2\)](#page-22-0). Instead of converting each segment **855** into a separate film file, we designated specific play- **856** back intervals to the respective DVDs using the **857** intervals as visual stimuli in each imaging session. **858** All films, with the sole exception of "Ghost in the **859** Shell" (originally produced in Japanese), were presented in the Japanese-dubbed version, considering 861 that all participants in our study were Japanese. **862**

A.1.2 Procedures **863**

fMRI BOLD signals were recorded as participants **864** viewed the audiovisual content (the film segments) **865** from 10 episodes across nine DVDs. The visual **866** stimuli were projected centrally with a visual angle **867** of 26.78×15.85 degrees at 25 or 30 Hz. MR- 868 compatible headphones delivered the auditory stim- **869** uli. Prior to the viewing sessions, the audio levels **870** were calibrated using non-experimental test clips **871** to ensure clarity and a comfortable volume for par- **872** ticipants. Participants were instructed to view the **873** film segments casually, mirroring their everyday **874** television-watching experience. For each partici- **875** pant, fMRI data were acquired over 10 distinct ses- **876** sions. During each session, participants watched **877** one or two episode segments over three to five seg- **878** ments (each segment lasting approximately 10 min- **879** utes) (Table [A.2\)](#page-22-0). Because of its extended length **880** (about 2 hours), "Dream Girls" was viewed over **881** two sessions. Each segment's film content was **882** displayed by cueing the respective DVD to play **883** at specific times using the VLC media player's **884**

 (VideoLAN, France) command line interface. This interface was set up to commence playback coin- ciding with the scan's start. Manual termination of 888 the scan followed the film segment's conclusion, thereby accommodating the varying durations of playback across segments and sessions. In total, around 9 hours (31905 seconds) of film content were presented to the participants across 10 ses-sions for fMRI data collection.

894 A.1.3 Preprocessing

 For individual preprocessing of EPI data for each participant, the Statisti- cal Parameter Mapping toolbox (SPM8, http://www.fil.ion.ucl.ac.uk/spm/software/spm8/) was used. EPI images were motion-corrected by aligning them to the initial image recorded in the first session for each participant. Voxel responses were standardized by deducting the average response over all time points. Subsequently, prolonged trends in the standardized responses were mitigated by detracting the outcome of median filter convolution with a 120-second time frame. Data standardization and detrending were conducted for each movie segment for each voxel. Data captured within the initial 20 seconds of the scan were deemed susceptible to artifacts from startup transients and thus excluded from the analysis. The analysis considered data from 20 seconds post-scan initiation to the conclusion of the film content.). To account for the hemodynamic response function (HRF), stimulus features were time-shifted by 8s and then averaged with the stimulus feature corresponding to each volume and the feature corresponding to the subsequent two-second volume. See Figure [A.6](#page-18-0)

920 A.1.4 Interpretation of PCA

 In the annotation process using GPT-4, we allowed the annotations to be associated with multiple se- mantic attributes. Then, we evaluated each PC ac- cording to the average scores for the five attributes. The five attributes depict a tense or peaceful envi- ronment ("Tense confrontations or crime" and "Ev- eryday interaction or peaceful living"), represent individual or collective decision-making ("Personal growth, change, or determination", and "Decision- making or role of leaders"), and illustrate inter- action or cooperation with others ("Mutual assis- tance or cooperation'). We also define these five attributes using GPT-4 by asking GPT-4 to identify common attributes across annotations.

To further interpret information content in the **935** PCs, we projected *Story* annotations on each PC. **936** Again, we observed consistent trends in PC1 and **937** PC2. Figure [4b](#page-6-1) shows that PC1 contrasts annota- **938** tions related to individual or collective decision- **939** making ("Decision-making or role of leaders" and **940** "Personal growth, change, or determination") with **941** annotations depicting environment or background **942** scenario ("Tense confrontations or crime" and "Ev- **943** eryday interaction or peaceful living"). Regarding **944** PC2, it contrasts annotations that indicate coop- **945** eration with others ("Decision-making or role of **946** leaders" and "Mutual assistance or cooperation") **947** with more personal scenarios ("Decision-making or **948** role of leaders", "Everyday interaction or peaceful **949** living," and "Tense confrontations or crime"). Re- **950** garding PC3, although there was a tendency among **951** participants to contrast cooperation ("Mutual as- **952** sistance or cooperation") with other attributes, the **953** variation across participants was large. **954**

A.1.5 Feature extraction **955**

We use bert-base-uncased, gpt2-large, **956** facebook/opt-6.7bm, meta-llama/Llama-2- **957** 7b-hf, MIT/ast-finetuned-audioset-10-10-0.4593, **958** facebook/mms-1b-models, facebook/deit-base- **959** distilled-patch16-224, microsoft/resnet-50, **960** microsoft/git-base, BridgeTower/bridgetower- **961** base, and llava-hf/llava-1.5-7b-hf models **962** available on Hugging Face for BERT, GPT2, **963** OPT, Llama2, AST, MMS, DeiT, ResNet, **964** GIT, BridgeTower, and Llava-v1.5. We use 965 GoogleNews-vectors-negative300 model available **966** on https://code.google.com/archive/p/word2vec/. **967**

A.2 Annotation procedure **968**

Each video was annotated for five types of semantic **969** content by annotators employed by external agen- **970** cies. The annotations were performed by one or **971** several annotators for each type of semantic con- **972** tent. Note that *Speech* annotations refer to the ex- **973** act content spoken by actors in a video (e.g., "Hey **974** John, how are you feeling?" "Great"). These can **975** indeed be expressed as language descriptions. On **976** the other hand, *Story* pertains not to the direct dia- **977** logue but to the context or background information **978** (e.g., "Mary and John, who have been childhood **979** friends, are reuniting after two years"). This allows **980** it to be described as a separate linguistic content **981** from the spoken dialogue. **982**

The overview of each annotation is as follows. **983** The details of the annotation procedures will be **984**

– (*Story*) *Harvey expressed surprise that* **1033**

985 more thoroughly explained in the documentation

996 narrative.

1025 displayed:

1026 • Scene from *Suits*:

1032 *on his face.*

13

 tanks with a machine gun and cannon. Unrest spreads among the workers and air traffic controllers. Ohba watches the scene from a short distance outside the fence.

 – (*TimePlace*) *Morning. Inside the Dome. Management Office.*

A.3 Quality control of the dataset

 To verify the quality of the dataset, we split the dataset and annotations as follows to ensure that the results were consistent when the encoding model was built separately for each split.

 First, we split the entire training dataset into two parts: runs of the first and second halves of the data used in the main analysis. We used the same videos for testing dataset. Regarding 'Breaking Bad,' because only one run of data was used in the main analysis, we excluded it from this control analysis. The comparison shows that the results for the two encoding models using different data splits produced quite similar results across cortical voxels (see Figure [A.8\)](#page-20-0).

 We also checked the quality at the annotation level. For our data, there were two annotators for *Story* and five for *Object*. Therefore, for *Story*, we split the two annotators and these split are used to create their respective encoding models. For *Ob- ject*, we split the annotators into groups of three and two and used to create their respective encod- ing models to compare the results. The comparison shows that the results for the two encoding models using different annotator splits produced quite sim-ilar results across cortical voxels (see Figure [A.9\)](#page-21-0).

 Finally, for the *Speech* annotations, we per- formed analysis to verify the consistency in the speech transcription between Japanese and English. Specifically, we compared the results for the encod- ing models when we used Japanese *Speech* annota- tion with the results when we used English *Speech* annotation with the latent representations of GPT2. In this analysis, we constructed the encoding model for the two languages, respectively, and compared the prediction accuracies across voxels for each participant. We then examined whether the predic- tion accuracies exhibited a similar pattern between two annotations. We observed strong correlation **across all participants (DM01: Pearson's r = 0.90, DM03:** $r = 0.85$, **DM06:** $r = 0.91$, **DM07:** $r = 0.90$, **DM09:** $r = 0.92$, **DM11:** $r = 0.82$), which indicates that the latent features for the two languages had similar information to explain brain activity.

A.4 Additional results of encoding models **1132**

Figures [A.1,](#page-14-0) [A.2,](#page-14-1) [A.4,](#page-16-0) and [A.5](#page-17-0) show additional **1133** results for all subjects for Figures [2,](#page-5-1) [3,](#page-6-0) [4,](#page-6-1) and [5,](#page-7-0) re- **1134** spectively. They show that our results were robust 1135 across subjects. **1136**

Figure A.1: All subject results for comparing prediction performances among different language models for different semantic contents.

Figure A.2: All subject results for comparing unique variance explained among different semantic contents using variance partitioning analysis.

Figure A.3: All subject results for unique variance explained of for *Story* feature for Llama 2 (Left) and Word2Vec (Right), respectively.

Figure A.4: All subject results for principal components analysis. We project each caption onto the PC space and then calculated the PC scores for each attribute assigned to the caption. The error bars represent the standard error of the mean PC scores across annotations belonging to each attribute.

Figure A.5: All subject results for comparing the prediction performance among semantics, audio, visual, and vision-semantic features.

HRF delays considered in the encoding models. (Llama2, Story)

Figure A.6: Results for the encoding models under the assumption of different BOLD signal time delays, using the Llama 2 with *Story* Feature. Changing the settings used in the main analysis (8-10s) does not affect the overall patterns of results.

Context window lengths (Llama2, Story)

Figure A.7: Result for the encoding models using the *Story* feature of Llama 2 with different context widths (w). Changing the setting used in the main analysis (w=1s) does not affect the overall patterns of results.

Figure A.8: Results for encoding models when training data are split in half (Split A and Split B) and the models are built independently. We observe no significant difference in the distribution of the flat map in both splits. Also, when comparing prediction performance across voxels between Split A and Split B, the results are generally reproduced in both splits (see scatter plots).

Figure A.9: Results for encoding models when annotations are divided into two splits (Split A and Split B) and the models are built independently. We observe no significant difference in the distribution of the flat map in both splits. Also, when comparing prediction performance across voxels between Split A and Split B, the results are generally reproduced in both splits (see scatter plots).

Table A.2: Videos used for the experiment.