The language network reliably 'tracks' naturalistic meaningful non-verbal stimuli

Abbreviated title: The language network and non-verbal meaning

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Acknowledgments: We would like to acknowledge the Athinoula A. Martinos Imaging Center at the McGovern Institute for Brain Research at MIT, and its support team (Steve Shannon and Atsushi Takahashi). We thank former and current EvLab members (especially Olessia Jouravlev, Zach Mineroff, Brianna Pritchett, and Caitlyn Hoeflin) for help with data collection, Amaya Arcelus for help with creating the Heider & Simmel style animation, and Jeanne Gallée and Caroline Arnold for help with recording the dialog.

Conflict of interest: The authors declare no competing financial interests.

Funding Sources: This research was supported in part by a grant from the Simons Foundation to the Simons Center for the Social Brain at MIT. EF was additionally supported by R01 awards DC016607 and DC016950 from NIDCD, U01 award NS121471, and research funds from the McGovern Institute for Brain Research, the Department of Brain and Cognitive Sciences at MIT, and the Middleton Professorship.

Abstract

The language network, comprised of brain regions in the left frontal and temporal cortex, responds robustly and reliably during language comprehension but shows little or no response during many non-linguistic cognitive tasks (e.g., Fedorenko & Blank, 2020). However, one domain whose relationship with language remains debated is semantics—our conceptual knowledge of the world. Given that the language network responds strongly to meaningful linguistic stimuli, could some of this response be driven by the presence of rich conceptual representations encoded in linguistic inputs? In this study, we used a naturalistic cognition paradigm to test whether the cognitive and neural resources that are responsible for language processing are also recruited for processing semantically rich non-verbal stimuli. To do so, we measured BOLD responses to a set of ~5-minute-long video and audio clips that consisted of meaningful event sequences but did not contain any linguistic content. We then used the inter-subject correlation (ISC) approach (Hasson et al., 2004) to examine the extent to which the language network 'tracks' these stimuli, i.e. exhibits stimulus-related variation. Across all the regions of the language network, non-verbal meaningful stimuli elicited reliable ISCs. These ISCs were higher than the ISCs elicited by semantically impoverished non-verbal stimuli (e.g., a music clip), but substantially lower than the ISCs elicited by linguistic stimuli. Our results complement earlier findings from controlled experiments (e.g., Ivanova et al., 2021) in providing further evidence that the language network shows some sensitivity to semantic content in non-verbal stimuli.

Keyword

Language network; Non-verbal semantics; fMRI; Naturalistic stimuli; Inter-subject correlation

1. Introduction

A set of brain regions in the left frontal and temporal cortex in the human brain respond robustly and reliably during language comprehension, both auditory and visual (e.g., Fedorenko et al., 2010; Silbert et al., 2014; Vagharchakian et al., 2012). In brain imaging studies, these regions exhibit highly selective responses to language processing over diverse cognitive tasks, including those that bear parallels to language and have long been argued to share resources with language. For example, language-responsive regions show little or no response to arithmetic (e.g., Fedorenko et al., 2011; Monti et al., 2012; Amalric & Dehaene, 2019), music (e.g., Fedorenko et al., 2011; Rogalsky et al., 2011; Chen et al., 2023), logic (e.g., Monti et al., 2009), executive control (e.g., Fedorenko et al., 2011; Mineroff, Blank et al., 2018), action/gesture observation (e.g., Pritchett et al., 2018; Jouravlev et al., 2019), Theory of Mind (e.g., Deen et al., 2015; Paunov, 2018; Paunov et al., 2022; Shain, Paunov, Chen et al., 2022), and even the processing of computer languages (e.g., Ivanova et al., 2020; Liu et al., 2020). Evidence from patients with aphasia converges with these findings, showing that the loss of language production and comprehension abilities can leave other cognitive abilities unimpaired (e.g., Lecours & Joanette, 1980; Varley & Siegal, 2000; Varley et al., 2001, 2005; Apperly et al., 2006; Bek et al., 2010; Willems et al., 2011; see Fedorenko & Varley, 2016, for a review).

However, one domain whose relationship with language remains debated is semantic knowledge—generalized, abstract conceptual information about objects/entities, actions, and events (Warrington, 1975; Patterson et al, 2007; Lambon Ralph et al, 2017). On the one hand, language understanding is inextricably linked to semantics. Whether producing or comprehending a sentence, accessing the meaning of words and constructions is an essential component of linguistic processing (e.g., Katz & Fodor, 1963; Pustejovsky, 2005; Goldberg,

2010). On the other hand, semantic knowledge is not restricted to language alone: non-verbal

stimuli, such as pictures and sounds, can also evoke rich conceptual representations. Here, we

ask: is the language network—or some of its components—sensitive to semantic knowledge

regardless of whether or not it is delivered linguistically?

Previous work provides conflicting evidence about the role of the language network in non-

verbal semantic processing. A number of brain imaging investigations have reported overlapping

activations in the lateral frontal and temporal brain areas for the processing of words and object

pictures (e.g., Visser et al., 2012; Devereaux et al., 2013; Handjaras et al., 2017), words and

actions (Wurm & Caramazza, 2019), or sentences and event pictures (e.g., Ivanova et al., 2021).

However, neuropsychological evidence from individuals with aphasia indicates that linguistic

and semantic processing are neurally dissociable, such that semantic processing can appear intact

in the presence of severe linguistic deficits (e.g., Whitehouse et al., 1978; Chertkow et al., 1997;

Saygin et al., 2004; Colvin et al., 2019; Ivanova et al., 2021; Warren & Dickey, 2021).

Most past brain imaging studies that have reported overlap between responses to verbal and

semantically meaningful non-verbal (typically, pictorial) stimuli have relied on traditional task-

based paradigms. In such paradigms, participants read words or view pictures and perform a

semantic task on those words/pictures. One possible explanation of these results is that language

regions respond during the processing of pictures because participants activate the corresponding

verbal labels as they come up with the response to the (often verbally presented) task prompt

(e.g., activating the word "hammer" when processing a picture of a hammer and deciding its

semantic category; Devereux et al., 2013). Activating the label may help hold the concept in

working memory or retrieve relevant semantic knowledge but not be *essential* to semantic

processing per se (see also Benn, Ivanova et al., 2023 for discussion).

In this study, we aimed to determine whether the language network responds to non-linguistic

semantically meaningful stimuli in the absence of an explicit task. To do so, we turned to

naturalistic stimuli (Hasson et al., 2018) and leveraged the inter-subject correlation (ISC)

approach (Hasson et al., 2004, 2008). In this approach, the similarity of neural fluctuations

during some naturalistic stimulus is computed across participants, and the degree of inter-subject

similarity is taken to reflect the degree to which a given voxel or brain region responds to

features of the relevant stimulus (or 'tracks' the stimulus).

Our critical stimuli consisted of ~5-minute-long video and audio clips that were rich in semantic

content but did not contain any language. The key operational criteria we used to select stimuli

with rich semantic content included the presence of (a) objects/entities/people, actions, and

events (e.g., "bird" depicted visually; "chasing" depicted visually; "brushing teeth" conveyed

auditorily with a prototypical sound, etc.), and (b) a storyline, such that the sequences of events

are sensible (e.g., a man falls asleep at church and rolls off the pew, or a sound of an alarm clock

is followed by a sound of a yawn) and interpretation would become more difficult if the event

order was shuffled. The latter criterion is another feature that distinguishes our study from most

prior neuroimaging studies examining verbal/non-verbal semantic processing (cf. Thierry &

Price, 2006; Baldassano et al., 2018), where participants typically view a series of discrete

temporally unconnected stimuli. Naturalistic meaningful stimuli that unfold over time in a task-

free setting provide a good approximation to many real-life scenarios and can yield important

insights about the role of the language network in semantic processing. In addition, a meaningful

storyline helps maintain the participants' attention even in the absence of an explicit task. For

comparison, we also included naturalistic linguistic stimuli, which have been previously shown to elicit high ISCs in the language network (e.g., Wilson et al., 2007; Lerner et al., 2011; Blank & Fedorenko, 2017; Fedorenko & Blank, 2020; Paunov et al., 2022), and non-verbal semantically impoverished stimuli, like music, which serve as negative controls. For simplicity, we refer to semantically rich stimuli as "meaningful", or +M and semantically impoverished stimuli as "non-meaningful", or -M.

To foreshadow the key results, we found that the language network shows significantly higher ISCs during the processing of non-verbal meaningful stimuli compared to non-verbal non-meaningful stimuli. These ISCs were nonetheless lower than those elicited during the processing of linguistic stimuli, in line with abundant evidence that linguistic stimuli are the preferred stimulus class for the language network. Our findings suggest that the language network is recruited for the processing of semantically rich inputs even in the absence of language.

2.   Materials and Methods

2.1. General Approach

To investigate whether the language brain regions track semantic content in non-verbal stimuli, we combined two methodologies commonly used in neuroimaging research (similar to e.g., Blank & Fedorenko, 2017): functional localization (e.g., Brett et al., 2002; Saxe et al., 2006; Fedorenko et al., 2010) and rich naturalistic stimuli analyzed with the inter-subject correlation (ISC) approach (Hasson et al., 2004, 2008). In this section, we motivate these methodological choices.

First, to account for inter-individual variability in the location of the language network (e.g., Amunts et al., 1999; Tomaiuolo et al., 1999; Fedorenko et al., 2010; Fedorenko & Blank, 2020; Lipkin et al., 2022), we defined language regions in each participant individually using a well-established functional localizer task (Fedorenko et al., 2010). This approach yields greater sensitivity, functional resolution, and interpretability compared to the traditional group-averaging approach, where functional correspondence across participants is assumed to hold voxel-wise (e.g., Nieto-Castañón & Fedorenko, 2012; Fedorenko, 2021).

And second, naturalistic stimuli are more ecologically valid and thus more likely to elicit neural responses that reflect how the target brain region or network is recruited during real-life cognitive processing. However, the less constrained nature of the stimuli poses a challenge when interpreting the observed blood oxygen-level dependent (BOLD) signal, namely that there are no well-defined conditions within a stimulus from which to construct model-based predictors of neural activity over time. Here, we rely on inter-subject correlations (ISCs), a method introduced

by Hasson et al. (2004) to tackle this issue. The reasoning behind the ISC approach is as follows:

if a voxel or a brain region tracks certain features of a stimulus, then the BOLD signal should be

time-locked to the appearance of those features in the stimulus, which would be reflected in

similar patterns of fluctuations across participants (i.e., reliable ISCs). Thus, the average

timecourse across participants serves as the "model" for a given left-out participant.

In the next sections, we detail each analysis method and describe other aspects of the study's

design and procedure. Data and code used for this study is available on OSF

(https://osf.io/t8sz5/?view_only=d5081a3bf15942c38c7d48f093eac16c).

2.2.Participants

Forty-nine native English speakers between the ages of 19 and 48, recruited from MIT and the

surrounding community, were paid for participation. Two participants were removed from the

analysis due to poor quality of the functional localizer data, with the exclusion criterion defined

as fewer than 100 suprathreshold voxels (at the $p < 0.001$ uncorrected whole-brain threshold)

across the language network's 'parcels' (**Figure 1B**). Of the remaining 47 participants (mean age

= 24.4, SD = 5.08; 29 females), seven participants were left-handed (based on the Edinburgh

Handedness Inventory; Oldfield, 1971), but all of those left-handed participants had a left-

lateralized language network (for motivation to include left-handers in cognitive neuroscience

research, see Willems et al., 2014). All participants gave informed written consent in accordance

with the requirements of MIT's Committee on the Use of Humans as Experimental Subjects

(COUHES).

2.3.Design and procedure

Each participant completed a language localizer and a subset of the naturalistic stimuli from the

critical experiment. As shown in **Table 1**, the majority of the participants (n=27, 57%)

watched/heard 8 of the 10 stimuli, one participant—all 10 stimuli, and the remaining 19

participants saw between 1 and 7 stimuli due to scan duration constraints (the differences in the

number of stimuli are accounted for in the analyses, as described below). Each stimulus was

presented to between 14 and 34 participants, and each +M stimulus was presented to at least 29

participants (**Table 2**). 40/47 participants completed the language localizer in the same session as

the critical experiment, the remaining 7 participants completed it in an earlier session (see

Mahowald & Fedorenko, 2016 and Lipkin et al., in prep. for evidence of high across-session

replicability; also Braga et al., 2020). Some participants completed additional experiments for

unrelated studies.

Number of Stimuli	Number of Participants
1	7
2	6
3	1
4	1
6	1
7	3
8	27
10	1

Table 1. *Number of participants who watched / heard each subset of naturalistic conditions.*

2.3.1.   Language localizer.

Participants read sentences (e.g., NOBODY COULD HAVE PREDICTED THE

EARTHQUAKE IN THIS PART OF THE COUNTRY) and lists of unconnected, pronounceable

nonwords (e.g., U BIZBY ACWORRILY MIDARAL MAPE LAS POME U TRINT WEPS

WIBRON PUZ) in a blocked design (**Figure 1A**). Each stimulus consisted of twelve

words/nonwords. For details of how the language materials were constructed, see Fedorenko et

al. (2010). The materials are available at https://evlab.mit.edu/funcloc/. The sentences >

nonword-lists contrast has been previously shown to reliably activate left-lateralized frontal and

temporal language processing regions and to be robust to changes in the materials, task, and

modality of presentation (Fedorenko et al., 2010; Mahowald & Fedorenko, 2016; Scott et al.,

2017). Stimuli were presented in the center of the screen, one word/nonword at a time, at the rate

of 450 ms per word/nonword. Each stimulus was preceded by a 100 ms blank screen and

followed by a 400 ms screen showing a picture of a finger pressing a button, and a blank screen

for another 100 ms, for a total trial duration of 6 s. Participants were asked to press a button

whenever they saw the picture of a finger pressing a button. This task was included to help

participants stay alert and awake. Condition order was counterbalanced across runs.

Experimental blocks lasted 18 s (with 3 trials per block), and fixation blocks lasted 14 s. Each

run (consisting of 5 fixation blocks and 16 experimental blocks) lasted 358 s. Each participant

completed 2 runs.

Figure 1. *Language Localizer Task.* **A.** An example sentence / nonword sequence presented during the language localizer task. Words / nonwords were presented one at a time for 450ms each. **B.** Five language parcels that were used to define the language network for each individual. IFGorb = inferior frontal gyrus, orbital portion; IFG = inferior frontal gyrus; MFG = middle frontal gyrus; AntTemp = anterior temporal lobe; PostTemp = posterior temporal lobe. Each participant's functional ROIs were defined as the top 10% of most language-responsive voxels within each parcel.

2.3.2. *Critical experiment.*

Participants passively watched or listened to a set of naturalistic stimuli (**Figure 2A**). Auditory stimuli were presented over scanner-safe Sensimetrics headphones. Each of 10 stimuli (conditions) belonged to one of 3 condition types: +Meaning/-Language, +Meaning/+Language, and -Meaning/-Language (**Figure 2**). The stimuli within each condition type were chosen to vary in their presentation modalities (visual/auditory) and styles (e.g., for visual stimuli: live action/animated movie/abstract shapes) to ensure generalizability within a condition type. The four stimuli from the critical condition were rich in semantic content but did not contain any

language (+Meaning/-Language; +M/-L): i) an animated short film ("Partly Cloudy" by Pixar),

ii) a clip from a live action film ("Mr. Bean", https://www.youtube.com/watch?v=bh__g-

ZZ6WA), iii) a custom-created Heider and Simmel-style animation (Heider & Simmel, 1944)

consisting of simple geometric shapes moving in ways as to suggest intentional interactions

designed to tell a story (e.g., a shape gets locked up inside a space, another shape goes on a quest

to get help to release it, etc.), denoted as "Shapes" hereafter, and iv) a custom-created audio

'story' consisting of a series of sounds that represents common events in a typical morning,

denoted as "Day" hereafter. Four stimuli from the positive control condition used semantically

rich verbal materials (+Meaning/+Language; +M/+L): i) a story ("Elvis" from the Natural

Stories corpus; Futrell et al., 2020), ii) an audio play (a segment from an HBO miniseries,

"Angels in America", from Chapter 1: https://www.imdb.com/title/tt0318997/), iii) a naturalistic

dialog—a casual unscripted conversation between two female friends, denoted as "Dialog"

hereafter, and iv) an expository text (a text about trees adapted from Wikipedia;

https://en.wikipedia.org/wiki/Tree), denoted as "Tree" hereafter. The two stimuli from the

negative control condition lacked both semantic and verbal content (-Meaning/-Language; -M/-

L): i) an audio clip of Paganini Caprice No. 24 arranged for solo flute, denoted as "Flute"

hereafter, and ii) a video consisting of continuously changing kaleidoscope images, denoted as

"Kaleidoscope" hereafter. Each stimulus, lasting ~5-7 minutes (see **Table 2** for detailed timing

information), was preceded and followed by 16 s of fixation. All the materials are available on

OSF (https://osf.io/t8sz5/?view_only=d5081a3bf15942c38c7d48f093eac16c), except "Partly

Cloudy" (for copyright reasons).

Figure 2. *Critical task and schematics of analysis.* **A.** Ten conditions used in the critical task. The speaker icons represent auditory stimuli, while others are visual stimuli. **B.** Schematics of ISC calculation. ISCs were computed by correlating each participant's BOLD time series for a particular condition in a particular fROI with the average of the other participants' BOLD time series for that condition in that fROI and Fisher-transforming the correlation coefficients. These ISCs were used for analysis with linear mixed effect models. **C.** Schematics for the peak-removal analysis. From each time course, peak, trough, or random time points were removed. These trimmed time courses were then used to compute the ISCs as shown in **B**.

Condition Type	Condition	Duration	N
	Partly Cloudy	5m 48s	33
	Mr. Bean	6m 10s	32
+M/-L	Shapes	4m 50s	32
	Day	4m 36s	31

	Elvis	5m 16s	34
+M/+L	Angels in America	6m 14s	31
	Dialog	5m 35s	29
	Tree	7m 6s	29
-M/-L	Flute	5m 44s	14
	Kaleidoscope	5m 48s	15

Table 2. *Details of the naturalistic conditions.* Each condition belonged to one of the three condition types. The duration of each stimuli, as well as number of participants who viewed / listened to each stimuli (N) are shown. Durations include 16s-long fixations at the beginning and the end of the scan (32s total). +M/-L = +Meaning/-Language; +M/+L = +Meaning/+Language; -M/-L = -Meaning/-Language.

2.3.3. *Resting state scan.*

Ten participants additionally performed a resting state scan, used in a control analysis. Participants were instructed to close their eyes and let their mind wander but to remain awake while resting in the scanner for 5 min (the scanner lights were dimmed, and the projector was turned off).

2.4.Data acquisition and preprocessing

2.4.1 Data acquisition.

Whole-brain structural and functional data were collected on a whole-body 3 Tesla Siemens Trio scanner with a 32-channel head coil at the Athinoula A. Martinos Imaging Center at the

McGovern Institute for Brain Research at MIT. T1-weighted structural images were collected in

176 axial slices with 1 mm isotropic voxels [repetition time (TR) = 2530 ms; echo time (TE) =

3.48 ms]. Functional, blood oxygenation level-dependent (BOLD) data were acquired using an

EPI sequence with a 90° flip angle and using GRAPPA with an acceleration factor of 2; the

following parameters were used: thirty-one 4-mm-thick near-axial slices acquired in an

interleaved order (with 10% distance factor), with an in-plane resolution of 2.1 x 2.1 mm, FoV in

the phase encoding (A >> P) direction 200 mm and matrix size 96 x 96 mm, TR = 2000 ms and

TE = 30 ms. The first 10 s of each run were excluded to allow for steady-state magnetization.

2.4.2. Spatial preprocessing.

Data preprocessing was performed with SPM12 (using default parameters, unless specified

otherwise) and custom scripts in MATLAB. Preprocessing of anatomical data included

normalization into a common space [Montreal Neurological Institute (MNI) template] and

segmentation into probabilistic maps of the gray matter (GM), white matter (WM), and cerebro-

spinal fluid (CSF). A GM mask was generated from the GM probability map and resampled to 2

mm isotropic voxels to mask the functional data. The WM and CSF maps were used as described

in *Temporal preprocessing* below. Preprocessing of functional data included motion correction

(realignment to the mean image using second-degree b-spline interpolation), normalization

(estimated for the mean image using trilinear interpolation), resampling into 2 mm isotropic

voxels, and smoothing with a 4 mm FWHM Gaussian filter.

2.4.3. Temporal preprocessing.

The localizer runs were high-pass filtered at 128 s. Additional preprocessing of data from the

naturalistic runs was performed using the CONN toolbox (Whitfield-Gabrieli & Nieto-Castañón,

2012; http://www.nitrc.org/projects/conn) with default parameters, unless specified otherwise.

BOLD signal time courses were extracted from white matter and cerebrospinal fluid. Five

temporal principal components were obtained from each, as well voxel-wise averages. These

were regressed out of each voxel's time course, along with additional noise regressors,

specifically, six motion parameters estimated during offline motion correction (three translations

and three rotations) and their first temporal derivatives, and artifact timepoints (based on global

signal outliers and motion).

2.5.Participant-specific functional localization of language network

2.5.1. *Modeling localizer data.*

For the localizer task, a standard mass univariate analysis was performed in SPM12 whereby a

general linear model estimated the effect size of each condition in each experimental run. These

effects were each modeled with a boxcar function (representing entire blocks) convolved with

the canonical hemodynamic response function. The model also included first-order temporal

derivatives of these effects, as well as nuisance regressors representing entire experimental runs,

offline-estimated motion parameters, and timepoints classified as outliers (i.e., timepoints where

scan-to-scan differences in global BOLD signal were above 5 standard deviations, or where the

scan-to-scan motion was above 0.9 mm). The obtained weights were then used to compute the

functional contrast of interest: sentences > nonwords.

2.5.2. *Defining fROIs.*

Language functional regions of interest (fROIs) were defined individually for each participant

based on functional contrast maps from the localizer experiments (a toolbox for this procedure is

available online; https://evlab.mit.edu/funcloc/). These maps were first restricted to include only

gray matter voxels by excluding voxels that were more likely to belong to either the WM or the

CSF based on SPM's probabilistic segmentation of the participant's structural data, as described

above.

Then, fROIs in the language network were defined using group-constrained, subject-specific

localization (Fedorenko et al., 2010). For each participant, the map of the sentences > nonwords

contrast was intersected with binary masks that constrained the participant-specific language

network to fall within areas where activations for this contrast are likely across the population.

These masks are based on a group-level representation of the contrast obtained from an

independent large (n=220) sample of participants. We used five such masks in the left-

hemisphere, including regions in the inferior frontal gyrus, in its orbital part, in the middle

frontal gyrus, in the anterior temporal lobe, and in the mid-to-posterior temporal lobe. These

masks are available online (https://evlab.mit.edu/funcloc/). In each of these five masks, a

participant-specific language fROI was defined as the 10% of voxels with the highest t-values for

the sentences > nonwords contrast (Note that this contrast allows for the inclusion of voxels in a

fROI that respond above baseline to the nonwords condition, as long as these responses are

weaker than to sentences.).

2.6.Critical analysis: ISCs

2.6.1. *Computing ISCs.*

For each participant, BOLD signal time courses recorded during each naturalistic condition were

extracted from each voxel beginning 6 s following the onset of the stimulus (to exclude an initial

rise in the hemodynamic response relative to fixation, which could increase ISCs). These time

courses were temporally z-scored in each voxel and then averaged across voxels within each

fROI. Then, for each fROI, participant, and condition we computed an ISC value, namely,

Pearson's moment correlation coefficient between the time course and the corresponding average

time course across the remaining participants (**Figure 2B**; Lerner et al., 2011). ISCs were Fisher-

transformed before statistical testing to improve normality (Silver & Dunlap, 1987).

We also tested whether the relatively high ISCs in +M/-L conditions could be attributed to

specific high-response time points. In particular, specific 'scenes' in the stimuli might activate

the language network across participants because they elicit some linguistic representations. In

other words, the tracking of the +M/-L conditions may be due not to the processing of

meaningful non-verbal information but instead driven by a few points where participants actually

engage in linguistic processing. To evaluate this possibility, ISCs were recomputed after peak

time points (or trough time points, as a control) of the BOLD signal were removed (peak- /

trough-removed ISCs, **Figure 2C**). To define peaks, a mean BOLD signal was constructed for

each condition by averaging the time course across participants and fROIs. Peak time points

were defined as those with values greater than 1 in the z-normalized average time course. The

number of time points removed was as follows: Partly Cloudy, 25 out of 158; Mr. Bean, 25 out

of 169; Shapes, 20 out of 129; Day, 19 out of 122. Similarly, trough time points were defined as

time points with values lower than -1 in the z-normalized average time course. The number of

time points removed was as follows: Partly Cloudy, 25 out of 158; Mr. Bean, 24 out of 169;

Shapes, 21 out of 129; Day, 16 out of 122.

2.6.2. *Statistical testing*.

In the critical analyses, we compared ISCs across condition types using linear mixed-effects

(LME) models (Barr et al., 2013), implemented in R. ISCs were modeled with condition type as

a fixed effect and fROI, participant, and condition (stimulus) as random intercepts. The model

was tested for significance in two-tailed hypothesis tests. Mixed-effects modeling is more robust

to missing-at-random data (i.e., the number of stimuli per participant, see **Table 1**), as well as to

unbalanced designs (i.e., different numbers of conditions per condition type). For all LME

analyses, we coded condition type using the dummy coding scheme, with +M/-L condition type

serving as a reference level, unless specified otherwise.

We additionally investigated ISCs for each +M/-L condition separately by treating each +M/-L

condition as individual condition types, which resulted in six condition types in total (+M/+L, -

M/-L, Partly Cloudy, Mr. Bean, Shapes, and Day). Here, the main goal was to compare the ISCs

during each condition to those observed during the zero baseline. ISCs were modeled with

condition type as a fixed effect and fROI and participant as random intercepts with the fixation

baseline as a reference level. Similarly, ISCs during each +M/-L condition were compared to

mean ISCs during +M/+L and -M/-L condition types. Here, mean ISCs during +M/+L and -M/-L

condition types were used as reference levels. P-values in this analysis are reported following

false discovery rate (FDR) correction for multiple (n=3; against zero-baseline, mean +M/+L, and

mean -M/-L) comparisons (Benjamini & Yekutieli, 1991).

The above network-level analysis was also performed for each fROI. Here, ISCs were modeled

for each fROI separately, with condition type as a fixed effect and participant and condition as

random intercepts, and p-values were FDR-corrected for multiple comparisons across fROIs

(n=5). To test that each condition was above baseline for each fROI, each +M/-L condition was

recoded into individual condition types, and ISCs were modeled with condition type as a fixed

effect and participant as random intercepts with the fixation baseline as a reference level. Again,

p-values were FDR-corrected for multiple comparisons across fROIs (n=5).

Finally, the peak-removed (and trough-removed as a control) ISCs for each condition were

compared against a distribution of ISCs (n=10,000) where n time points in the timecourse were

pseudo-randomly removed (n matched the number of peak time points for each condition). These

adjusted timecourses were generated in MATLAB 2018a. The peak-removed and trough-

removed ISCs were also tested against each other using a two-sample t-test for each condition.

For the latter analysis, trough-removed ISCs were adjusted so that the number of timepoints

removed (the ones with the lowest values) matched the number of peak timepoints removed for

each condition. P-values were FDR-corrected for multiple comparisons across conditions (n=4).

2.7.Content Unit (CU) Analysis

To measure the degree of semantic content in a given stimulus, we quantified the number of

Content Units (CUs) in each clip. We defined a CU as a unique concept (object, entity, action,

property, etc.) referred to in verbal descriptions of each stimulus (Agis et al., 2016; Gallée et al.,

2021). To estimate the number of CUs in each clip, we conducted an online behavioral study

with an independent pool of participants.

The task was implemented as an online Qualtrics survey that presented a randomly chosen

stimulus to each participant. The stimulus was cut into ~30s subclips and the subclips were

presented in chronological order. The splitting of stimuli into subclips was done manually to

minimize abrupt cuts that would split natural events in the middle; the same subclips were used

for all participants for a given stimulus. Each subclip presentation page (participants could only

watch each subclip once) was followed by a text box page, where participants were asked to

describe the stimulus they just watched / listened to. The transition to the text box page was

enabled five seconds after the clip ended. At the end of the survey, as an attention check,

participants were asked two questions about the content of the stimulus they had been presented.

For this experiment, 250 native English speakers between the ages of 19 and 77 were recruited

online via the Prolific platform. Three participants were removed for failing attention checks at

the end of the survey and providing minimal, low-effort responses. Of the 247 remaining

participants, twenty participants per stimulus were randomly selected (for a total of 200

participants; n=20 x 10 stimuli) for further analyses.

Before analyzing the descriptions for the number of content units, the following (content-

irrelevant) categories of phrases were manually removed: explicitly self-referential language ("I

think", "I believe", etc.), meta-descriptive language ("Same as before", "In this clip", "the

camera", "screen", etc.), and language regarding levels of confidence/belief states ("It appears to

be", "seems like", etc.). The remaining portions of the descriptions were stripped of 'stop words'

(high-frequency function words) using the nltk package in Python, lemmatized using the spaCy

package in Python, and split into individual words. Words that served as subcomponents of

proper nouns (e.g., "Mr. Bean", "Elvis Presley") were merged and counted as a single concept.

The same word that appeared multiple times within the response to a single subclip was treated

as different concepts because the same entity could participate in multiple events within the

clip. Words that appeared in descriptions of three or more participants for a given subclip were

defined as CUs.

To compare CU counts across conditions, CU counts were averaged across participants to obtain

a single CU count value per subclip. These CU counts were further averaged across subclips to

yield a single CU count value for each condition. To statistically compare CU counts between

condition types, we used an LME to model average (across participants) subclip CU counts with

condition type as a fixed effect and condition (stimulus) as random intercepts. The relationship

between CU counts and the ISCs was evaluated, first, with a Pearson correlation coefficient

between the average CU count and the average ISCs for each condition. Second, a model

comparison examined whether semantic richness (as approximated by CU counts) explained

additional variance in ISCs over condition type. We created two models to predict ISCs of

stimuli from the three condition types: one adding normalized CU count (centered around 0) as a

fixed effect to the original model and the other – replacing condition type with normalized CU

count for the fixed effect. The first model was compared with the original model using the

likelihood ratio test. The second model was compared with the original model using AIC

(Akaike information criterion) given that the two models were not nested. The above analyses

were also performed using pairwise shared CU count, defined as the average number of CUs that

were shared between each participant pair.

3. Results

3.1. The language regions reliably track meaningful non-verbal stimuli

Figure 3. *ISCs in the language network.* **A.** Average ISCs across the five language fROIs. Dots indicate individual participants' data points, and error bars indicate standard error of mean by participant. Black horizontal lines indicate the mean ISC values for each of the three condition types. **B.** Average ISCs were computed for each fROI separately (on the brains, we show the parcels used to define the fROIs; individual fROIs comprise 10% of each parcel, as described in the text). IFGorb = inferior frontal gyrus, orbital portion; IFG = inferior frontal gyrus; MFG = middle frontal gyrus; AntTemp = anterior temporal cortex; PostTemp = posterior temporal cortex.

Meaningful non-verbal (+M/-L) conditions elicited ISCs that were significantly higher than the

zero baseline (mean ISCs = 0.193, beta = 0.168, SE = 0.0434, p = 0.00151; **Figure 3A**). As a

sanity check, we also examined the BOLD signal during the resting state condition to ensure that

spurious correlations do not arise from the data acquisition and analysis procedures. The ISCs

during rest averaged across fROIs were not greater than 0 (one-tailed t-test, $t(9) = -1.53$, p =

0.920), suggesting that the ISCs for the other conditions reflect stimulus-related activity.

To characterize this effect in greater detail, we next tested individual +M/-L conditions against

the zero baseline. Each of the four +M/-L conditions elicited above-baseline ISCs (**Table 3, top**).

Interestingly, the language fROIs tracked these non-verbal stimuli regardless of whether they

were visual (Partly Cloudy, Mr. Bean, Shapes) or auditory, made up of sound effects (Day).

Table 3. *LME model statistics for the +M/-L conditions.* For each condition (stimulus), ISCs were compared against the zero baseline, average +M/+L ISCs, and average -M/-L ISCs using LME models with condition as a fixed effect and participant and fROI as random intercepts. For each analysis, the following three values are reported: beta, standard error of the mean (SE), p-value (FDR-corrected for multiple comparison across baselines (n=3)). For p-values, *<0.05, **<0.01, ***<0.001.

	Day	-0.229	0.0282	<0.001	****
+M/-L vs. -M/-L	Partly Cloudy	0.196	0.0281	<0.001	***
	Mr. Bean	0.173	0.0282	<0.001	***
	Shapes	0.107	0.0282	0.00475	**
	Day	0.113	0.0282	0.00460	**

475 We next asked whether the recruitment of the language network by +M/-L stimuli can be

476 observed at the level of individual fROIs (**Figure 3B**). Indeed, these conditions elicited ISCs that

477 were significantly higher than the zero baseline in each of the five fROIs (**Table 4**). These results

478 also held for each condition individually, except for Day in MFG (**Table A.1**).

fROI	beta	SE	p-value	
IFGorb	0.127	0.0278	0.00126	**
IFG	0.149	0.0353	0.00186	**
MFG	0.0976	0.0380	0.0260	*
AntTemp	0.192	0.0337	<0.001	***
PostTemp	0.262	0.0428	<0.001	***

Table 4. *LME model statistics for each fROI.* For each fROI, ISCs were compared across conditions with condition type as a fixed effect and participant and condition as random intercepts. +M/-L condition type was used as reference. For each fROI, the following three values are reported: beta, standard error of mean (SE), p-value (FDR-corrected for multiple comparison across fROIs (n=5)). IFGorb = inferior frontal gyrus, orbital portion; IFG = inferior frontal gyrus; MFG = middle frontal gyrus; AntTemp = anterior temporal lobe; PostTemp = posterior temporal lobe. For p-values, *<0.05, **<0.01, ***<0.001.

Taken together, these analyses show that naturalistic meaningful non-verbal stimuli, including

both visual and auditory ones, elicit reliable stimulus-related activity across the language

network, as indexed by reliable ISCs.

3.2. The language regions track meaningful non-verbal stimuli more reliably than non-

meaningful stimuli, but less reliably than verbal stimuli

We next asked how the ISCs elicited by the +M/-L conditions differ from the ISCs elicited by the

other two condition types. We found that the +M/-L conditions elicited ISCs (mean ISCs = 0.193,

beta = 0.168, SE = 0.0434, p = 0.00151) that were higher than those elicited by non-meaningful

non-verbal (-M/-L) conditions (mean ISCs = 0.00795, beta = 0.146, SE = 0.0597, p = 0.0350)

but lower than those elicited by meaningful linguistic (+M/+L) conditions (mean ISCs = 0.350,

beta = 0.118, SE = 0.0483, p = 0.0353). This pattern also held for each individual condition

(**Table 3, middle, bottom**), and when each fROI was analyzed separately (**Table A.2**; the

differences among the language fROIs in the exact patterns of ISCs are likely due to differences

among the regions with respect to their sensitivity to stimulus dimensions other than the presence

of semantic / verbal content). Taken together, these analyses show that meaningful non-verbal

stimuli elicit stimulus-related activity across the language network that is stronger than that

elicited by non-meaningful non-verbal stimuli (e.g., a musical piece) but weaker than that

elicited by meaningful verbal stimuli (e.g., a story).

3.3.Elevated ISCs in the +L conditions cannot be explained by the amount of semantic content

Does the difference in ISCs elicited by the +M/+L versus the +M/-L conditions reflect a

difference in semantic richness? To test this idea, we quantified the degree of semantic richness

for each stimulus using the content unit (CU) metric—the number of referenced concepts in

verbal descriptions of the stimuli (**Figure 4A**; Agis et al., 2016; Gallée et al., 2021). As a sanity

check, we first examined the CU counts for the -M conditions. Because participants are

prompted to provide a verbal description for each portion of the stimulus, the CU count does not

go to zero for any given stimulus. Nonetheless, the CU count is significantly lower in the -M/-L

conditions compared to both the +M/-L (beta = 6.48, SE = 2.19, p = 0.0143) and the +M/+L

conditions (beta = 5.68, SE = 2.18, p = 0.0267), in line with our classification of +M versus -M

stimuli.

We then tested whether the +M/+L conditions were more semantically rich compared to the +M/-

L conditions. These two conditions did not differ statistically (beta = -0.800, SE = 1.96, p =

0.694; +M/-L as reference level). Furthermore, the average CU count did not reliably correlate

with ISC strength for the conditions in these two condition types (**Figure 4B**; r = 0.196, p =

0.642). To test this effect more rigorously, we created two models that use CU count as a

predictor of ISC strength. In the first model, we added normalized CU count as fixed effect on

top of the condition type. In this model, the CU count did not have a significant effect (beta =

0.0101, SE = 0.00785, p = 0.227), and the likelihood ratio test showed that adding this extra

fixed effect did not significantly improve the model ($X^2(1)$ = 1.54, p = 0.214). In the second

model, we replaced the fixed effect: from condition type to normalized CU count. The

normalized CU count had significant explanatory power in the ISCs (beta = 0.0196, SE =

0.00869, p = 0.0479), in line with the low CU count for -M stimuli. Nonetheless, the model with

condition type as the fixed effect had a lower AIC (ΔAIC = -4.79), suggesting that condition type

explains the ISCs better than the CU count.

To assess the generalizability of this result across metrics, we performed the same analysis using

average pairwise shared CU count, which measures the similarity in the verbal description across

participants and thus parallels (conceptually) the ISC measure for BOLD signals. This analysis

also revealed no significant difference in the shared CU count between the two condition types

(beta = -0.0348, SE = 0.823, p = 0.967; +M/-L as reference level) and no significant correlation

between the average shared CU count and the ISCs (**Figures 4C, D**; r = 0.324, p = 0.433). Next,

we tested the effect of shared CU count using the two LME models described above. Adding a

normalized shared CU count as a fixed effect did not have a significant effect (beta = 0.0295, SE

= 0.0184, p = 0.141), and the likelihood ratio test showed that adding this extra fixed effect did

not significantly improve the model ($X^2(1)$ =2.29, p = 0.130). In the second model, the

normalized shared CU count had significant explanatory power in the ISCs (beta = 0.0541, SE =

0.197, p = 0.0210) but the model with condition type as the fixed effect had a lower AIC (ΔAIC

= -3.31). Altogether, these analyses rule out the interpretation that the elevated ISCs in +L

conditions result from these stimuli being semantically richer.

Figure 4. *CU count cannot explain the elevated ISCs in +L stimuli.* **A.** Average CU count across participants. Dots indicate individual subclips that comprise each stimulus, and error bars indicate standard error of the mean by subclip. Black horizontal lines indicate the mean CU counts for each of the three condition types. **B.** The correlation between the average CU count and the ISC across the +M stimuli. Dashed line indicates best fit. line. **C, D**. Same as A and B, but using average shared CU count.

3.4.The language network's tracking of meaningful non-verbal stimuli cannot be explained by

the peak timepoints

In the final analysis, we asked whether the relatively high ISCs in the language network for

meaningful non-verbal conditions could be explained by a small number of peak timepoints

(when language processing may be likely to be engaged). We recomputed the ISCs after

removing peak (and, for comparison, trough) time points (**Figure 2C**). The peak-/trough-

removed ISCs were compared against ISCs computed after random time points were removed

(matched in number to the peak time points removed) and to each other (**Figure 5**). The peak-

removed ISCs were significantly lower than random-timepoints-removed ISCs for each of the

four +M/-L conditions (ps < 0.001, FDR corrected (n = 4)). The trough-removed ISCs were also

lower than random-timepoints-removed ISCs (ps < 0.001, FDR corrected). However, although

numerically, peak removal led to a larger reduction in the strength of ISCs than trough removal

across conditions, this difference was only significant in one of the four conditions (Mr. Bean,

t(338) = -3.68, p = 0.00108; FDR-corrected). These results suggest that although in some cases

occasional strong responses in the language regions during the processing of meaningful non-

verbal stimuli (perhaps related to activating linguistic representations) may contribute to the

strength of ISCs for those conditions, these peak points cannot fully explain reliable tracking of

these stimuli. In fact, in the +M/-L condition that elicited the highest ISCs in the language

regions (Partly Cloudy), peak removal and trough removal resulted in a similar reduction in ISC

strength.

Figure 5. *Peak-removal analysis.* Peak- / trough-removed ISCs were compared against random-timepoints-removed ISCs and against each other for each +M/-L condition. The histograms show the random-timepoints-removed ISCs (generated 10,000 times; averaged across fROIs/participants) with bin width of 0.0001. The blue lines correspond to the true ISCs, the red lines – to the peak-removed ISCs, and the yellow lines – to the trough- removed ISCs. For p-values, *<0.05, n.s. = non-significant (p > 0.05).

4. Discussion

A left-lateralized network of frontal and temporal areas has long been implicated in language comprehension. However, the role of the language network in non-verbal semantic processing remains debated. Using the inter-subject correlation (ISC) approach (Hasson et al., 2008), we examined the degree of 'tracking' of meaningful (i.e., semantically rich) non-verbal stimuli by language areas, identified functionally in each individual (e.g., Fedorenko et al., 2010). We found that i) the language regions reliably track meaningful non-verbal stimuli (both visual and auditory); ii) the degree of tracking of such stimuli is higher than for non-meaningful stimuli (like music or dynamically-changing kaleidoscope images) but lower than for verbal stimuli, in spite of the verbal and non-verbal meaningful stimuli being similarly semantically rich; and iii) the tracking of meaningful non-verbal stimuli cannot be explained by the presence of occasional scenes that elicit a strong response in the language regions (e.g., due to activating some linguistic representations).

The strong tracking of naturalistic verbal stimuli by the language network replicates several past findings (e.g., Wilson et al., 2007; Lerner et al., 2011; Blank & Fedorenko, 2017, 2020). Importantly, our analysis of content units (Agis et al., 2016; Gallée et al., 2021) demonstrated that such elevated tracking (relative to non-verbal meaningful stimuli) is not merely a result of verbal stimuli containing higher semantic content That said, we acknowledge that verbal and non-verbal meaningful stimuli (in general, or for the particular set used in the current study) may differ under other metrics of semantic content. The reliably stronger tracking of verbal than non-verbal stimuli in the language network adds to the growing body of evidence suggesting that the language network is highly selective for language processing relative to diverse non-linguistic

functions (e.g., Monti et al., 2009; Fedorenko et al., 2011; Pritchett et al., 2018; Ivanova et al.,

2020; Paunov et al., 2022).

The observed difference between the verbal and non-verbal meaningful stimuli requires care in

its interpretation. Lower ISCs in the +M/-L compared to the +M/+L conditions imply *lower*

consistency in responses to these stimuli across participants, but not necessarily lower evoked

responses. In other words, this result on its own does not rule out the possibility that the

language network is similarly responsive to linguistic and non-linguistic meaningful content.

However, previous work argues against this possibility. Specifically, Ivanova et al. (2021)

found that event pictures activate the language network to a lesser degree compared to

semantically-matched sentences (discussed in more detail below). A similar result was

obtained using auditory meaningful stimuli (Humphries et al., 2001). These finding suggest

that the more likely explanation for the lower ISCs for the meaningful non-verbal (+M/-L)

stimuli is the language network's lower degree of engagement with those stimuli rather than

merely a lower degree of response consistency.

Worth a special mention is a very low (near-zero) degree of tracking by the language network of

a naturalistic musical stimulus. Although a number of neuroimaging studies have now provided

evidence against the role of the language network in music perception, including in the

processing of music structure (e.g., Fedorenko et al., 2011; Rogalsky et al., 2011; Deen et al.,

2015; Chen et al., 2023), many researchers continue to argue for overlapping mechanisms

between language and music (e.g., Sammler et al., 2013; Kunert et al., 2015). The lack of

stimulus-related activity in the language network (including its inferior frontal components

('Broca's area')) during naturalistic listening of a musical piece provides compelling evidence

that the language areas are not performing computations related to the musical stimulus,

including its structure (the most common claim; e.g., Kunert et al., 2015). Future research using

intra-subject correlations based on repeated exposure to the same music stimulus can further

clarify whether this result is due to the lack of engagement of the language network during music

listening or due to the interpretive freedom associated with music stimuli.

Our main finding—above-baseline tracking by the language network of meaningful non-verbal

stimuli—is in line with recent work showing that a) event pictures elicit a reliable response in the

language network, but b) this response is lower than that elicited by semantically matched

sentences (Ivanova et al., 2021). Here, we extend these results in an important way by ruling out

the possibility that the responses in the language network to visual events are task-driven. In

particular, it has been suggested that when viewing visual objects and events, participants may

activate words related to those stimuli in order to facilitate task performance (Trueswell &

Papafragou, 2010; Greene & Fei-Fei, 2014). However, naturalistic stimuli presented under

passive-viewing instructions are unlikely to lead to verbal re-coding given no obvious

advantages of such re-coding. And the possibility of occasional verbal re-coding—perhaps in the

parts of the stimuli that impose high processing or memory demands—is further ruled out by our

peak-removal analysis, which showed that the observed ISCs are not driven by a small number

of time points with elevated activity in the language network.

Together, our results suggest that the language network exhibits continuous and automatic

tracking of semantic content in non-verbal stimuli. What does this tracking reflect? Data from

neuropsychological investigations of patients with acquired brain damage (e.g., Whitehouse et al.,

1978; Chertkow et al., 1997; Saygin et al., 2004; Colvin et al., 2019; Ivanova et al., 2021;

Warren & Dickey, 2021) demonstrate that damage to the language network does not

impair visual / abstract semantic processing. For example, Ivanova et al. (2021; see also Dickey

& Warren, 2015) showed that some individuals with aphasia (including severe aphasia) perform

well on a challenging semantic task on event pictures (judging event plausibility for events with

two animate participants; e.g., a jester entertaining a king vs. a king entertaining a jester).

However, it is still possible that the language network contributes to semantic processing—

redundantly with other systems—without being crucial for it. Another possibility, suggested by a

reviewer, is that the relatively high ISCs in the language areas during the processing of

meaningful non-verbal stimuli reflect the processing of communicative elements present in those

stimuli, like facial expressions or body language. However, previous studies have found that the

language network does not respond to facial expressions, eye gaze, or even speech-

accompanying gestures (e.g., Deen et al., 2015; Pritchett et al., 2018; Jouravlev et al., 2019),

which makes this possibility unlikely.

Understanding what precise semantic computations or aspects of meaning drive the language

network's response to non-verbal meaningful stimuli is an important future endeavor, which can

provide important clues about the relationship between linguistic and semantic processing. One

constraint on this space of hypotheses has to do with the size of the language network's

'temporal integration (or receptive) window' (e.g., Lerner et al., 2011). In particular, previous

work has shown that the temporal integration window of the language network is relatively short,

on the order of a clause or sentence (e.g., Lerner et al., 2011; Blank & Fedorenko, 2020; Regev,

Casto et al., 2022; Shain, Kean et al., 2023). It is therefore likely that non-verbal meanings that

the language system is concerned with have to do with individually described states or agent-

patient interactions, but not longer-timescale representations like situation models whose

construction can span long sequences of events (Johnson-Laird, 1983; Zwaan & Radvansky,

1998; Loschky et al., 2019). But whether the language network has a preference for particular

kinds or aspects of semantic content remains to be determined. Future work that manipulates in

more controlled ways various properties of visual or auditory events may help uncover such

preferences, including potential dissociations among the different components of the language

network.

5. Conclusions

Our study provides evidence that the language network reliably tracks non-verbal meaningful stimuli. The use of naturalistic stimuli and control analyses allowed us to rule out explanations in terms of broad differences in semantic richness and task-driven linguistic re-coding. Overall, these results demonstrate a role of the language network in naturalistic non-verbal semantic processing and set the stage for future work on the precise nature and functions of its contributions.

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Appendix A: Supplementary Data

Condition	fROI	beta	SE	p-value	
	IFGorb	0.206	0.0215	<0.001	***
	IFG	0.188	0.0254	<0.001	***
Partly Cloudy	MFG	0.0952	0.0265	<0.001	***
	AntTemp	0.249	0.0246	<0.001	***
	PostTemp	0.314	0.0274	<0.001	***
	IFGorb	0.116	0.0219	<0.001	***
	IFG	0.132	0.0258	<0.001	***
Mr. Bean	MFG	0.140	0.0268	<0.001	***
	AntTemp	0.215	0.0249	<0.001	***
	PostTemp	0.336	0.0278	<0.001	***
	IFGorb	0.0997	0.0219	<0.001	***
	IFG	0.147	0.0258	<0.001	***
Shapes	MFG	0.0883	0.0268	0.00112	**
	AntTemp	0.101	0.0249	<0.001	***
	PostTemp	0.174	0.0278	<0.001	***
	IFGorb	0.0748	0.0222	0.00105	**
	IFG	0.115	0.0262	<0.001	***
Day	MFG	0.0498	0.0272	0.0686	
	AntTemp	0.192	0.0253	<0.001	***
	PostTemp	0.205	0.0282	<0.001	***

Table A.1. *LME model statistics for each condition-fROI pair.* For each fROI, ISCs were compared across conditions/fROIs with condition type as a fixed effect and participant as random intercepts (Here, each +M/-L condition are recoded into individual condition types). Zero-baseline was used as a reference. For each fROI, the following three values are reported: beta, standard error of mean (SE), p-value (FDR-corrected for multiple comparison across fROIs (n=5)). IFGorb = inferior frontal gyrus, orbital portion; IFG = inferior frontal gyrus; MFG = middle frontal gyrus; AntTemp = anterior temporal lobe; PostTemp = posterior temporal lobe. For p-values, *<0.05, **<0.01, ***<0.001.

Contrast	fROI	beta	SE	p-value	
	IFGorb	-0.0783	0.0380	0.0831	
	IFG	-0.0885	0.0486	0.0997	
+M/-L vs. +M/+L	MFG	-0.168	0.0521	0.0233	*
	AntTemp	-0.151	0.0464	0.0233	*
	PostTemp	-0.129	0.0591	0.0831	
	IFGorb	0.109	0.0490	0.0570	
	IFG	0.142	0.0621	0.0570	
+M/-L vs. -M/-L	MFG	0.0800	0.0662	0.252	
	AntTemp	0.183	0.0594	0.0330	*
	PostTemp	0.219	0.0747	0.0330	*

Table A.2. *LME model statistics for each fROI on condition type comparison.* For each fROI, ISCs were compared across fROIs with condition type as a fixed effect and participant and condition as random intercepts. For each fROI, the following three values are reported: beta, standard error of mean (SE), p-value (FDR-corrected for multiple comparison across fROIs (n=5)). IFGorb = inferior frontal gyrus, orbital portion; IFG = inferior frontal gyrus; MFG = middle frontal gyrus; AntTemp = anterior temporal lobe; PostTemp = posterior temporal lobe. For p-values, *<0.05.