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

Abbreviated title: The language network and non-verbal meaning

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Contributions

AP, IB, and EF developed the concept for the study. AP and IB selected / created experimental materials. YS, AP, AI, and IB collected and analyzed the data. YS, AP, and AI performed formal statistical analyses. YS, AP, AI, and EF wrote the manuscript; IB provided comments.

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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. Across all the regions of the language network, non-verbal meaningful stimuli elicited reliable ISCs. These ISCs were higher than the ISCs elicited by non-verbal stimuli without semantic content (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 responds to meaningful content in non-verbal stimuli.

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 for 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., 2021), 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., in prep.), 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., Broca, 1861; 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 semantics. When we process language, we activate rich conceptual structures—meanings of objects/entities, actions, and events. Of course, these conceptual representations can also get activated by non-verbal input, including visual stimuli (e.g., pictures or videos) and auditory stimuli (e.g., environmental sounds). Is the language network—or some of its components—sensitive to meaning, whether or not it is delivered linguistically, or do language brain regions respond exclusively to linguistic input?

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).

Most past brain imaging studies that have reported overlap between the processing of linguistic meaning and meaning derived from 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 possibility 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; Devereaux 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., 2021 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 structure and meaning but did not contain any language. The key operational criteria we used to define "meaningfulness" in these stimuli include 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 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. 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 non-meaningful stimuli, like music, which serve as negative controls.

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 that 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. These findings suggest that the language network is recruited for the processing of semantically meaningful inputs,

even in the absence of language.

Materials and Methods

General Approach

To investigate whether the language brain regions track meaning-related information 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 also 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.

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. 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).

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., 2019). Some participants completed some 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*.

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.

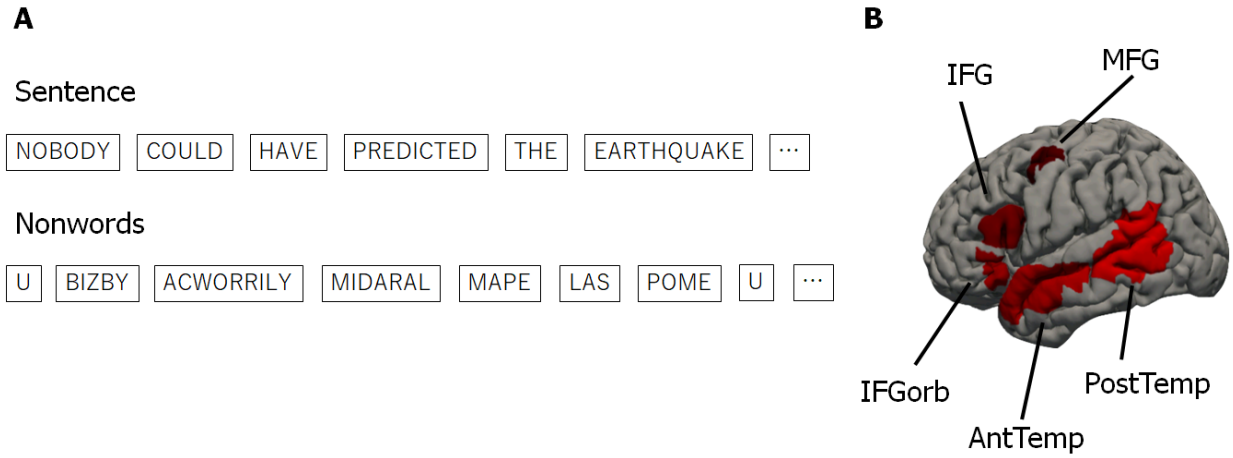

Figure 1. *Language Localizer Task.* **A.** An example sentence / nonword sequence presented during the language localizer task. Words / nonwords were presented one at a time for 450ms each. **B.** Five language parcels that were used to define the language network for each individual. IFGorb = inferior 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.

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. The four critical conditions were rich in structure and meaning 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 additional conditions used meaningful 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 remaining two conditions lacked both meaningful 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, except "Partly Cloudy" (for copyright reasons).

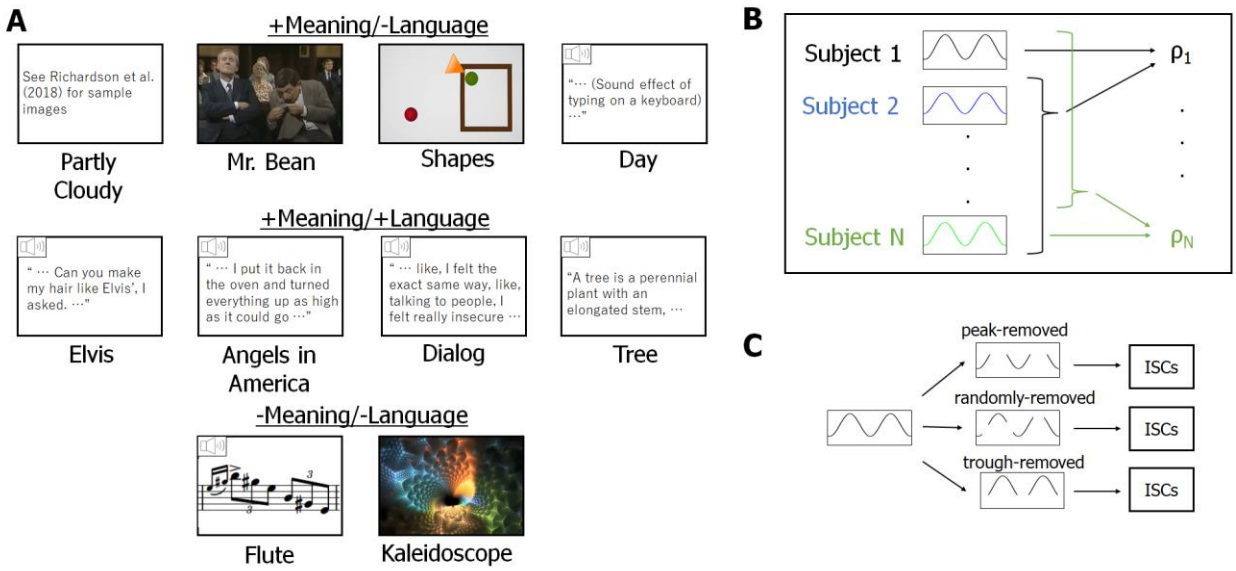

Figure 2. *Critical task and schematics of analysis.* **A.** Ten conditions used in the critical task. The speaker icons represent auditory stimuli, while others are visual stimuli. **B.** Schematics of ISC calculation. ISCs were computed by correlating each participant's BOLD time series for a particular 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
+M/-L	Partly Cloudy	5m 48s	33
	Mr. Bean	6m 10s	32
	Shapes	4m 50s	32
	Day	4m 36s	31
+M/+L	Elvis	5m 16s	34
	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.

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).

Data acquisition and preprocessing

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.

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.

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).

Participant-specific functional localization of language network

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.

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.

Critical analysis: ISCs

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).

To test whether the relatively high ISCs in +M/-L conditions could be explained by lower-level perceptual processing, we computed another set of ISCs: for these, BOLD signal from primary visual and auditory areas was regressed out from each original time course. For visual regions, we used anatomical masks

covering the inferior, middle, and superior occipital cortex bilaterally (six ROIs in total; masks available from http://fmri.wfubmc.edu/software/PickAtlas; Tzourio-Mazoyer et al., 2002). For auditory regions, we used anatomical masks covering the posteromedial and anterolateral sections of Heschl's gyrus bilaterally (four ROIs in total; Morosan et al., 2001). Same statistical testing, detailed below, was performed on these ISCs.

Finally, we 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.

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 allows us to account for the difference in the number of stimuli per person (see **Table 1**), as well as other imbalances in the data. 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).

Results

The language regions reliably track meaningful non-verbal stimuli

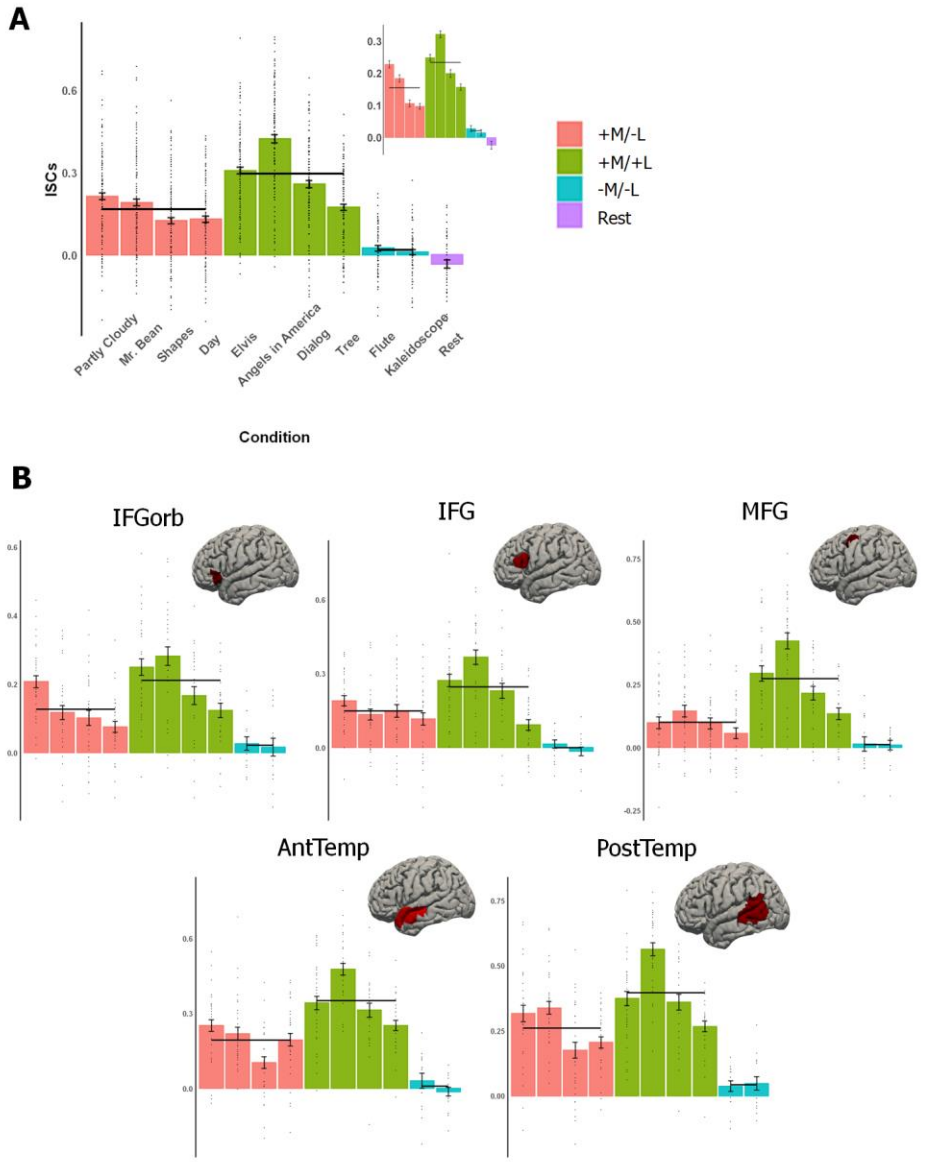

Figure 3. *ISCs in the language network.* **A.** Average ISCs across the five language fROIs. Dots indicate individual participants' data points, and error bars indicate standard error of mean by participant. Black horizontal lines indicate the mean ISC values for each of the three condition types. Inset shows the ISC values computed after regressing out from the original signal the BOLD signal extracted from the visual and auditory cortices. **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 are meaningful.

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).

Contrast	Condition	beta	SE	p-value	
+M/-L vs. 0	Partly Cloudy	0.204	0.0281	<0.001	***
	Mr. Bean	0.181	0.0282	<0.001	***
	Shapes	0.115	0.0282	0.00314	**
	Day	0.121	0.0282	0.00306	**
+M/-L vs. +M/+L	Partly Cloudy	-0.145	0.0281	<0.001	***
	Mr. Bean	-0.169	0.0282	<0.001	***
	Shapes	-0.235	0.0282	<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	**

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.

We next asked whether the recruitment of the language network by +M/-L stimuli can be observed at the level of individual fROIs (**Figure 3B**). Indeed, these conditions elicited ISCs that were significantly higher than the zero baseline in each of the five fROIs (**Table 4**). These results also held for each

condition individually, except for Day in MFG (**Table S1**).

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.

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 S2**).

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).

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

processing

Next, we asked whether the relatively high ISCs in the language network for meaningful non-verbal conditions could be explained by the perceptual (visual or auditory) processing of the stimuli. The fact that non-meaningful non-verbal conditions do not elicit much stimulus-related activity in the language network already argues against this possibility. However, we additionally recomputed the ISCs after regressing out the BOLD signal from the visual and auditory cortices (**Figure 3A, inset**). Like in the original analysis, these new ISCs were significantly above the zero baseline (mean ISCs = 0.155, beta = 0.153, SE = 0.0357, $p < 0.001$) and stronger than those elicited by the -M/-L conditions (mean ISCs = 0.0209, beta = 0.127, SE = 0.0486, $p = 0.0263$). Unlike in the original analysis, the comparison between the +M/-L conditions and the +M/+L conditions was not significant (mean ISCs for the +M/+L conditions = 0.234, beta = 0.0754, SE = 0.0392 $p = 0.0850$). This pattern of results was similar for each individual +M/-L condition (**Table S3**) and for each fROI (**Table S4**). Taken together, these analyses suggest that the stimulus-related activity in the language network for meaningful non-verbal stimuli cannot be explained by lower-level perceptual (visual/auditory) processing demands.

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 4**). 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.

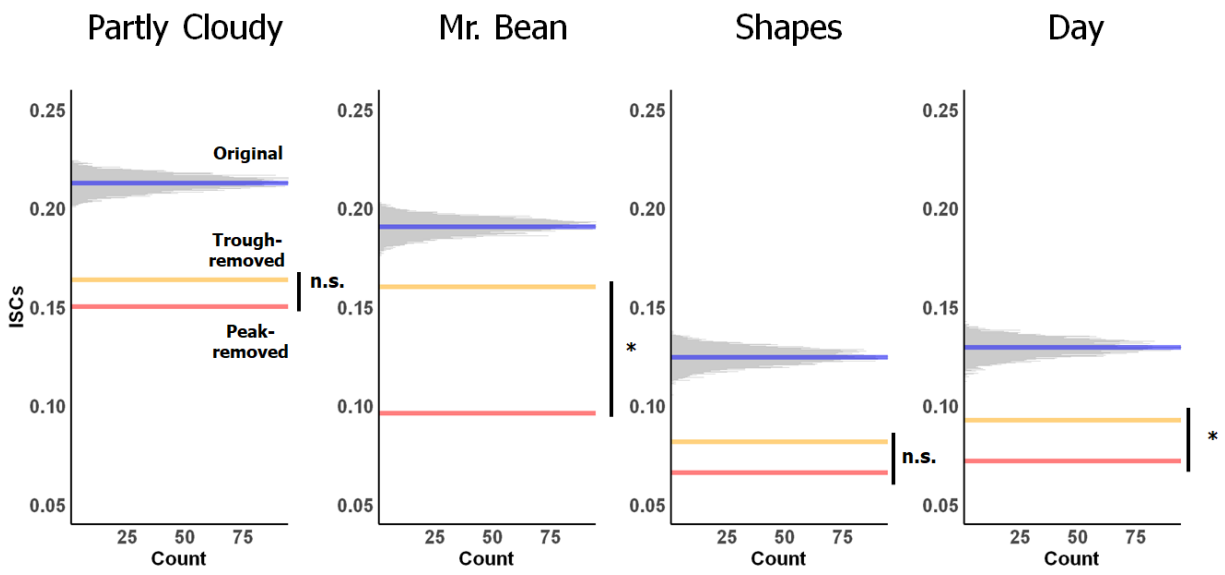

Figure 4. *Peak-removal analysis.* Peak- / trough-removed ISCs were compared against random-timepoints-removed ISCs and against each other for each +M/-L condition. The histograms show the random-timepoints-removed ISCs (generated 10,000 times; averaged across fROIs/participants) with bin width of 0.0001. 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).

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 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; and iii) the tracking of meaningful non-verbal stimuli cannot be explained by low-level perceptual processing or 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). 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 fact that a preference for linguistic inputs is maintained even in the context of complex naturalistic stimuli suggests that no amount of non-verbal information, however semantically rich, is sufficient to drive the language network's responses to the same extent as linguistic stimuli.

Worth a special mention is a very low 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., 2021), many continue to argue for overlapping mechanisms for processing aspects of language and music (e.g., Sammler et al., 2013; Kunert et al., 2015). The lack of stimulus-linked 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).

Our main finding—above-baseline tracking by the language network of meaningful non-verbal stimuli—is in line with recent work showing that event pictures elicit a reliable response in the language network, but 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, these results suggest that the language network exhibits continuous and automatic tracking of non-verbal semantics. 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) demonstrate that damage to the language network does not impair visual / abstract semantic processing. For example, Ivanova et al. (2021) showed that individuals with 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. Understanding what aspects of meaning drive the language network's response may provide important clues about the relationship between linguistic and conceptual processing.

One constraint in 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; Shain et al., 2021). It is therefore likely that non-verbal meanings that the language system is concerned with have to do with events, 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 events remains to be determined. Future work that manipulates in more controlled ways various properties of visual events may help uncover such preferences, including potential dissociations among the different components of the language network.

In sum, 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 task-driven linguistic re-coding and lower-level perceptual processing. Overall, these results demonstrate a role of the language network in naturalistic non-verbal processing, and set the stage for future work on the precise nature and functions of its contributions.

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Supplementary Information

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

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

Supplementary Table 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.

Contrast	Condition	beta	SE	p-value	
+M/-L vs. 0	Partly Cloudy	0.221	0.0239	<0.001	***
	Mr. Bean	0.174	0.0239	<0.001	***
	Shapes	0.0957	0.0239	0.00472	**
	Day	0.0877	0.240	0.00577	**
+M/-L vs. +M/+L	Partly Cloudy	-0.0130	0.0239	0.600	
	Mr. Bean	-0.0593	0.0239	0.0491	*
	Shapes	-0.138	0.0239	<0.001	***
	Day	-0.146	0.0240	<0.001	***
+M/-L vs. -M/-L	Partly Cloudy	0.200	0.0239	<0.001	***
	Mr. Bean	0.154	0.0239	<0.001	***
	Shapes	0.0748	0.0239	0.0176	*
	Day	0.0668	0.0240	0.0223	*

Supplementary Table 3. *LME model statistics for +M/-L conditions after regressing out perceptual ROIs.* For each condition, ISCs were compared against a zero-baseline, mean +M/+L ISCs and mean -M/-L ISCs using LMEM, 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 mean (SE), p-value (FDR-corrected for multiple comparison across baselines (n=3)). For p-values, *<0.05, **<0.01, ***<0.001.

Contrast	fROI	beta	SE	p-value	
+M/-L vs. 0	IFGorb	0.110	0.0212	<0.001	***
	IFG	0.140	0.0281	<0.001	***
	MFG	0.109	0.0303	0.00395	**
	AntTemp	0.172	0.0295	<0.001	***
	PostTemp	0.236	0.0383	<0.001	***
+M/-L vs. +M/+L	IFGorb	-0.0534	0.0296	0.171	
	IFG	-0.0518	0.0392	0.251	
	MFG	-0.0873	0.0411	0.150	
	AntTemp	-0.130	0.0409	0.0486	*
	PostTemp	-0.0653	0.0535	0.251	
+M/-L vs. -M/-L	IFGorb	0.0850	0.0389	0.0602	
	IFG	0.112	0.0507	0.0602	
	MFG	0.0910	0.0527	0.110	
	AntTemp	0.147	0.0525	0.0394	*
	PostTemp	0.211	0.0677	0.0394	*

Supplementary Table 4. *LME model statistics for each fROI on condition type comparison after regressing out perceptual ROIs.* 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, **<0.01, ***<0.001.