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Identifying moments of peak audience engagement from brain responses during story listening

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ABSTRACT
Stories in general, and peak moments within a single story in particular, can evoke strong responses across recipients. Between the content of a story and these shared audience responses lies an explanatory gap that neuroimaging can help close. Accordingly, this study examined how the brains of an audience responded during a story. We performed two types of analyses: First, we correlated the story's physical characteristics to brain activity. Second, we reverse-correlated moments of peak brain engagement to story segments. We found that activity peaks in the temporo-parietal junction identify socially engaging points within the story, such as a pie-in-the-face scene, hyperbole, and sexual references. We discussed how these results and reverse correlation neuroimaging more broadly advance communication science.

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A good story can engage and entertain many listeners by captivating their attention, carefully orchestrating cognitive and emotional processes, and prompting overt reactions (Boyd, 2009; Brown, 2004; Bruner, 1986; Green et al., 2002). These phenomena are well known and have been studied extensively across the fields of communication, psychology, and linguistics, to name only a few. However, there are still key gaps in our theoretical understanding of how stories affect audiences. Specifically, we have only fragmentary knowledge about how listening to a story evokes strong responses that are shared across many listeners, and which content elements are especially apt to do so.

Within this context, functional neuroimaging shows promise as an approach to elucidate the reception process while people are exposed to stories (Cascio & Falk, 2016; Floyd & Weber, 2020). Specifically, neuroimaging enables studying audience responses over time while circumventing the need for verbal questioning, introspection, and retrospective reporting. This helps close the gap between story content and reception mechanisms by providing novel data that can yield new insights to refine, clarify, and improve theory related to narrative processing and other social processes (Falk et al., 2015; Greenwald, 2012; Huskey et al., 2020; Mather et al., 2013; Schmälzle & Meshi, 2020). For example, exposure to stories can affect recipients' attitudes and behaviors (Braddock & Dillard, 2016) and several theories aim to explain these effects (Green et al., 2002).

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Analyzing how story content is processed by the brain to produce these psychological effects can greatly inform such theories, although this is not the goal of the present study. Rather, we focused more directly on the link between the story stimulus with its auditory and narrative content and brain activity.

A challenge, however, is that while a neuroimaging approach is comparatively easy to execute with simple stimuli like isolated sounds or words, the complex content of stories makes them more difficult to connect to brain responses (Ferstl et al., 2008; Hasson & Honey, 2012). As a result, few studies have investigated the neural processing of stories (Willems et al., 2020), and even fewer have approached the topic from a communication perspective (Grall et al., 2021).

This study examines how an audience processes an engaging story, focusing on the story moments that maximize specific regional brain responses consistently across many recipients. We suggest a novel approach, called reverse correlation analysis (Hasson et al., 2004; Ringach & Shapley, 2010), to link brain responses back to the moments of the story and the content that likely evoked these responses. Reverse correlation analysis uses neural responses to a story to identify salient moments, such as peaks that are significantly expressed among a group of listeners while their brains respond to the story (Hasson et al., 2004; Wagner et al., 2016). This reverse correlation approach has not yet received much attention in communication, despite its theoretical and practical potential for understanding audience responses.

Capitalizing on this reverse correlation approach as a way to confirm predicted functional associations between story elements and brain responses, we examine data from a test audience whose brains were scanned while listening to a story with many social elements. Our primary focus is on the reverse correlation between the temporo-parietal junction (TPJ) and the content of the test story that maximally engaged this region. The theoretical rationale behind this focus is that the TPJ has been associated with social cognition (Schurz et al., 2014; Van Overwalle, 2009), defined as processes related to thinking about self or others. Research on the neural basis of social cognition, however, has largely been conducted outside of the context of story processing and topics related to communication and audience engagement. Considerable benefits from addressing this gap can be gained for our field, such as what the term "engaging" means and how conceptions overlap and differ between fields (Grall et al., 2021). Work using neural measures typically links engagement to the enhanced recruitment of brain systems (e.g., Dmochowski et al., 2012; Jääskeläinen et al., 2020; Schmälzle et al., 2015), whereas work using self-reports tends to emphasize subjective experiences, such as feeling engaged. Although these differences are an inevitable consequence of different methodologies (e.g., Cummins, 2010), it is clear that brain responses to stories and subjective effects are both rooted in the incoming stimuli, that is, the stream of words that describe the story characters and events. In this way, the study here can extend previous work bridging neuroscience and communication to better understand how a story's content (i.e., the stream of auditory stimuli and the narrative information it conveys) engages the brains of an audience.

Of note, as this is a secondary analysis of an existing neuroimaging dataset (Nastase et al., 2019), we did not select the original story or manipulate its content. However, this specific dataset was chosen because preliminary inspection of the story and previous findings related to the dataset (Huth et al., 2016) suggested that it was capable of eliciting

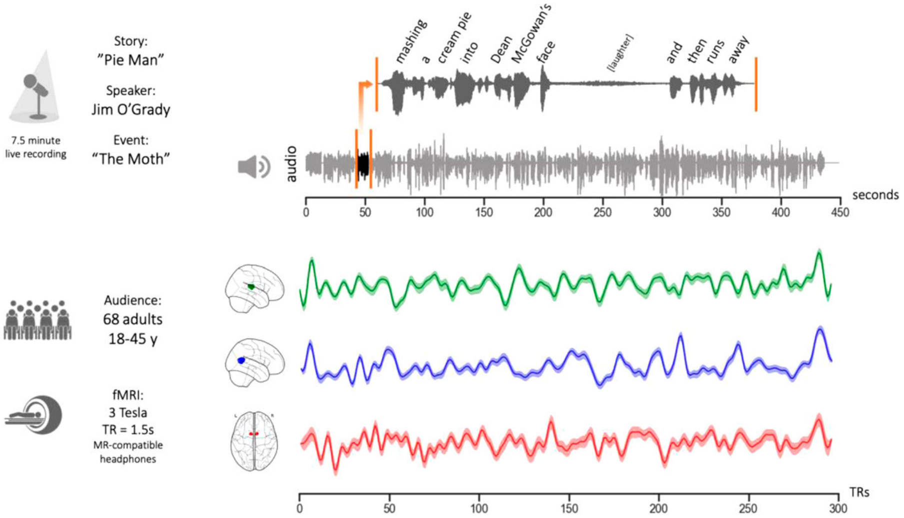


Figure 1. Illustration of the study and the time-aligned nature of the neuroimaging recordings. The 7.5 min long story "Pie Man" was recorded at the live storytelling event "The Moth" in New York and played to fMRI participants listening to it via headphones. Onset times of individual words were transcribed for coding. fMRI data were recorded concurrently with the story stimulus, preprocessed and time-aligned to the story, and regional data were extracted. Shaded corridors around the fMRI time series represent standard error of the mean at each time point.

strong and convergent audience responses that we assumed to be driven by the specific social events described in the story. In addition to our focus on social cognitive processing, the fact that these events were also funny (for instance, a cream pie being mashed into a high-powered dean's face) motivated a secondary focus on humor and reward processing, although this was not the primary goal.

The paper is organized as follows: First, we briefly introduce previous research on the social and affective responses to powerful stories. We specify what we know and what we don't know about the neural underpinnings of these effects, and why gaining such insight constitutes theoretical progress for communication science. We highlight how work on communication neuroscience may help connect the fields of rhetoric, social cognition, and audience response measurement by elucidating how a given story evokes shared responses across many recipients. Next, we provide readers with the relevant theoretical and empirical background on the neurocognitive basis of auditory, social, and affective brain processes. Finally, we introduce the specific study that measured brain activity from 68 participants listening to an authentic, 7.5-minute-long story, which we use to "reversely" identify those sections that evoked strong and consistent responses in selected brain regions of this sample audience (see Figure 1).

Background

It is well known that stories are able to convey a wealth of conceptual information to large audiences, keeping listeners attentive and often also entertained (Boyd, 2009; Busselle & Bilandzic, 2009; Green et al., 2002; Schank, 1995). Although there has always been debate on how to best define the concept of story (Braddock & Dillard, 2016; Graesser et al., 2002; Stein, 1982), there is general consensus that most stories include descriptions of characters and events that happen to them, especially social interactions between characters or how the events enable or prevent them from achieving their goals (Abelson & Schank, 1977; Bower & Rinck, 1999). Extant research has examined the processing of complex narratives with a focus on discourse and social cognitive processes (Graesser et al., 1994; Green et al., 2002; Kintsch, 1998; Schank, 1979). This all has led to a large and cross-disciplinary body of knowledge about stories and the experiences and behaviors they produce.

However, it is worth acknowledging what we do not know yet, as specifying the existing ignorance is a necessary step for theoretical progress (Merton, 1987). With this in mind, we start with Schramm (1971), who stated that "Most of the communication process is in the 'black box' of the central nervous system, the contents of which we understand only vaguely" (p. 24–25). Decades after this remark, advances in cognitive neuroscience produced numerous insights into how the central nervous system processes communication in general and stories in particular (Floyd & Weber, 2020; Mar, 2011), but scholars are still far away from precisely understanding all relevant subprocesses. Furthermore, relevant knowledge tends to be dispersed across several fields, such as rhetoric, narratology, psychology, or neuroscience. As a result, a comprehensive neural theory of story processing has not yet emerged, although this is becoming an active area of theoretical development (Willems et al., 2020; Yeshurun et al., 2021) and researchers do actually know a lot about constitutive subprocesses like auditory neurocognition (focusing on explaining hearing), neurolinguistics (focusing on explaining language), and social cognitive and communication neuroscience (Hickok & Small, 2015; Lieberman, 2015; Schmälzle & Meshi, 2020).

In the following paragraphs, we will therefore introduce three selected brain systems that are integral to different aspects of story processing: hearing (the ability to sense sound), social cognition (thinking about oneself or others), and reward processing (processing of positively valenced stimuli that can influence hedonic experience and behavior).[1] The goal of this section is to theoretically motivate the choice of brain regions whose activity will later be examined.

Auditory cortex

It is clear that if people do not hear a spoken story, subsequent effects cannot emerge. In this sense, the brain systems for audition are a logical starting point to examine the reception of a story. One key brain region that is central to hearing is the auditory cortex. The term *auditory cortex* is an umbrella term for cortical regions involved in processing the incoming sound information from the ear, which instantiate various spectrotemporal analyses. Anatomically, the primary auditory cortex is located in the superior temporal lobe and extends into Heschl's gyrus (Brodman area 41/42; Humphries et al., 2010; Moerel et al., 2014).

Hundreds of functional neuroimaging studies have examined how responses in the auditory cortex vary based on properties of sound, language, and other auditory stimuli. In sum, when listeners process a spoken narrative, their auditory cortices will respond to spectrotemporal properties of the incoming speech signal, which then provides the input for further processes involved in linguistic analysis. Also, it is worth noting that hearing is a general neurocognitive function. Thus, although individual differences in auditory anatomy and function exist, the basic neural responses to auditory stimuli are largely similar among listeners (Watson & Breedlove, 2012). This evidence can be accessed and condensed via automated meta-analyses. In brief, automated meta-analyses of the cumulative results of neuroimaging studies enable researchers to enter a search term (e.g., "auditory") into a database and then receive a brain map that displays which regions are reliably activated in studies that mention this search term. As shown in Figure 2, an automated meta-analysis of fMRI studies of auditory processing indeed identifies bilateral superior temporal regions, which is compatible with the anatomical and neuropsychological literature (Humphries et al., 2010; Moerel et al., 2014).

Temporoparietal junction

The reasons why people seek out, continue listening to, or enjoy stories are arguably less related to hearing speech sounds than to the content these sounds convey, which is often

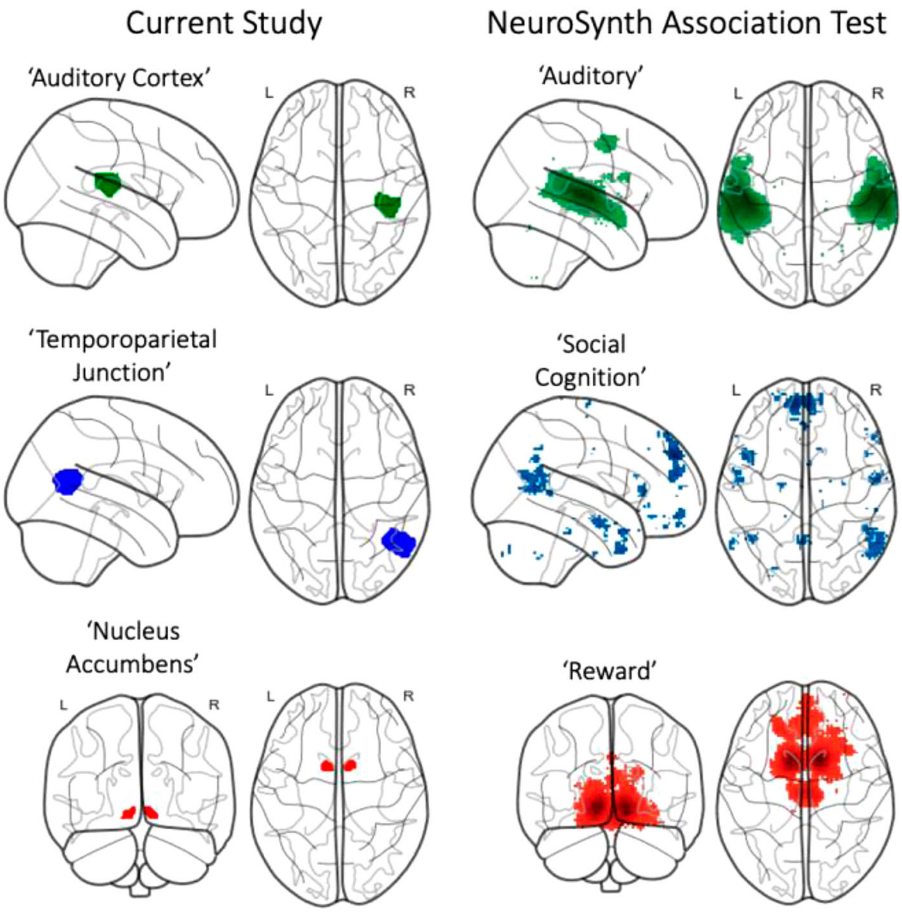


Figure 2. Anatomical location of key a-priori regions examined in this study and meta-analytic results for theoretical concepts motivating region selection. Meta-analysis maps are based on NeuroSynth.org and represent the association test maps, thresholded at $z = 5$. For details see Method.

social in nature (Busselle & Bilandzic, 2009; Tamborini et al., 2021). *Social cognition*, which can be defined as the study of processes that enable people to think about other people and social situations (Fiske & Taylor, 2013), has become an area of intense neuroscience research (Cacioppo et al., 2002; Lieberman, 2015). Such work also interfaces more and more with communication topics (Kranzler et al., 2019; O'Donnell et al., 2015; Pei et al., 2019; Schmälzle et al., 2017), although much work remains to be done to more fully connect this research with fields like media effects and entertainment research more broadly.

In the brain, social cognition has long been linked to the right temporoparietal junction (rTPJ) (Decety & Lamm, 2007; Schurz et al., 2017). Anatomically the temporoparietal junction (TPJ) is, as the name suggests, located where the temporal and parietal regions meet (see Figure 2, middle left panel). Functionally, tasks that manipulate mentalizing, perspective taking, and similar social-cognitive processes consistently evoke TPJ activations (Decety & Lamm, 2007; Schurz et al., 2017). As for the auditory cortex, we can again perform an automated meta-analysis, but this time searching for the term "social cognition" instead of "auditory." As shown in Figure 2 (middle panel), these results also identify the temporoparietal junction.

To avoid potential misunderstanding, we note that the TPJ does not act in isolation from other brain regions, and that TPJ activity does not correspond to a single function in a one-to-one fashion (Schmälzle & Meshi, 2020). Instead, the TPJ is associated with higher-level processes that encompass social understanding, attention shifts, and higher-level language processing, although these literatures are barely integrated (Alcalá-López et al., 2017; Carter & Huettel, 2013; Geng & Vossel, 2013; Mars et al., 2012). In fact, it is likely that there exists commonality between these topics in terms of the information transformations the TPJ helps to accomplish, such as integrating information across space, time, or between perspectives (e.g., Dohmatob et al., 2020; Yeshurun et al., 2021). However, despite these complexities, the theoretical link between TPJ and social cognition is extremely robust.

Zooming in more specifically on communication, the TPJ appears to be implicated in exposure to messages and production and retransmission of social language (Kranzler et al., 2019; O'Donnell et al., 2015). Although more preliminary, some work has suggested the TPJ plays a role in understanding punchlines and resolving expectancy violations in social situations (Amir et al., 2015; Franklin & Adams, 2011; Jääskeläinen et al., 2016). For instance, Jääskeläinen et al. (2016) found that there was decreased activity in the TPJ upon reviewing humorous content when the violation of the jokes became more expected. In sum, this evidence suggests that a spoken narrative should engage the TPJ, especially if it conveys a story with a wealth of social information. Of note, in this specific context the term engage does not refer to a psychological experience, but rather to the recruitment of this region's activity (Grall et al., 2021).

Nucleus Accumbens

The Nucleus Accumbens (NAcc) is a key structure in the brain's reward system (Knutson & Greer, 2008; Salgado & Kaplitt, 2015). The bottom-left panel in Figure 2 shows the anatomical location of the NAcc according to the popular Pauli-Atlas (Pauli et al., 2018). This again matches precisely with an automated meta-analysis of fMRI studies using the term “reward” (bottom-right panel). Although these functional associations of the NAcc are extensively researched and strongly supported, it is important to note that many underlying studies come from animal research that is separate from the task of story listening. Moreover, neuroimaging studies with humans often rely on economic and gambling tasks to interrogate NAcc function. In comparison, studies of the TPJ-social-cognition link often use text or speech stimuli to present social vignettes, and thus, have a closer relationship to the current study.

Although the NAcc has been mentioned less often in the literature on story processing, its foundational nature for reward-related processing and anticipation makes it a key candidate to explore within this context. In fact, several neuroimaging studies have found that the NAcc is involved in processes related to the surprise, anticipation, and affective value of short texts or musical pieces (Berns & Moore, 2012; Mobbs et al., 2003; Salimpoor et al., 2013). Although, as argued above, the specific story that will be examined below was not chosen because of its humor, humor does play a role. Prior work on humor and the NAcc has looked at the role of reward pathway in humor and found higher levels of NAcc activation when participants viewed humorous content (Amir et al., 2015; Franklin & Adams, 2011; Mobbs et al., 2003). In sum, there appears to be a link between humor processing and the NAcc, which justifies further examination.

To summarize, the auditory cortex, the rTPJ, and the NAcc are candidate regions for examining the reception of a story. We selected the auditory cortex because it is a starting point for sensory-perceptual analysis, and we wanted to probe whether measured brain activity is actually related to expected properties of the sound stimulus. Our main analytical focus was on the TPJ, however, because its putative functions seem closest to the collective engagement of audience brain activity that we were interested in here. Additionally, we explored the role of the NAcc in particular. Results for many other brain regions can be found in the Online Supplement Materials. Whereas past insights into these three key regions’ functions have many implications for closing the explanatory gap between story content and story reception processes, one should keep in mind that what we know to date comes either from ex-vivo anatomical studies, animal research, or from studies that do not contain narrative-level information. If narratives are used as stimuli in neuroimaging, the focus has often been on language processes, ignoring higher-level narrative content (Huth et al., 2016). As such, only a few studies have examined related issues and those that did took different analytical approaches (Grall et al., 2021; O’Donnell et al., 2015). Hence, testing hypotheses in the present study about assumed brain/content relationships using stories as stimuli is even more relevant. At the same time, theoretically, this endeavor can help further refine concepts and predictions in narrative theories, and yield a better understanding and explanation of the reception process.

The present study and hypotheses

The current study examined how listeners’ brains respond to an engaging story, focusing on story-evoked brain responses in the three brain regions discussed above. Importantly, the emphasis of this study was on shared or general brain responses to the same story content, not on individual differences. The motivation behind this is that a story basically presents the same input to all listeners, who therefore face similar processing demands. Therefore, we expected that when people perceive and process the same story, this should be accomplished by similar neural responses.

We tested hypotheses about the role of three primary regions (auditory cortex, TPJ, and Nucleus accumbens) during story processing via two general types of analyses. These two types of analyses, forward analysis and reverse correlation, are introduced next along with relevant hypotheses and research questions:

The first type of analysis is called forward analysis because it links stimulus features to evoked brain responses via a forward-logic. For instance, we can assume that specific physical characteristics (e.g., sound frequency, amplitude) of the story should evoke brain responses that "track with" variations of this stimulus characteristic (Huettel, 2008). In the case of a spoken story, one easily quantifiable physical characteristic is the sound waveform's energy, roughly equal to the loudness. The so-called root mean squared energy (RMSE) can be extracted as a continuous measure from the raw story recording. Based on knowledge that the auditory cortex is involved in the sensory analysis of sound and prior studies, we can assume that over-time variations in sound energy content will be associated with fluctuations in the fMRI signal (Alho et al., 2014). Therefore, we advanced our first hypothesis:

> H_1: Variations in RMSE should be associated with the fMRI signal's strength in the superior temporal lobe.

There are, of course, numerous other quantifiable aspects beyond the sound's energy, which are psychologically more interesting: We could quantify word types, word length, their syntactic role, or even their semantics. Such analyses are possible (Huth et al., 2016; Wehbe et al., 2014), albeit this approach has many difficulties getting at narrative-level information. Therefore, we used a different approach for the present study than this forward-analysis: reverse correlation.

The reverse correlation approach (Gosselin & Schyns, 2010; Hasson et al., 2004; Huettel, 2008; Ringach & Shapley, 2010) essentially inverts the sequential logic of the analysis. Instead of varying stimulus-features and revealing associated brain systems via forward mapping, this approach starts from the recorded brain activity and identifies its peaks and troughs; then, it "links back" these responses to the moments in the stimulus that elicited them.[2] As an analogy, imagine that one could track the moment-to-moment fuel consumption of a car during a hilly terrain trip. Then, one might perhaps find out that periods of peak fuel consumption occur during segments with high uphill slopes. This type of information can provide a lot of insight into functional selectivities and the general system function. This reverse correlation approach has been prominent in visual neuroscience (Hubel & Wiesel, 1962). In social cognition, however, the approach is less common, which may again have to do with the fact that few studies have used naturalistic stories or other continuously varying stimuli that lend themselves to reverse correlation. However, this approach has been successful in neighboring areas, such as to map brain responses back to specific movie scenes (Hasson et al., 2004; Wagner et al., 2016).

We therefore adopted the reverse correlation approach for the current study, assuming that signal peaks in the TPJ and NAcc should point us to scenes that feature especially social or affective content. In other words, our strategy involved creating brain-based trailers comprising those parts of the story that maximally engaged individual brain regions, which we then examined in terms of their content. For the temporoparietal junction (TPJ), we hypothesized:

> H_2: The TPJ signal peaks will correspond to scenes that describe socially engaging story parts.

Specifically, for the present study, occurrences of laughter were used to index such parts.[3] Finally, for the NAcc, we formulated a research question. Although one might argue that the robust literature on NAcc-involvement in reward and anticipation processes, and even its role in humor could warrant an actual hypothesis, the fact that this work is largely based on very different, non-narrative kinds of stimuli and different analytical approaches led us to proceed more cautiously.

> *RQ*: How will the NAcc activation peaks relate to scene content, particularly regarding anticipation and reward?

Method

This study is a secondary analysis of a dataset that is part of a collection of fMRI data about narratives (Nastase et al., 2019; Willems et al., 2020). Specifically, we used the data for the story Pie Man because this story has a large sample size, is long and complete, and was given in a realistic storytelling context during a The Moth live event in New York City. Data from this story have been examined before, but with a focus on language processing (Huth et al., 2016; Lerner et al., 2011) that is distinct from the current focus on communication and audience engagement.

Sample

The sample included data from 68 participants (*age range* = 18–45 years, $M = 22.5$, $SD = 4.7$; 42 females). Data were originally collected at Princeton University, and all participants provided informed consent to the IRB-approved study. Further details on the sample and inclusion criteria can be found in the data paper (Nastase et al., 2019).

Story stimulus

All participants listened to the same story, titled Pie Man, which featured a recording from the live storytelling event The Moth in New York City in 2008. The Pie Man story is a humorous piece about a “pastry avenger” at Fordham University, told by its author, Jim O’Grady, from a first-person narrator perspective (see the transcript in the supplementary material and recording at https://osf.io/qw2sp). The entire story is 7.5 min long, with a brief introduction and end periods. Overall, 300 functional scans were recorded while participants listened to this auditory-only stimulus. The recording is freely available at https://themoth.org/stories/pie-man and was transcribed automatically into 957 words, and the exact temporal onsets of each word are marked.

In terms of content, the story is about O’Grady’s experiences as a journalist when he reported a series of pastry attacks in the student newspaper. His decision to exaggerate the story leads to some unforeseen twists and turns. The piece follows a linear path starting with Pie Man's first pie-in-the-face attack on a high-powered college dean. The next segment describes how O'Grady gave Pie Man his name and embellished the original events. He is then surprised to receive an invitation from the real Pie Man, inviting him to another planned attack. This all then leads to Pie Man becoming a sensation on campus. The story ends with an anecdote in a bar, where O'Grady pretends to be Pie Man as his alter ego to seduce an attractive woman.

Data acquisition and analysis

MRI data were collected using a 3T Siemens Magnetom Skyra scanner. Functional data were acquired with a TR of 1.5 s and an in-lane resolution of 3*3 mm (slice thickness = 4 mm). Preprocessing was done using fMRIPrep 20.0.5 (Esteban et al., 2019). More details can be found in the data descriptor paper (Nastase et al., 2019).

Subsequent analyses were then carried out using the NiLearn package (Abraham et al., 2014) and in-house code. The analysis pipeline is documented in the form of reproducible Jupyter-notebooks at github.com/nomcomm/narratives_pieman. In brief, functional data were downloaded, high-pass filtered at 0.01 Hz, detrended, and standardized, and averaged regional time series were extracted from individual brain regions.

We extracted functional time series using the Shen-parcellation, which features 268 parcels across the cortex and has been used for analyzing fMRI data during movie-watching and narrative listening (Shen et al., 2013). We further added 25 anatomically defined regions from the atlases by Pauli et al. (2018) and Edlow et al. (2012). Thus, the basic data structure comprised 300 functional volumes, 293 regions, and data from 68 participants.

The three primary regions of interest – the auditory cortex, the right TPJ (rTPJ), and the NAcc – were identified based on their overlap with the NeuroSynth meta-analysis maps (Yarkoni et al., 2011; Figure 2) and their anatomical location (e.g., NAcc in the Pauli-atlas). Additionally, we carried out data-driven analyses for all other regions, which are reported in the Supplementary Materials.

For the forward correlation analysis, we quantified the RMSE sound energy via the RMSE extractor from the pliers package (McNamara et al., 2017). RMSE scores were extracted from the raw audio recording, downsampled to match the resolution of the fMRI signal, and shifted by 3 TRs to account for delays in the hemodynamic response function. The resampled and shifted RMSE time course was then correlated against all 293 time courses from each brain region. The resulting correlation values were mapped back onto the brain (see Figure 3).

For reverse correlation analysis, we focused on the fMRI signal recorded from the auditory cortex, TPJ, and NAcc. To identify moments of significant activation across the group of listeners, we computed – for each volume/moment – a *t*-score based on the mean divided by the standard error of the mean (see Hasson et al., 2004). This procedure was used to identify significant peaks and troughs in each region's fMRI signal across the audience (see Figure 4). Specifically, the vector of point-by-point *t*-scores was thresholded at a value of two, which corresponds to a 95% confidence interval around the data points at each story moment, or a significance threshold of $p = .025$ (two-sided testing).

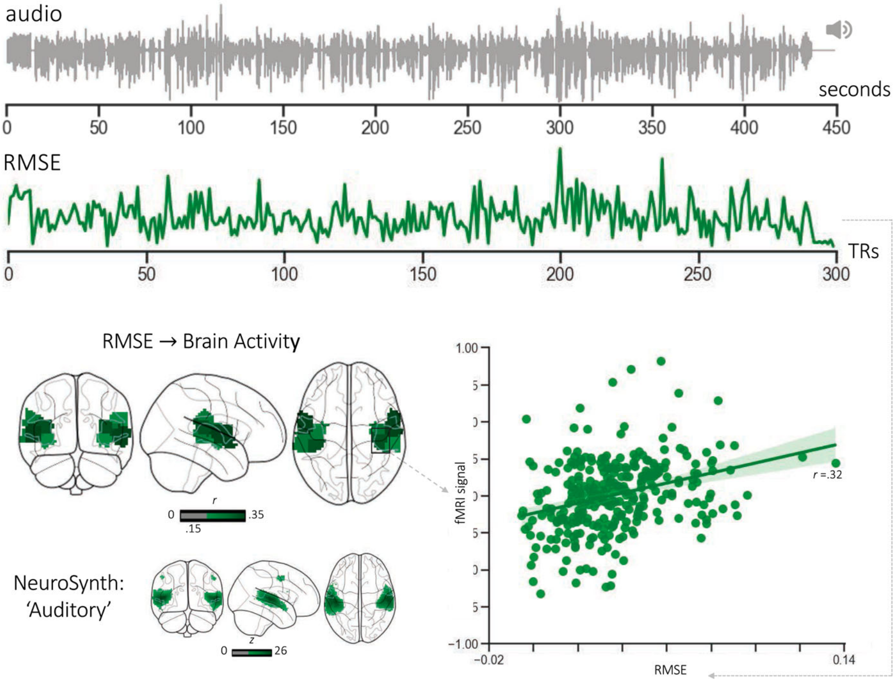


Figure 3. Result for forward correlation analysis. The sound waveform's (top panel) auditory signal energy (RMSE-panel, resampled to match the resolution of fMRI) predicts fMRI activity strength in bilateral auditory cortex (bottom left). The figure at the very bottom illustrates the result of a NeuroSynth meta-analysis for the term "auditory" (see also Figure 2). As can be seen, the results match almost perfectly. The scatterplot on the right represents the correlation between the RMSE feature and the fMRI signal from the right auditory cortex.

To reverse-correlate peak and trough moments back to the stimulus, we used (a) the textual transcript with time-stamps for each word, and (b) the original audio recording of the story. Specifically, we identified all words and all story segments that fell within the interval identified by the peak- and trough-significance-thresholding analyses. We then inspected the resulting text and recreated a trailer that concatenated the respective "story snippets" into one new recording, such as the "TPJ-peak-hot-takes."

Results

Forward correlation of sound energy to brain activity

H_1 stated that variations in RMSE, a measure of a sound's physical property, should be associated with the fMRI signal's strength in the superior temporal lobe. The underlying logic is that the soundwave is the medium that carries the stimulus content to the brain, so that subsequent psychological processes are logically contingent on the fact that the sound reaches the brain, gets transduced into neural signals, and analyzed along a gradient from sensation to cognition. To assess how the sound drives the brain signal, we first extracted the RMSE of the recording. Computing the correlation between the RMSE-sound-feature and the time-varying brain activity confirmed a highly robust

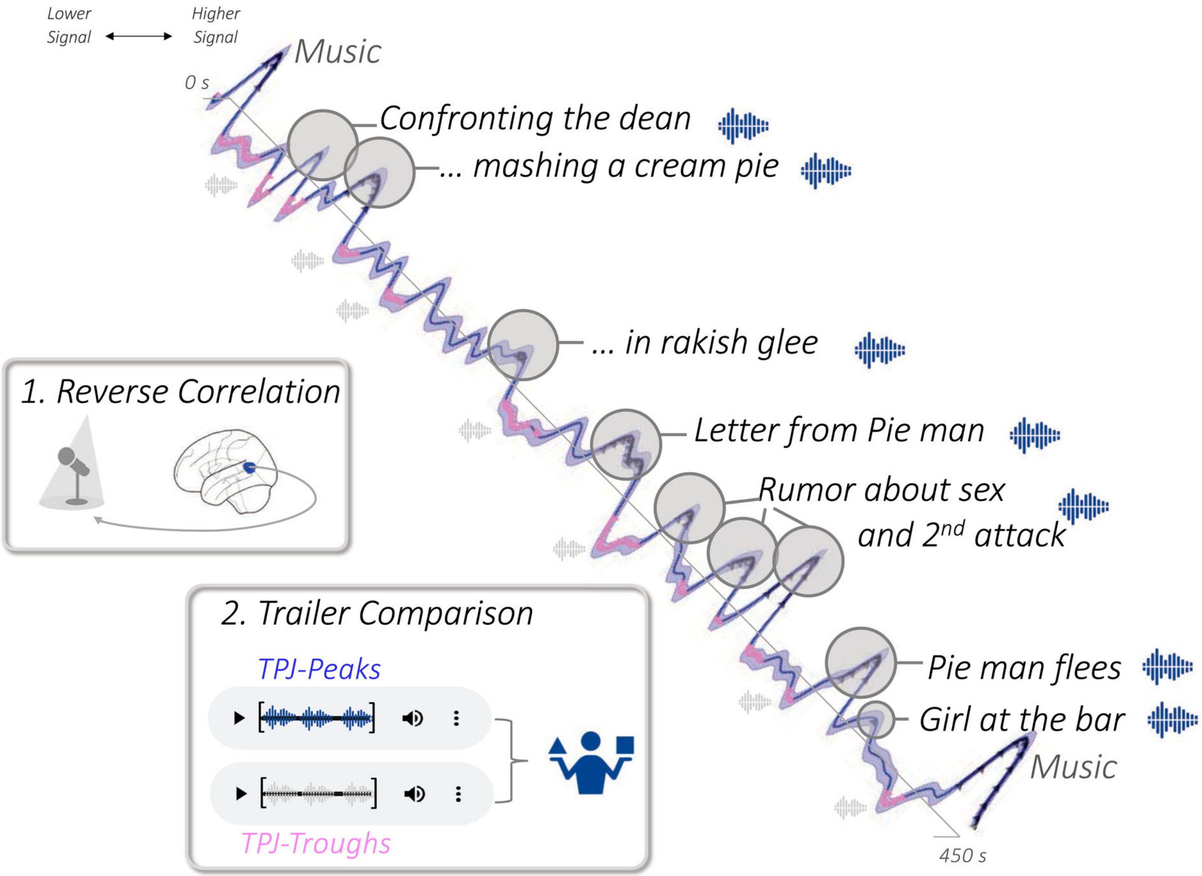


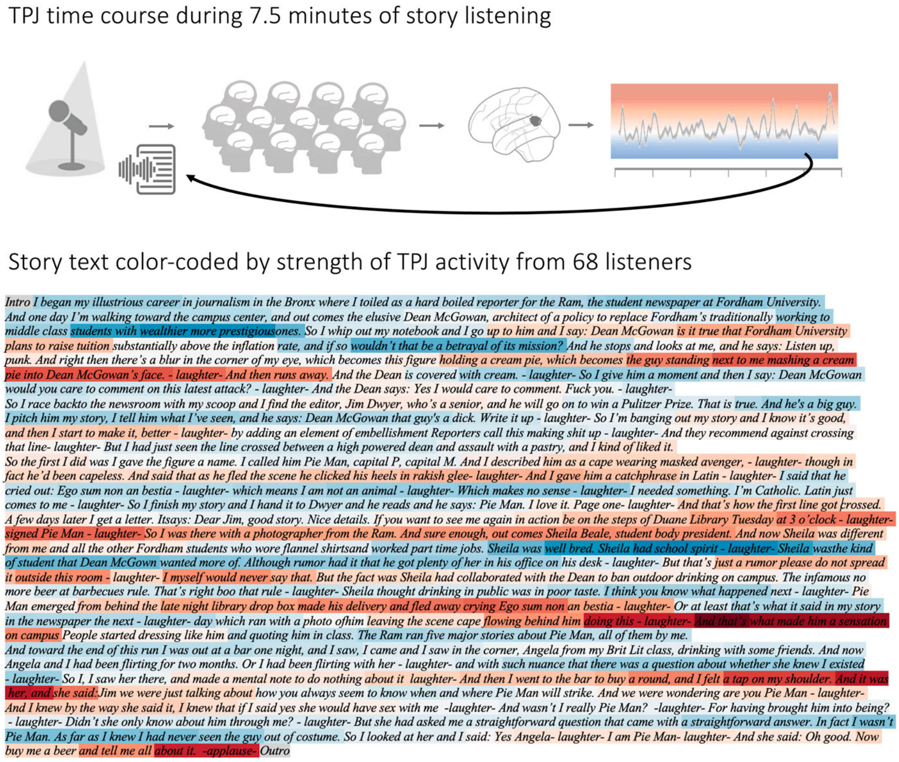
Figure 4. Reverse correlation results for the Temporoparietal Junction. Shaded regions around the group-averaged rTPJ signal represent SEM. Colored peaks and troughs indicate significant signal increases or decreases, respectively. Based on the time points of these peaks, we reversely identified (reverse-correlated) the corresponding scenes from the story transcripts, and rearranged the raw audio recording to produce a brain-based trailer, i.e., scenes that produce significant activations or deactivations ($p < .025$) in the rTPJ. These trailers can be listened to at https://osf.io/qw2sp.

correlation between the sound energy and activity in the primary auditory cortex – bilaterally. These results, which supported H_1, are shown in Figure 3.

Reverse correlation of audience brain activity back to story moments

H_2 examined the relationship between rTPJ peak activity and story scenes, whereas the *RQ* focused on the NAcc peaks. Figure 4 (TPJ) and Supplemental Figure 1 (NAcc) illustrate the results from the reverse-corelation analysis for these two regions. Specifically, we reverse-correlated both the words that fell within each region's peak or trough window and created brain-based trailers ("TPJ-hot-takes"). We provided these trailers for listening in an online repository (https://osf.io/qw2sp) because it is difficult to convey the overall impression. Figure 4 also shows the text segments associated with the rTPJ peaks and Figure 5 provides an additional visualization of the entire story text color-coded by rTPJ activity level.

The picture that emerges for the rTPJ is that this region's peaks point to socially sensitive and engaging moments in the Pie Man story. Specifically, reading the text-segments or listening to the trailer revealed that TPJ peaks identify a surprising norm violation,


TPJ time course during 7.5 minutes of story listening

Story text color-coded by strength of TPJ activity from 68 listeners

Intro I began my illustrious career in journalism in the Bronx where I toiled as a hard boiled reporter for the Ram, the student newspaper at Fordham University. And one day I'm walking toward the campus center, and out comes the elusive Dean McGowan, architect of a policy to replace Fordham's traditionally working to middle class students with wealthier more prestigiousones. So I whip out my notebook and I go up to him and I say: Dean McGowan is it true that Fordham University plans to raise tuition substantially above the inflation rate, and if so wouldn't that be a betrayal of its mission? And he stops and looks at me, and he says: Listen up, punk. And right then there's a blur in the corner of my eye, which becomes this figure holding a cream pie, which becomes the guy standing next to me mashing a cream pie into Dean McGowan's face. - laughter- And then runs away. And the Dean is covered with cream. - laughter- So I give him a moment and then I say: Dean McGowan would you care to comment on this latest attack? - laughter- And the Dean says: Yes I would care to comment. Fuck you. - laughter-

So I race backto the newsroom with my scoop and I find the editor, Jim Dwyer, who's a senior, and he will go on to win a Pulitzer Prize. That is true. And he's a big guy. I pitch him my story, I tell him what I've seen, and he says: Dean McGowan that guy's a dick. Write it up - laughter- So I'm banging out my story and I know it's good, and then I start to make it, better - laughter- by adding an element of embellishment Reporters call this making shit up - laughter- And they recommend against crossing that line- laughter- But I had just seen the line crossed between a high powered dean and assault with a pastry, and I kind of liked it.

So the first I did was I gave the figure a name. I called him Pie Man, capital P, capital M. And I described him as a cape wearing masked avenger, - laughter- though in fact he'd been capeless. And said that as he fled the scene he clicked his heels in rakish glee- laughter- And I gave him a catchphrase in Latin - laughter- I said that he cried out: Ego sum non an bestia - laughter- which means I am not an animal - laughter- Which makes no sense - laughter- I needed something. I'm Catholic. Latin just comes to me - laughter- So I finish my story and I hand it to Dwyer and he reads and he says: Pie Man. I love it. Page one- laughter- And that's how the first line got crossed. A few days later I get a letter. Itsays: Dear Jim, good story. Nice details. If you want to see me again in action be on the steps of Duane Library Tuesday at 3 o'clock - laughter- signed Pie Man - laughter- So I was there with a photographer from the Ram. And sure enough, out comes Sheila Beale, student body president. And now Sheila was different from me and all the other Fordham students who wore flannel shirtsand worked part time jobs. Sheila was well bred. Sheila had school spirit - laughter- Sheila wasthe kind of student that Dean McGown wanted more of. Although rumor had it that he got plenty of her in his office on his desk - laughter- But that's just a rumor please do not spread it outside this room - laughter- I myself would never say that. But the fact was Sheila had collaborated with the Dean to ban outdoor drinking on campus. The infamous no more beer at barbecues rule. That's right boo that rule - laughter- Sheila thought drinking in public was in poor taste. I think you know what happened next - laughter- Pie Man emerged from behind the late night library drop box made his delivery and fled away crying Ego sum non an bestia - laughter- Or at least that's what it said in my story in the newspaper the next - laughter- day which ran with a photo ofhim leaving the scene cape flowing behind him doing this - laughter- And that's what made him a sensation on campus People started dressing like him and quoting him in class. The Ram ran five major stories about Pie Man, all of them by me.

And toward the end of this run I was out at a bar one night, and I saw, I came and I saw in the corner, Angela from my Brit Lit class, drinking with some friends. And now Angela and I had been flirting for two months. Or I had been flirting with her - laughter- and with such nuance that there was a question about whether she knew I existed - laughter- So I, I saw her there, and made a mental note to do nothing about it laughter- And then I went to the bar to buy a round, and I felt a tap on my shoulder. And it was her, and she said: Jim we were just talking about how you always seem to know when and where Pie Man will strike. And we were wondering are you Pie Man - laughter- And I knew by the way she said it, I knew that if I said yes she would have sex with me -laughter- And wasn't I really Pie Man? -laughter- For having brought him into being? - laughter- Didn't she only know about him through me? - laughter- But she had asked me a straightforward question that came with a straightforward answer. In fact I wasn't Pie Man. As far as I knew I had never seen the guy out of costume. So I looked at her and I said: Yes Angela- laughter- I am Pie Man- laughter- And she said: Oh good. Now buy me a beer and tell me all about it. -applause- Outro

Figure 5. Illustration of rTPJ brain activity time course and story text. The story text is presented in color-coded fashion, such that warmer colors represent higher fMRI activity levels (based on the group-averaged time course). Color-coding is based on the normalized and centered activations to range between zero (blue) to one (red). Note that e.g., the introductory music, pauses, and emphases are part of the original audio stimulus, but these are not visualized. A higher-resolution image can be found at https://osf.io/qw2sp.

moments that call for social inferences and perspective-taking, and sexual innuendo. One potential criticism of this descriptive result is that labeling the scenes as containing norm violation, sexual innuendo, etc. could be open to interpretation. We acknowledge this issue, which is due to the fact that we examined here only a single, short story consisting of less than 1000 words and a rather peculiar set of scenes. In principle, one would want to quantify and compare textual characteristics associated with peaks and troughs by submitting the identified text segments to automated analysis methods or more well-defined coding categories. However, we noted that dictionary-based methods are not suitable for this because the meaning emerges at the story rather than the word level.

In lieu of computerized methods, we used human-based content analysis that coded the TPJ-trailers for occurrences of laughter. Laughter provides a strong criterion for audience impact and one that is clearly codeable. We found that out of the 11 segments identified by the rTPJ-peak-analysis, eight contained laughter. For the trough-segments, of which there were 14 in total, there were only four containing audience laughter, and two of these were not very strong. A chi-squared test suggested that these ratios (peaks: 8:3, troughs: 4:10) were significantly different ($\chi^2 = 4.81$; $p = 0.028$). Thus, the peak trailers contained more socially engaging (or laughter-evoking) content, which supported H_2. This pattern of results was thus compatible with the putative functions of the TPJ. However, the results were still somewhat surprising because the Pie Man story was quite engaging throughout, which could have masked effects.

The same methods as for the TPJ were also used to analyze data from the NAcc, and a similar figure as for the TPJ (Figure 4) is reported in Online Supplemental Figure 1. The results indicated the NAcc activates more strongly during segments that one could characterize as anticipatory or references to future states (e.g., So the first thing I did … , A few days later … .). Again, listening to the compiled snippets trailer can provide a better impression (see https://osf.io/qw2sp) since the trailer also conveys prosodic cues like emphasis and rising vocal features. It should be noted, however, that the signal in the NAcc is more noisy than for the TPJ, the peaks are less pronounced, and the overall picture is not as clear cut as for the TPJ. Also, given the limits of fMRI's temporal resolution, these results should be interpreted with some caution (Sabatinelli et al., 2009).

Discussion

There is no shortage of popular science, conventional wisdom, and expert advice that a good story keeps the audience engaged. However, little work has studied these mechanisms from a neural perspective that can examine brain responses across audiences during story listening on a moment-to-moment basis. Here, we examined how a story engaged the brains of over 60 listeners.

First, H_1 stated that variations in RMSE should be associated with the fMRI signal's strength in the superior temporal lobe. The result that the auditory cortex activity tracked well with the sound energy feature, as shown in Figure 2, supports H_1. Although this result is unsurprising, it confirms predictions about how the auditory system works. Moreover, given the complexity of real-world stories compared to the simple, isolated sound stimuli used in most previous fMRI studies, it is encouraging to replicate these findings in the ecologically more valid context of listening to a naturalistic story in its entirety (Hasson & Honey, 2012; Miller et al., 2019).

Perhaps the most important result of this study is that the reverse correlation analysis of the rTPJ identifies key scenes of the story. This link between the rTPJ and socially engaging story parts is compatible with a large body of research from the past 20 years of neuroimaging that has demonstrated a role for the rTPJ in social cognition. Numerous studies manipulating social-cognitive functions, such as empathy, theory-of-mind, agency, or attentional reorienting, have consistently observed increased rTPJ activation (Decety & Lamm, 2007). However, due to many methodological challenges of studying the reception of natural stories via neuroimaging, virtually no study has examined how the TPJ responses of an audience relate to a story's content. Instead, comparisons have always been made only between different messages, such as speeches rated as strong vs. weak (Schmälzle et al., 2015), or health messages perceived as subjectively effective vs. less effective (Imhof et al., 2017, 2020). Critically, as we discuss further below, it is not the goal of this study with a story stimulus to isolate any of the TPJ's specific subfunctions, or to claim that the TPJ is exclusively related to any single verbalizable or operationalized task role. However, listening to the audio-scenes associated with the TPJ peaks (see https://osf.io/qw2sp) demonstrates that peak points happen during socially engaging scenes, as defined by their ability to evoke audience laughter. Of course, we acknowledge that laughter is only one way to operationally define social engagement. Moving forward, we foresee an increased use of natural language processing tools to analyze these scenes' textual content, although this remains a challenging task (Bisk et al., 2020). In any case, the current results are compatible with a role for the TPJ in attentional regulation and social processes, and whatever specific representational content the TPJ operates over, these functions' demand is highest during these particular scenes.

These results are also relevant in the context of recent results by Huth et al. (2016). Briefly, they also used stories from The Moth in fMRI experiments, but they relied on a different methodological approach than ours. Specifically, they used very few subjects ($N = 7$), but hours of The Moth stories, for which they annotated every word based on a word embedding model (Hirschberg & Manning, 2015). This leads to a similar approach as the one we used for the RMSE-audio-feature, but at the level of word-meanings. This can yield associations between word-level meaning and regional brain activity. Inspecting the results of these analyses specifically for the rTPJ reveals that this region is responsive to social words, such as husband, brother, father, died, or remarried, to name a few. However, it is essential to note that Huth et al. (2016) approach operates only at the level of single words, which is different from a story that builds a context over words. Nevertheless, the results from various studies – including task-based activation (Decety & Lamm, 2007), word-level encoding (Huth et al., 2016), and the current reverse correlation study – all show that the rTPJ is involved in functions that seem critical for listeners' ability to follow and respond to the social content of a story.

Moving on to the reverse correlation results for the NAcc, our findings are also compatible with its putative theoretical functions regarding reward and anticipation. As shown in Supplemental Figure 1, the peak-trailers could be understood as moments of funny surprise or mounting anticipation (e.g., the "listen up, punk" scene or the ending, where O'Grady claims to be Pie Man and the girl says "tell me all about it"). These observations are certainly promising, but we want to exert some caution at this point: Whereas the result for the auditory cortex provides a robust validation and the TPJ result confirms our prediction, our confidence in the NAcc findings would be strengthened if we had more evidence about NAcc activity during stories, which will ultimately require more data.

Despite these caveats, it is promising that one can produce these trailers using an objective analytic procedure, and the reverse correlation approach also has the theoretical potential to bring communication and neuroscience into better contact. However, in doing so, there is potential for misunderstanding the reverse correlation approach and its theoretical underpinnings, and thus we will next distinguish it from the potentially problematic reverse inference.

The theoretical distinction between reverse correlation and reverse inference

In the forward correlation analysis, we quantified a property of the stimulus (RMSE). We then predicted that this property should track with brain activity in regions known to be involved in sound analysis, which it did. This forward correlation follows the logical causal sequence of information flow that goes from message content to the brain.

Things get more complicated when interpreting the reverse correlation analysis, and there is danger that it could be confused with reverse inference, which points to something different. In particular, reverse inference refers to conclusions that are drawn about a hypothetical psychological process based on observed brain activation (Schmälzle & Meshi, 2020). For instance, if we took the activation of the TPJ as an indication that listeners were mentalizing (or any other psychological task or experience), then that would be a reverse inference.

The reverse correlation procedure, however, is distinct from reverse inferencing. Specifically, reverse correlation links back from the response to a stimulus to the actual content of the stimulus that produced the response. Reverse correlation is primarily about the brain response and its relationship to stimulus content. Thus, it does not involve inferring what psychological experience the participants in the scanner may or may not have had. However, when we interpret the trailers in terms of their content, then one is easily drawn to make inferences, like the observation that the rTPJ-peak-trailer contains moments of the story that are critical and funny points for the plot. Interpreting these results in light of the putative function of the TPJ is fine and can offer many interesting insights, or even discoveries of new functional associations, but we must proceed with caution.

Broader implications

Having clarified the reverse correlation analysis, we next discuss why this approach has potential for communication science – theoretically and in terms of applications. Theoretically, the approach is so attractive because it focuses on something central for stories: content. Indeed, stories are so popular because they feature rich content that produces strong effects, and the same could be said about communicative messages and media more broadly. However, much of the experiments done in social and cognitive neuroscience are still extremely weak in their content richness, featuring only a few isolated words or images. Stimuli with such impoverished meaning are not appropriate to engage the kinds of social-cognitive and affective processes that narrative and communication scholars are interested in (Grall et al., 2021; Wilcox et al., 2020).

As more and more neuroimaging studies use stories and related stimuli, however, the reverse correlation provides a principled way to examine the nexus between content and audience responses, and to link back and forth between these domains. Given that the reverse correlation is relatively underused, we see the potential for synergies here. In particular, content analysis is a traditional strength of communication science. Thus, as larger datasets with many different stories and hundreds of listeners become available, opportunities for linking content features of messages to objectively measured brain responses will increase and the current approach could be further merged with entertainment theory. For instance, several theories, such as affective disposition theory (Zillman & Cantor, 1977) or dual-process models of entertainment (Tamborini et al., 2021) suggest ways to analyze content that could be integrated with the present approach of measuring how such content engages audiences' brains. Given that these models also make predictions about psychological experiences and outcomes (e.g., story enjoyment, character liking etc.), neural data may be helpful for testing their predictions at a more mechanistic level. The current study of forward (auditory content/RMSE → brain activity) and especially reverse (higher-level social content ← rTPJ) correlations, however, deliberately placed the issue of these psychological processes aside, in part because no data about audience experiences was available, but also because both forms of data (i.e., content properties and brain responses) are in the realm of observables, not psychological constructs.

In terms of potential applications, perhaps the most obvious one is that the approach can be used to produce automated trailers based on reverse correlations from brain activity. It is an interesting question, also from a theoretical point of view, whether experts would create similar trailers, or how expert-created trailers would differ from the ones that are created based on audience brain responses. Of course, this approach can be applied not only to data for spoken stories, but also for book previews, album outtakes, and so forth. Indeed, several studies have shown promise in predicting the success of cultural products from brain activity data (Berns & Moore, 2012; Salimpoor et al., 2013) and recent work points to the potential of neural data to forecast real-world message effects (Coronel et al., 2021; Dmochowski et al., 2014; Falk & Scholz, 2017; Imhof et al., 2020; Schmälzle et al., 2020; Weber et al., 2015). However, these studies all measured brain responses to existing messages, whereas the reverse correlation approach allows one to select subsections of a message that maximize regional brain activity. Future work might thus link brain-based trailers to their success in the field, and doing so could give us more insights into the mechanisms by which specific content aspects of stories produce brain responses, which then make messages successful among large audiences.

Limitations and future directions

One limitation is that since this study uses a social-cognitive and communication perspective to examine a pre-existing dataset, it would have been desirable to have more data about how the participants responded to the story at the subjective level (e.g., story liking). Since this is not possible, all we can know about participants is their demographics and the fact that they could understand the story – or else their data were excluded (Nastase et al., 2019). Having such data would also be beneficial to study individual differences, whereas we focused here only on the common response of an audience.

Another limitation is the limited temporal resolution of fMRI as well as potential time lags. A single fMRI volume spans an entire short sentence, thereby blurring over any fast-paced changes. This fundamental limitation of fMRI invites new measures, such as electroencephalography, which could offer further insight into the neuromodulatory systems that are engaged by surprise, social cognition, or other socio-motivational responses to dynamic media (Imhof et al., 2020).

The current study also focused primarily on three regions that were selected for theoretical, *a-priori* reasons. However, the brain includes other regions, and regions interact in complex ways to accomplish comprehension, engagement, and so on (Fisher et al., 2021; Huskey, et al., 2018a). Although this does not invalidate our approach, future research could examine responses in other regions or perform network-based analyses. That said, we do provide results for other areas in the supplementary online results.

On a related note, one could also compute the reverse correlation analysis for other features of the fMRI time series. For instance, although the current study focused on the regional response time courses and their peaks, one could use this approach to focus in on the connectivity between regions. One might then find that the connectivity or coactivation of specific regions, or configurations of regional activity, might be particularly associated with highly engaging scenes. Such results would be theoretically interesting for theories that link networked brain activity to media effects (Huskey et al., 2018b), and again, eminently applicable from a practical perspective.

Last, given the context of audiences listening to entertaining stories, one would wish for a more diverse sample of different stories, and possibly also different settings beyond The Moth. For instance, an interesting extension might be to consider how fluctuations in language difficulty throughout a story affect how subjectively engaged audiences are, and ultimately, how effective stories are (Bullock et al., 2019; Busselle & Bilandzic, 2009; Schmälzle et al., 2015). Thus, by studying how audiences' brains respond to stories across contents and contexts, we can expect more profound and more generalizable insights into the phenomenon of how stories are processed.

Conclusion

In the present study, we used neuroimaging to examine the reception of an entertaining story. Using a reverse correlation approach, we found that consistent response peaks of the rTPJ across listeners' brains identified peak moments in the story. These findings add insight into the social-cognitive mechanism of story processing and particularly the remarkable sensitivity of the TPJ for socially engaging content. That the TPJ is a hub for social cognitive processes was already known, but with very few exceptions, the body of knowledge on social neuroscience has not been linked to communication and audience response measurement. Consequently, this study illustrates how stories offer fruitful ground for studying these phenomena in ecologically relevant settings and linking them to communication theory in order to more fully understand communication processes.

Research transparency statement

Code to reproduce and document the analyses is accessible online at https://osf.io/qw2sp and github.com/nomcomm/narratives_pieman.

Notes

1. Critically, we provide macro-level overview rather than a microscopic account of these subsystems. There are other relevant systems that we skip over here, particularly the complex topic of neurolinguistics. The supplementary materials provide analyses of hundreds of additional regions. Also, this is a somewhat simplified theoretical account of how the brain transforms information from simple sounds into complex meaning, emphasizing modularity and serial processing.
2. Please also see the extensive argument about the distinction between reverse correlation and reverse inference in the Discussion.
3. Laughter provides an objective criterion for strong audience impact and one that is clearly codeable. The decision to use laughter as an index of socially engaging content as opposed to other operationalized indicators has to do with the fact that only one particular story is used in this study, which naturally limits the number of peaks and story segments that are available for reverse correlation, including the contents that are covered by the story. In the future, we envision that larger datasets will enable to reverse-correlate from corpora containing hours of story content with thousands of brain activation peaks, enabling analyses that go beyond laughter. For this study, however, we use laughter as an objective criterion, but we encourage readers to examine the sound trailers and text segments.

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References

Abelson, R., & Schank, R. C. (1977). *Scripts, plans, goals and understanding: An inquiry into human knowledge structures*. Lawrence Erlbaum.

Abraham, A., Pedregosa, F., Eickenberg, M., Gervais, P., Mueller, A., Kossaifi, J., Gramfort, A., Thirion, B., & Varoquaux, G. (2014). Machine learning for neuroimaging with scikit-learn. *Frontiers in Neuroinformatics*, *8*, 1–10. https://doi.org/10.3389/fninf.2014.00014.

Alcalá-López, D., Smallwood, J., Jefferies, E., Van Overwalle, F., Vogeley, K., Mars, R. B., Turetsky, B. I., Laird, A. R., Fox, P. T., Eickhoff, S. B., & Bzdok, D. (2017). Computing the social brain connectome across systems and states. *Cerebral Cortex*, *28*(7), 1–26. https://doi.org/10.1093/cercor/bhx121.

Alho, K., Rinne, T., Herron, T. J., & Woods, D. L. (2014). Stimulus-dependent activations and attention-related modulations in the auditory cortex: A meta-analysis of fMRI studies. *Hearing Research*, *307*, 29–41. https://doi.org/10.1016/j.heares.2013.08.001.

Amir, O., Biederman, I., Wang, Z., & Xu, X. (2015). Ha ha! Versus aha! A direct comparison of humor to nonhumorous insight for determining the neural correlates of mirth. *Cerebral Cortex*, *25*(5), 1405–1413. https://doi.org/10.1093/cercor/bht343.

Berns, G. S., & Moore, S. E. (2012). A neural predictor of cultural popularity. *Journal of Consumer Psychology*, *22*(1), 154–160. https://doi.org/10.1016/j.jcps.2011.05.001.

Bisk, Y., Holtzman, A., Thomason, J., Andreas, J., Bengio, Y., Chai, J., Lapata, M., Lazaridou, A., May, J., Nisnevich, A., Pinto, N., & Turian, J. (2020). Experience grounds language. In *arXiv [cs.CL]*. arXiv. https://arxiv.org/abs/2004.10151v3.

Bower, G. H., & Rinck, M. (1999). Goals as generators of activation in narrative understanding. In S. R. Goldman, A. C. Graesser, & P. van den Broek (Eds.), *Narrative comprehension, causality, and coherence: Essays in honor of Tom Trabasso* (pp. 111–134). Routledge.

Boyd, B. (2009). *On the origin of stories: Evolution, cognition, and fiction*. Harvard University Press.

Braddock, K., & Dillard, J. P. (2016). Meta-analytic evidence for the persuasive effect of narratives on beliefs, attitudes, intentions, and behaviors. *Communication Monographs*, *83*(4), 446–467. https://doi.org/10.1080/03637751.2015.1128555.

Brown, D. E. (2004). Human universals, human nature & human culture. *Daedalus*, *133*(4), 47–54. https://doi.org/10.1162/0011526042365645.

Bruner, J. (1986). *Actual minds, possible worlds*. Harvard University Press. https://doi.org/10.4159/9780674029019.

Bullock, O. M., Colón Amill, D., Shulman, H. C., & Dixon, G. N. (2019). Jargon as a barrier to effective science communication: Evidence from metacognition. *Public Understanding of Science*, *28*(7), 845–853. https://doi.org/10.1177/0963662519865687.

Busselle, R., & Bilandzic, H. (2009). Measuring narrative engagement. *Media Psychology*, *12*(4), 321–347. https://doi.org/10.1080/15213260903287259.

Cacioppo, J. T., Berntson, G. G., Adolphs, R., Sue Carter, C., McClintock, M. K., Meaney, M. J., Schacter, D. L., Sternberg, E. M., Suomi, S., & Taylor, S. E. (2002). *Foundations in social neuroscience*. MIT Press.

Carter, R. M., & Huettel, S. A. (2013). A nexus model of the temporal–parietal junction. *Trends in Cognitive Sciences*, *17*(7), 328–336. https://doi.org/10.1016/j.tics.2013.05.007.

Cascio, C. N., & Falk, E. B. (2016). Neuroscience. In K. B. Jensen & R. T. Craig (Eds.), *The international encyclopedia of communication theory and philosophy* (pp. 1351–1359). Wiley. https://doi.org/10.1002/9781118766804.wbiect171.

Coronel, J. C., O'Donnell, M. B., Pandey, P., Delli Carpini, M. X., & Falk, E. B. (2021). Political humor, sharing, and remembering: Insights from neuroimaging. *Journal of Communication*, *71*(1), 129–161. https://doi.org/10.1093/joc/jqaa041.

Cummins, R. (2010). *The world in the head*. Oxford University Press.

Decety, J., & Lamm, C. (2007). The role of the right temporoparietal junction in social interaction: How low-level computational processes contribute to meta-cognition. *The Neuroscientist*, *13*(6), 580–593. https://doi.org/10.1177/1073858407304654.

Dmochowski, J. P., Bezdek, M. A., Abelson, B. P., Johnson, J. S., Schumacher, E. H., & Parra, L. C. (2014). Audience preferences are predicted by temporal reliability of neural processing. *Nature Communications*, *5*(1), 4567. https://doi.org/10.1038/ncomms5567.

Dmochowski, J. P., Sajda, P., Dias, J., & Parra, L. C. (2012). Correlated components of ongoing EEG point to emotionally laden attention–a possible marker of engagement? *Frontiers in Human Neuroscience*, *6*, 112. https://doi.org/10.3389/fnhum.2012.00112

Dohmatob, E., Dumas, G., & Bzdok, D. (2020). Dark control: The default mode network as a reinforcement learning agent. *Human Brain Mapping*, *41*(12), 3318–3341. https://doi.org/10.1002/hbm.25019.

Edlow, B. L., Takahashi, E., Wu, O., Benner, T., Dai, G., Bu, L., Grant, P. E., Greer, D. M., Greenberg, S. M., Kinney, H. C., & Folkerth, R. D. (2012). Neuroanatomic connectivity of the human ascending arousal system critical to consciousness and its disorders. *Journal of Neuropathology and Experimental Neurology*, *71*(6), 531–546. https://doi.org/10.1097/NEN.0b013e3182588293.

Esteban, O., Markiewicz, C. J., Blair, R. W., Moodie, C. A., Ilkay Isik, A., Erramuzpe, A., Kent, J. D., Goncalves, M., DuPre, E., Snyder, M., Oya, H., Ghosh, S. S., Wright, J., Durnez, J., Poldrack, R. A., & Gorgolewski, K. J. (2019). fMRIPrep: A robust preprocessing pipeline for functional MRI. *Nature Methods*, *16*(1), 111–116. https://doi.org/10.1038/s41592-018-0235-4.

Falk, E. B., Cascio, C. N., & Coronel, J. C. (2015). Neural prediction of communication-relevant outcomes. *Communication Methods and Measures*, *9*(1-2), 30–54. https://doi.org/10.1080/19312458.2014.999750.

Falk, E., & Scholz, C. (2017). Persuasion, influence, and value: Perspectives from communication and social neuroscience. *Annual Review of Psychology*, *69*(1), 329–356. https://doi.org/10.1146/annurev-psych-122216-011821.

Ferstl, E. C., Neumann, J., Bogler, C., & von Cramon, D. Y. (2008). The extended language network: A meta-analysis of neuroimaging studies on text comprehension. *Human Brain Mapping*, *29*(5), 581–593. https://doi.org/10.1002/hbm.20422.

Fisher, J. T., Hopp, F. R., & Weber, R. (2021). A practical introduction to network neuroscience for communication researchers. *Communication Methods and Measures*, *15*(1), 60–79. https://doi.org/10.1080/19312458.2020.1860206.

Fiske, S. T., & Taylor, S. E. (2013). *Social cognition: From brains to culture*. SAGE.

Floyd, K., & Weber, R. (2020). *The handbook of communication science and biology*. Routledge.

Franklin, R. G., & Adams, R. B. (2011). The reward of a good joke: Neural correlates of viewing dynamic displays of stand-up comedy. *Cognitive, Affective & Behavioral Neuroscience*, *11*(4), 508–515. https://doi.org/10.3758/s13415-011-0049-7.

Geng, J. J., & Vossel, S. (2013). Re-evaluating the role of TPJ in attentional control: Contextual updating? *Neuroscience and Biobehavioral Reviews*, *37*(10 Pt 2), 2608–2620. https://doi.org/10.1016/j.neubiorev.2013.08.010.

Gosselin, F., & Schyns, P. G. (2010). Bubbles: A new technique to reveal the use of information in recognition tasks. *Journal of Vision*, *1*(3), 333–333a. https://doi.org/10.1167/1.3.333.

Graesser, A. C., Olde, B., & Klettke, B. (2002). How does the mind construct and represent stories? In M. C. Green, J. J. Strange, & T. C. Brock (Eds.), *Narrative impact: Social and cognitive foundations* (pp. 229–262). Psychology Press.

Graesser, A. C., Singer, M., & Trabasso, T. (1994). Constructing inferences during narrative text comprehension. *Psychological Review*, *101*(3), 371–395. https://doi.org/10.1037/0033-295X.101.3.371.

Grall, C., & Finn, E. S. (2021, July 27). Leveraging the power of media to drive cognition: A media-informed approach to naturalistic neuroscience. https://doi.org/10.31234/osf.io/c8z9t

Grall, C., Tamborini, R., Weber, R., & Schmälzle, R. (2021). Stories collectively engage listeners' brains: Enhanced intersubject correlations during reception of personal narratives. *Journal of Communication*, *71*(2), 332–355. https://doi.org/10.1093/joc/jqab004.

Green, M. C., Strange, J. J., & Brock, T. C. (2002). *Narrative impact: Social and cognitive foundations*. Psychology Press. https://doi.org/10.4324/9781410606648.

Greenwald, A. G. (2012). There is nothing so theoretical as a good method. *Perspectives on Psychological Science*, *7*(2), 99–108. https://doi.org/10.1177/1745691611434210.

Hasson, U., & Honey, C. J. (2012). Future trends in neuroimaging: Neural processes as expressed within real-life contexts. *NeuroImage*, *62*(2), 1272–1278. https://doi.org/10.1016/j.neuroimage.2012.02.004.

Hasson, U., Nir, Y., Levy, I., Fuhrmann, G., & Malach, R. (2004). Intersubject synchronization of cortical activity during natural vision. *Science*, *303*(5664), 1634–1640. https://doi.org/10.1126/science.1089506.

Hickok, G., & Small, S. L. (2015). *Neurobiology of language*. Academic Press.

Hirschberg, J., & Manning, C. D. (2015). Advances in natural language processing. *Science*, *349*(6245), 261–266. https://doi.org/10.1126/science.aaa8685.

Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *Journal of Physiology*, *160*(1), 106–154. https://doi.org/10.1113/jphysiol.1962.sp006837.

Huettel, S. A. (2008). *Functional magnetic resonance imaging* (2nd ed.). Sinauer Associates.

Humphries, C., Liebenthal, E., & Binder, J. R. (2010). Tonotopic organization of human auditory cortex. *NeuroImage*, *50*(3), 1202–1211. https://doi.org/10.1016/j.neuroimage.2010.01.046.

Huskey, R., Bue, A. C., Eden, A., Grall, C., Meshi, D., Prena, K., Schmälzle, R., Scholz, C., Turner, B., & Wilcox, S. (2020). Marr's tri-level framework integrates biological explanation across communication subfields. *Journal of Communication*, *70*(3), 356–378. https://doi.org/10.1093/joc/jqaa007.

Huskey, R., Craighead, B., Miller, M. B., & Weber, R. (2018a). Does intrinsic reward motivate cognitive control? A naturalistic-fMRI study based on the synchronization theory of flow. *Cognitive, Affective & Behavioral Neuroscience*, *18*(5), 902–924. https://doi.org/10.3758/s13415-018-0612-6.

Huskey, R., Wilcox, S., & Weber, R. (2018b). Network neuroscience reveals distinct neuromarkers of flow during media use. *Journal of Communication*, *68*(5), 872–895. https://doi.org/10.1093/joc/jqy043.

Huth, A. G., de Heer, W. A., Griffiths, T. L., Theunissen, F. E., & Gallant, J. L. (2016). Natural speech reveals the semantic maps that tile human cerebral cortex. *Nature*, *532*(7600), 453–458. https://doi.org/10.1038/nature17637.

Imhof, M. A., Schmälzle, R., Renner, B., & Schupp, H. T. (2017). How real-life health messages engage our brains: Shared processing of effective anti-alcohol videos. *Social, Cognitive, and Affective Neuroscience*, *12*(7), 1188–1196. https://doi.org/10.1093/scan/nsx044.

Imhof, M. A., Schmälzle, R., Renner, B., & Schupp, H. T. (2020). Strong health messages increase audience brain coupling. *NeuroImage*, *216*, 116527. https://doi.org/10.1016/j.neuroimage.2020.116527.

Jääskeläinen, I. P., Pajula, J., Tohka, J., Lee, H.-J., Kuo, W.-J., & Lin, F.-H. (2016). Brain hemodynamic activity during viewing and re-viewing of comedy movies explained by experienced humor. *Scientific Reports*, *6*(1), 27741. https://doi.org/10.1038/srep27741.

Jääskeläinen, I. P., Sams, M., Glerean, E., & Ahveninen, J. (2020). Movies and narratives as naturalistic stimuli in neuroimaging. *NeuroImage*, *224*, 117445. https://doi.org/10.1016/j.neuroimage.2020.117445.

Kintsch, W. (1998). *Comprehension: A paradigm for cognition*. Cambridge University Press.

Knutson, B., & Greer, S. M. (2008). Anticipatory affect: Neural correlates and consequences for choice. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *363*(1511), 3771–3786. https://doi.org/10.1098/rstb.2008.0155.

Kranzler, E. C., Schmälzle, R., Pei, R., Hornik, R. C., & Falk, E. B. (2019). Message-elicited brain response moderates the relationship between opportunities for exposure to anti-smoking messages and message recall. *Journal of Communication*, *69*(6), 589–611. https://doi.org/10.1093/joc/jqz035.

Lerner, Y., Honey, C. J., Silbert, L. J., & Hasson, U. (2011). Topographic mapping of a hierarchy of temporal receptive windows using a narrated story. *Journal of Neuroscience*, *31*(8), 2906–2915. https://doi.org/10.1523/JNEUROSCI.3684-10.2011.

Lieberman, M. D. (2015). Introduction to social cognitive neuroscience. *Brain Mapping*, *3*, 1–2. https://doi.org/10.1016/b978-0-12-397025-1.09992-9.

Mar, R. A. (2011). The neural bases of social cognition and story comprehension. *Annual Review of Psychology*, *62*(1), 103–134. https://doi.org/10.1146/annurev-psych-120709-145406.

Mars, R. B., Sallet, J., Schüffelgen, U., Jbabdi, S., Toni, I., & Rushworth, M. F. S. (2012). Connectivity-based subdivisions of the human right "temporoparietal junction area": Evidence for different areas participating in different cortical networks. *Cerebral Cortex*, *22*(8), 1894–1903. https://doi.org/10.1093/cercor/bhr268.

Mather, M., Cacioppo, J. T., & Kanwisher, N. (2013). How fMRI can inform cognitive theories. *Perspectives on Psychological Science*, *8*(1), 108–113. https://doi.org/10.1177/1745691612469037.

McNamara, Q., De La Vega, A., & Yarkoni, T. (2017, August). *Developing a comprehensive framework for multimodal feature extraction*. Proceedings of the 23rd ACM SIGKDD International Conference on Knowledge Discovery and Data Mining, Halifax, Nova Scotia – Canada. pp. 1567–1574. https://doi.org/10.1145/3097983.3098075

Merton, R. K. (1987). Three fragments from a sociologist's notebooks: Establishing the phenomenon, specified ignorance, and strategic research materials. *Annual Review of Sociology*, *13*(1), 1–29. https://doi.org/10.1146/annurev.so.13.080187.000245.

Miller, L. C., Shaikh, S. J., Jeong, D. C., Wang, L., Gillig, T. K., Godoy, C. G., Appleby, P. R., Corsbie-Massay, C. L., Marsella, S., Christensen, J. L., & Read, S. J. (2019). Causal inference in generalizable environments: Systematic representative design. *Psychological Inquiry*, *30*(4), 173–202. https://doi.org/10.1080/1047840X.2019.1693866.

Mobbs, D., Greicius, M. D., Abdel-Azim, E., Menon, V., & Reiss, A. L. (2003). Humor modulates the mesolimbic reward centers. *Neuron*, *40*(5), 1041–1048. https://doi.org/10.1016/S0896-6273(03)00751-7.

Moerel, M., De Martino, F., & Formisano, E. (2014). An anatomical and functional topography of human auditory cortical areas. *Frontiers in Neuroscience*, *8*, 225. https://doi.org/10.3389/fnins.2014.00225.

Nastase, S. A., Liu, Y. F., Hillman, H., Zadbood, A., Hasenfratz, L., Keshavarzian, N., Chen, J., Honey, C. J., Yeshurun, Y., Regev, M., & Husson, U. (2019). Narratives: fMRI data for evaluating models of naturalistic language comprehension. *OpenNeuro*. https://doi.org/10.18112/openneuro.ds002345.v1.1.4.

O'Donnell, M. B., Falk, E. B., & Lieberman, M. D. (2015). Social in, social out: How the brain responds to social language with more social language. *Communication Monographs*, *82*(1), 31–63. https://doi.org/10.1080/03637751.2014.990472.

Pauli, W. M., Nili, A. N., & Tyszka, J. M. (2018). A high-resolution probabilistic in vivo atlas of human subcortical brain nuclei. *Scientific Data*, *5*(1), 180063. https://doi.org/10.1038/sdata.2018.63.

Pei, R., Schmälzle, R., Kranzler, E. C., O'Donnell, M. B., & Falk, E. B. (2019). Adolescents' neural response to tobacco prevention messages and sharing engagement. *American Journal of Preventive Medicine*, *56*(2S1), S40–S48. https://doi.org/10.1016/j.amepre.2018.07.044.

Ringach, D., & Shapley, R. (2010). Reverse correlation in neurophysiology. *Cognitive Science*, *28*(2), 147–166. https://doi.org/10.1207/s15516709cog2802_2.

Sabatinelli, D., Lang, P. J., Bradley, M. M., Costa, V. D., & Keil, A. (2009). The timing of emotional discrimination in human amygdala and ventral visual cortex. *Journal of Neuroscience*, *29*(47), 14864–14868. https://doi.org/10.1523/JNEUROSCI.3278-09.2009.

Salgado, S., & Kaplitt, M. G. (2015). The nucleus accumbens: A comprehensive review. *Stereotactic and Functional Neurosurgery*, *93*(2), 75–93. https://doi.org/10.1159/000368279.

Salimpoor, V. N., van den Bosch, I., Kovacevic, N., McIntosh, A. R., Dagher, A., & Zatorre, R. J. (2013). Interactions between the nucleus accumbens and auditory cortices predict music reward value. *Science*, *340*(6129), 216–219. https://doi.org/10.1126/science.1231059.

Schank, R. C. (1979). Interestingness: Controlling inferences. *Artificial Intelligence*, *12*(3), 273–297. https://doi.org/10.1016/0004-3702(79)90009-2.

Schank, R. C. (1995). *Tell me a story: Narrative and intelligence*. Northwestern University Press.

Schmälzle, R., Brook O'Donnell, M., Garcia, J. O., Cascio, C. N., Bayer, J., Bassett, D. S., Vettel, J. M., & Falk, E. B. (2017). Brain connectivity dynamics during social interaction reflect social network structure. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(20), 5153–5158. https://doi.org/10.1073/pnas.1616130114.

Schmälzle, R., Cooper, N., O'Donnel, M., Tompson, S., Lee, S., Cantrell, J., Vettel, J., & Falk, E. (2020). The effectiveness of online messages for promoting smoking cessation resources: Predicting nationwide campaign effects from neural responses in the EX campaign. *Frontiers in Human Neuroscience*, *14*, 381. https://doi.org/10.3389/fnhum.2020.565772.

Schmälzle, R., Häcker, F., Honey Christopher, J., & Hasson, U. (2015). Engaged listeners: Shared neural processing of powerful political speeches. *Social, Cognitive, and Affective Neurosciences*, *1*, 168–169. https://doi.org/10.1093/scan/nsu168

Schmälzle, R., & Meshi, D. (2020). Communication neuroscience: Theory, methodology and experimental approaches. *Communication Methods and Measures*, *14*(2), 105–124. https://doi.org/10.1080/19312458.2019.1708283.

Schramm, W. (1971). The nature of communication between humans. In D. R. Wilbur Schramm (Ed.), *The process and effects of mass communication*. University of Illinois Press.

Schurz, M., Radua, J., Aichhorn, M., Richlan, F., & Perner, J. (2014). Fractionating theory of mind: A meta-analysis of functional brain imaging studies. *Neuroscience and Biobehavioral Reviews*, *42*, 9–34. https://doi.org/10.1016/j.neubiorev.2014.01.009.

Schurz, M., Tholen, M. G., Perner, J., Mars, R. B., & Sallet, J. (2017). Specifying the brain anatomy underlying temporo-parietal junction activations for theory of mind: A review using probabilistic atlases from different imaging modalities. *Human Brain Mapping*, *38*(9), 4788–4805. https://doi.org/10.1002/hbm.23675.

Shen, X., Tokoglu, F., Papademetris, X., & Constable, R. T. (2013). Groupwise whole-brain parcellation from resting-state fMRI data for network node identification. *NeuroImage*, *82*, 403–415. https://doi.org/10.1016/j.neuroimage.2013.05.081.

Stein, N. L. (1982). The definition of a story. *Journal of Pragmatics*, *6*(5–6), 487–507. https://doi.org/10.1016/0378-2166(82)90022-4.

Tamborini, R., Grady, S. M., Baldwin, J., McClaran, N., & Lewis, R. (2021). The narrative enjoyment and appreciation rationale. *The Oxford Handbook of Entertainment Theory*, https://doi.og/10.1093/oxfordhb/9780190072216.013.3.

Van Overwalle, F. (2009). Social cognition and the brain: A meta-analysis. *Human Brain Mapping*, *30*(3), 829–858. https://doi.org/10.1002/hbm.20547.

Wagner, D. D., Kelley, W. M., Haxby, J. V., & Heatherton, T. F. (2016). The dorsal medial prefrontal cortex responds preferentially to social interactions during natural viewing. *Journal of Neuroscience*, *36*(26), 6917–6925. https://doi.org/10.1523/JNEUROSCI.4220-15.2016.

Watson, N. V., & Breedlove, S. M. (2012). *The mind's machine: Foundations of brain and behavior*. Sinauer Associates.

Weber, R., Huskey, R., Mangus, J. M., Westcott-Baker, A., & Turner, B. O. (2015). Neural predictors of message effectiveness during counterarguing in antidrug campaigns. *Communication Monographs*, *82*(1), 4–30. https://doi.org/10.1080/03637751.2014.971414.

Wehbe, L., Murphy, B., Talukdar, P., Fyshe, A., Ramdas, A., & Mitchell, T. (2014). Simultaneously uncovering the patterns of brain regions involved in different story reading subprocesses. *PloS One*, *9*(11), e112575. https://doi.org/10.1371/journal.pone.0112575.

Wilcox, S., Dorrance Hall, E., Holmstrom, A. J., & Schmälzle, R. (2020). The emerging Frontier of interpersonal communication and neuroscience: Scanning the social synapse. *Annals of the International Communication Association*, https://doi.org/10.1080/23808985.2020.1843366..

Willems, R. M., Nastase, S. A., & Milivojevic, B. (2020). Narratives for neuroscience. *Trends in Neurosciences*, *43*(5), 271–273. https://doi.org/10.1016/j.tins.2020.03.003.

Yarkoni, T., Poldrack, R. A., Nichols, T. E., Van Essen, D. C., & Wager, T. D. (2011). Large-scale automated synthesis of human functional neuroimaging data. *Nature Methods*, *8*(8), 665–670. https://doi.org/10.1038/nmeth.1635.

Yeshurun, Y., Nguyen, M., & Hasson, U. (2021). The default mode network: Were the idiosyncratic self meets the shared social world. *Nature Reviews Neuroscience*, *22*(3), 181–192. https://doi.org/10.1038/s41583-020-00420-w.

Zillman, D., & Cantor, J. R. (1977). Affective responses to the emotions of a protagonist. *Journal of Experimental Social Psychology*, *13*(2), 155–165. https://doi.org/10.1016/S0022-1031(77)80008-5