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Processing Narratives Concerning Protected Values: A Cross-Cultural Investigation of Neural Correlates

Jonas T. Kaplan^{1,2}, Sarah I. Gimbel¹, Morteza Dehghani^{1,2,3},
Mary Helen Immordino-Yang^{1,5}, Kenji Sagae^{3,4}, Jennifer D. Wong¹,
Christine M. Tipper¹, Hanna Damasio^{1,2}, Andrew S. Gordon^{3,4}
and Antonio Damasio^{1,2}

¹Brain and Creativity Institute, ²Department of Psychology, ³Department of Computer Science, ⁴Institute for Creative Technologies and ⁵Rossier School of Education, University of Southern California, Los Angeles, CA, USA

Address correspondence to Jonas T. Kaplan, Brain and Creativity Institute, University of Southern California, Los Angeles, CA, USA. Email: jtkaplan@usc.edu

Abstract

Narratives are an important component of culture and play a central role in transmitting social values. Little is known, however, about how the brain of a listener/reader processes narratives. A receiver's response to narration is influenced by the narrator's framing and appeal to values. Narratives that appeal to "protected values," including core personal, national, or religious values, may be particularly effective at influencing receivers. Protected values resist compromise and are tied with identity, affective value, moral decision-making, and other aspects of social cognition. Here, we investigated the neural mechanisms underlying reactions to protected values in narratives. During fMRI scanning, we presented 78 American, Chinese, and Iranian participants with real-life stories distilled from a corpus of over 20 million weblogs. Reading these stories engaged the posterior medial, medial prefrontal, and temporo-parietal cortices. When participants believed that the protagonist was appealing to a protected value, signal in these regions was increased compared with when no protected value was perceived, possibly reflecting the intensive and iterative search required to process this material. The effect strength also varied across groups, potentially reflecting cultural differences in the degree of concern for protected values.

Key words: default mode network, fMRI, narrative, protected values

Introduction

Narratives play a central role in human psychology (Bruner 2002). Stories organize our experiences and memories, imbue events with meaning, and share values and ideas. The ancient practice of storytelling is both uniquely human and universal. Although narratives are instrumental in human culture (Miller et al. 2007), little is known about the neural machinery that supports their processing. Reading or hearing stories involve a multitude of mental components including memory, imagination, emotion, abstract inference, and social knowledge. It also requires coordination among the systems that support these components to arrive at an understanding of the depicted events, themes, characters, and their relationships (Gerrig 1993; Oatley 1999; Gerrig and Egidi 2003).

Stories are particularly important, because they are often used to capture and express moral values (Nelson 2003; Mar and Oatley 2008). The association of stories with moral values is so close that the word "moral" often refers to the meaning of a story, as in "the moral of the story." Reading stories with moral content also affects subsequent moral decision-making (Prasad 2007; Dehghani, Gentner, et al. 2009). Of particular interest are personal narratives, stories that we use to conceptualize the episodes of our lives and which form the basis of our autobiographical selves. In using stories to explain our histories, we weave moral values directly into our identity.

Recent research has revealed that values that are closely tied to core personal, national, and cultural identities take on a special cognitive status. Known as "protected" or "sacred" values,

these values are non-negotiable and transcend the cost-benefit logic of rational choice models (Baron and Spranca 1997; Tetlock 2003; Atran and Ginges 2012). Recent research has shown that protected values play an important role in sustaining intractable political and cultural conflicts by impeding intergroup negotiations (Atran et al. 2007; Dehghani et al. 2010; Atran and Ginges 2012). Examples include sovereignty over Jerusalem, Gaza, and the West Bank (Ginges et al. 2007; Rozin and Wolf 2008), conflict over the Babri Mosque in India (Sachdeva et al. 2009), and the Iranian nuclear dispute (Dehghani, Iliev, et al. 2009; Dehghani et al. 2010). Protected values are often historically embedded in one's culture, but the targeted use of sacred rhetoric in narratives (Marietta 2008; Dehghani et al. 2010) can facilitate beliefs achieving protected status (Marietta 2009). Narratives are thus a centrally important vehicle for the creation and transmission of protected values.

While there has been much recent interest in the neural systems that underlie moral cognition (Anderson et al. 1999; Greene et al. 2001; Heekeren et al. 2003; Koenigs et al. 2007), there has been little work aimed specifically at understanding the brain's processing of naturally occurring narratives, especially with embedded moral and protected values. Berns et al. (2012) conducted one of the few studies that directly investigated the neural foundation of protected values. They found that reading statements about protected values (defined as values that participants refused to abandon at any cost) led to increased engagement of the left temporo-parietal junction and ventrolateral prefrontal cortices, which they interpreted as related to semantic rule retrieval, since protected values invoke fixed principles rather than calculations of costs and benefits. Other work has established the involvement of emotional brain systems when people react to tradeoffs involving protected values; Duc et al. (2013) found increased activity in amygdala nuclei and anterior temporal cortices when participants confronted "taboo" tradeoffs that involved violating protected values in favor of mundane values. These early findings are important, but they do not speak to some critical aspects of protected values: that they are distilled in the context of personal or cultural narratives and tied to our core identities.

In the present study, we aimed to understand how the brain processes personal narratives that the individual perceives to have embedded protected values. Striving for ecological validity, we used methods from computer science and computational linguistics to gather millions of real-world personal narratives written by people describing their experiences on Internet weblogs. In the current digital world, people are engaged more than ever in generating, sharing, and reading personal narratives. Advances in computer science allowed us to harvest this rich source of data to study the real-world process of understanding narratives. From a set of 20 million Internet weblog posts, we identified stories in which the author appealed to protected values and presented these stories to readers inside the fMRI scanner. In these stories, people not only describe events that happen to them, but they frame the events by invoking the values that motivated their choices. Given the complex interaction between narratives, moral values, culture, and identity, we expected that the neurocognitive processes of responding to these stories would differ across people with varied personal and cultural backgrounds. Accordingly, we translated our stories into Chinese and Farsi, and tested American, Chinese, and Iranian subjects living in the Los Angeles area, all reading these stories in their native language. Our aim was to understand how the neural systems engaged by narrative processing and moral cognitive processes might differ depending on how the reader reacted to the values in the story,

and how these reactions might differ depending on the culture of the readers. Specifically, we were looking for brain activity that related to whether the reader perceived the protagonist of the story as being motivated by a protected value. We predicted that reading stories would engage brain networks involved in integrating processes of recall, imagination, and the evocation of emotions and feelings, including cortical midline structures such as the precuneus, posterior cingulate (collectively, the posterior medial cortices or PMC), and the medial prefrontal cortex (MPFC). These are structures known to be engaged in social and moral cognition (Greene et al. 2001; Greene 2009; Mars et al. 2012; Yoder and Decety 2014; Hyatt et al. 2015; Koelsch et al. 2015; Spunt et al. 2015; van Bavel et al. 2015), autobiography (Araujo et al. 2014), and in general, self-related processes (Northoff and Berman 2004), making them good candidates for responding to the complex protected values embedded within our personal narratives. These brain regions, along with regions in the lateral inferior parietal cortices, are unique in that they are widely linked via long-range connections with association cortices elsewhere in the brain (Parvizi et al. 2006; Hagmann et al. 2008), placing them in an ideal position to interrelate processes of perception, imagination, and emotions/feelings in order to process complex ideas, such as those that are central to cultural values.

Materials and Methods

Participants

Ninety-five healthy participants with no history of psychological or neurological disorders were recruited from the University of Southern California community and the surrounding Los Angeles Area. Five American participants, 6 Chinese participants, and 6 Iranian participants were excluded for excessive motion, insufficient responses, or to match for age and gender between the 3 groups. This left 26 American participants (mean age: 24.61 ± 0.97 , 13 male), 26 Chinese participants (mean age: 23.92 ± 0.36 , 13 male), and 26 Iranian participants (mean age: 26.00 ± 0.53 , 15 male). Subjects were paid \$20 per hour for their participation and gave informed consent approved by the Institutional Review Board of the University of Southern California. All American participants were born in the United States of America and were native English speakers who grew up in exclusively English-speaking households. All Chinese and Iranian participants were born and raised in their native country, and had been in the United States of America for fewer than 5 years. Chinese and Iranian participants were all fluent in English in addition to their native languages.

Stimuli—Story Selection

As described in Sagae et al. (2013), a corpus of over 20 million weblog story posts aggregated from the internet (via Spinn3r.com) was used as the base for our story search. The corpus was queried via a text retrieval engine (Apache Lucene) for stories of questionable behavior (e.g., cheating on a spouse, having an abortion, crossing a picket line, or getting into a physical fight), expecting that bloggers who write about this kind of behavior might justify their actions by relying on moral and protected values. Each topic was queried by writing a paragraph-sized fictional prototype that retrieved similar blog posts, then each retrieved post was annotated as to its relevance; this information was fed back into the search algorithm (Rocchio 1971). Using this approach, 460 posts were identified that contained narratives of socially questionable

behavior. From these, 100 posts were condensed into paragraphs ranging from 145 to 155 words, and were behaviorally piloted in 208 University of Southern California undergraduate students (mean age: 20.94 ± 3.51 years, 63 male). Each story was then assessed based on the responses given by the participants about evocativeness, protected nature of the value to the protagonist, and protected nature of the value to the participant himself. Forty narratives were selected to be the most highly evocative in each of the protected value categories and spanning all 5 moral foundation categories (Graham et al. 2011). The 40 stories were used as the stimuli for the fMRI experiment. These 40 stories and all accompanying materials for the fMRI sessions were translated into Mandarin Chinese and Farsi by professional translators and back-translated to English and checked for their match to the original English stimuli.

Stimuli—Story Annotation

Three raters read the stories and rated them for subjective versus objective language content. The details of the annotation process are provided in [Supplementary Material](#).

fMRI Experiment

In preparation for the study, participants filled out a survey of demographic information, a Protected Values Questionnaire (PVQ) based on that used by Berns et al. (2012), the Moral Foundations Questionnaire (Graham et al. 2011), the handedness questionnaire (Oldfield 1971), and the Interpersonal Reactivity Index questionnaire (Davis 1983). All questionnaires were completed in the participant's native language (English, Mandarin, or Farsi). Upon arrival for the scan, participants read study instructions in their native language and were given the opportunity to ask questions to the experimenter. Following the pre-scan session, participants underwent blood-oxygenation level-dependent (BOLD) fMRI. For each participant, there were 5 story-reading scans (556 s), 1 resting-state scan (360 s), and 1 additional task run not presented here. During the story scans, each story was preceded by a context slide (2 s) identifying the protagonist of the story (e.g., American Mother). Following a 1.5-s delay, the story was presented, divided into 3 screens each displayed for 12 s. After a variable delay (1.25–4.75 s), a question appeared asking the participant to decide whether the protagonist would change his or her action for any amount of money (see [Supplementary Fig. 1](#)). This question was specifically tailored to the content of each story, for example, "Do you think this nurse would accept any amount of money to refrain from crossing the picket line?" The participant indicated his or her response via a button press on an MRI-compatible button box held in the right hand. Later, outside the scanner, participants saw each story again, and answered 4 questions about the story (How strongly did you react to this story? Would the protagonist accept any amount of money to change their action? In this scenario, would you do the same thing as the protagonist? Would you change your position on what to do in this scenario for any amount of money?).

fMRI Parameters

Imaging was performed using a 3-T Siemens MAGNETOM Trio System with a 12-channel matrix head coil at the Dana and David Dornsife Neuroscience Institute at the University of Southern California. Functional images were acquired using a gradient-echo, echo-planar, T_2^* -weighted pulse sequence (TR = 2000 ms, one shot per repetition, TE = 25 ms, flip angle = 90° , 64×64

matrix). Forty slices covering the entire brain were acquired with a voxel resolution of $3.0 \times 3.0 \times 3.0$ mm with no interslice gap. Functional data were continuously acquired for each run, with a short break between runs. A T_1 -weighted high-resolution ($1 \times 1 \times 1$ mm) image was acquired using a three-dimensional magnetization-prepared rapid acquisition gradient (MP-RAGE) sequence (TR = 2530 ms, TE = 3.09 ms, flip angle = 10° , 256×256 matrix). Two hundred and eight coronal slices covering the entire brain were acquired with a voxel resolution of $1 \times 1 \times 1$ mm. We also collected a T_2 -weighted anatomical scan (TR = 10 000 ms, TE = 88 ms, flip angle = 120° , 256×256 matrix) with 40 transverse slices with a voxel resolution of $0.82 \times 0.82 \times 3.5$ mm. Total scan time for each participant was approximately 80 min.

fMRI Data Analysis

Data were analyzed using a combination of FSL (FMRIB's Software Library; <http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/>) and custom tools developed at the Dornsife Neuroimaging Institute. Data were pre-processed using standard steps: motion correction (Jenkinson et al. 2002), 8-mm FWHM spatial smoothing, high-pass temporal filtering using Gaussian-weighted least-squares straight line fitting with a sigma of 60 s (corresponding to a period of 120 s), and slice-timing correction. Data were also corrected for magnetic field inhomogeneities using field maps acquired for each subject. Each component of the task (context, story screen 1, story screen 2, story screen 3, and the question) was modeled by convolving the task design with a double-gamma hemodynamic response function. The temporal derivative of each task regressor and 6 motion correction parameters were also included in the design.

We used FLIRT to register the functional data to the atlas space in 2 stages (Jenkinson and Smith 2001; Jenkinson et al. 2002). First, functional images were aligned with the T_1 -weighted MP-RAGE using a 6 degrees of freedom rigid-body warp. Next, the MP-RAGE was registered to the standard MNI atlas with a 12 degrees of freedom affine transformation, and then this transformation was refined using FNIRT nonlinear registration (Andersson et al. 2007a, 2007b).

Data were then analyzed within the general linear model using a multilevel mixed-effects design. At the individual subject level, statistical maps were generated for each functional scan. These were then combined into individual participant-level maps in a fixed-effects analysis across each subject's 5 scans. In the event that one scan did not contain more than a single trial of a given type, that run was excluded from the analysis. This resulted in 14% of the runs excluded from the final analysis. Subject-level maps were then entered into a higher-level group analysis to examine group-level effects. We computed 3 main contrasts at the whole-brain level: (1) Reading stories versus resting baseline, (2) reading stories versus answering questions, and (3) reading stories perceived as appealing to protected values versus reading stories not perceived as appealing to protected values. Statistical thresholding was performed using FSL's cluster correction algorithm to correct for multiple comparisons. This algorithm estimates the probability of clusters of a given size using Gaussian Random Field theory. We used an initial threshold of $Z = 2.3$ and a cluster size probability threshold of $P < 0.05$.

Due to our a priori hypotheses about the involvement of the PMC, MPFC, and inferior parietal lobes, we analyzed resting-state data with the goal of generating regions of interest to then apply to analyses of the narrative data. Resting-state data were analyzed using a seed-based correlation approach similar to

the one used by Biswal et al. (2010). First, raw data were motion-corrected and temporally filtered using a band-pass temporal filter with a high-pass cutoff of 0.01 Hz and a low-pass cutoff of 0.1 Hz and spatially smoothed with an 8-mm Gaussian kernel. Next, mean white matter and CSF signals across time were calculated by segmenting the T_1 volume with FSL's FAST segmentation tool and transforming the resulting tissue masks into the functional space. Motion parameters, CSF signal, and white matter signal were regressed out of the resting-state data and subsequent analysis was performed in the residuals. The time course of a seed region in the precuneus was extracted using a 7.5-mm sphere around the coordinates $(-5, -49, 40)$ from Fox et al. (2005). We then used FEAT to generate individual subject-level maps of correlation with the seed region, and combined these maps in a higher-level mixed-effects GLM. For each node of the default mode network [PMC, MPFC, and left and right temporo-parietal junction (TPJ)], we defined a sphere with radius 8 mm centered around the maximum coordinate from the group-level resting-state maps. We then performed analyses on the story-related data by extracting parameter estimates from these 4 regions and performing statistical tests on the resulting values.

Post-Scan Questionnaire

After exiting the scanner, each participant completed a post-scan questionnaire in which they saw the 40 stories again, and answered 4 questions about each story. The exact text of the questions is provided in [Supplementary Material](#). Briefly, participants were asked how strong their emotional reaction to the story was, whether they would have performed the same action as the protagonist, and how important the value was to them and to the protagonist.

Results

Behavioral results, including responses inside the scanner and responses to questionnaires, are described in [Supplementary Material](#).

Neuroimaging Results

Reading Stories and Answering Questions

Relative to resting baseline, when reading stories there was increased BOLD signal in a widespread network of regions including the PMC, ventromedial prefrontal cortex, temporal poles, superior temporal sulcus, inferior frontal gyrus, basal ganglia, amygdala, hippocampus, thalamus, midbrain, pons, cerebellum, and occipital lobe (see [Supplementary Fig. 2](#)). Signal decreased, compared with resting baseline, in the insula, cingulate gyrus, inferior parietal lobule, and lateral orbitofrontal cortex (not pictured). Cultural differences were noted in medial and lateral occipital cortices, probably related to the fact that the groups read the stories in different languages with different orthographies: Americans showed greater signal compared with Chinese and Iranians in medial occipital cortex, whereas Chinese showed greater signal compared with Americans in lateral occipital cortex.

A comparison of reading the stories to answering the questions about the stories revealed differential brain networks involved in these 2 tasks (see [Supplementary Fig. 3](#)). While answering questions about the stories (questions minus stories contrast), there was a greater BOLD signal covering much of the cerebral cortex (except for MPFC). There was a greater signal for reading stories compared with answering questions in the MPFC, hippocampus, parahippocampal gyrus, superior temporal gyrus, and occipital lobe. During the question period, there were

regions of greater activity when participants responded that the story did not contain a protected value compared with when they responded that the story did contain a protected value (see [Supplementary Fig. 4](#)).

Protected Values

While reading stories that were later judged by the participant as containing protected values (compared with stories that were judged by the participant as not containing protected values), there was increased signal in PMC, bilateral temporo-parietal junction, MPFC, and anterior temporal lobe (Fig. 1). Separate analysis of each of the 3 story segments showed that this pattern of activation was most pronounced during the third segment of the story. Whole-brain analysis showed no significant cultural differences among the 3 subject groups for this contrast.

To analyze how activity changed in these structures over time, we used a region-of-interest approach to extract signal from 4 regions during the 3 story segments (PMC, left TPJ, right TPJ, and MPFC). To avoid circularity, we used an independent dataset to define the regions of interest. Since our a priori regions form a network that shows coordinated fluctuations at rest, these regions can be identified by a functional connectivity analysis on resting-state data. The regions of interest were defined as 8 mm spheres around the peak coordinates from a functional connectivity analysis of the resting-state scans, using the precuneus as a seed region (see Materials and Methods). Beta values during the 3 parts of the story were extracted for stories judged as containing protected values and stories judged as containing mundane values, and were converted to percent signal change. We then analyzed these data using a repeated-measures ANOVA with 2 within-subject variables (value type and story segment) and 1 between-subject variable (cultural group).

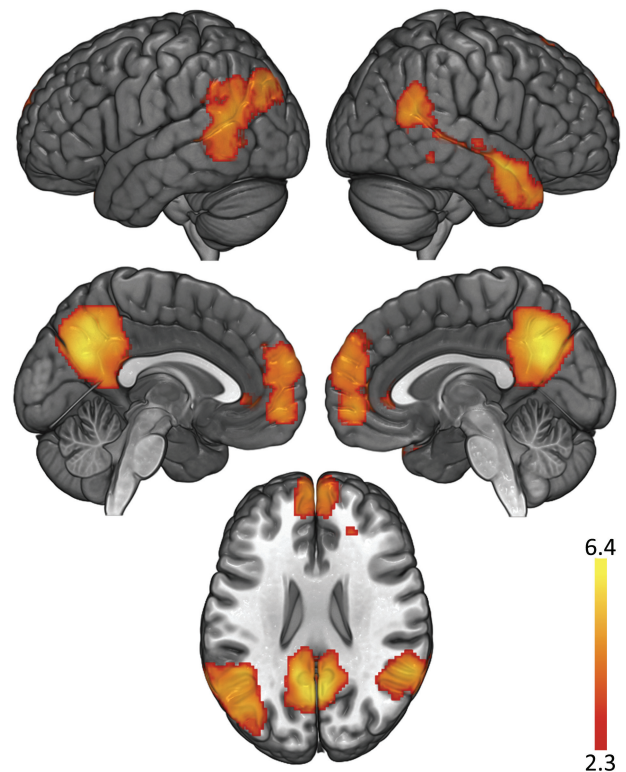


Figure 1. Greater BOLD activity in the default mode network during the third part of the story when participants perceive an appeal to protected values compared with when they do not perceive an appeal to protected values.

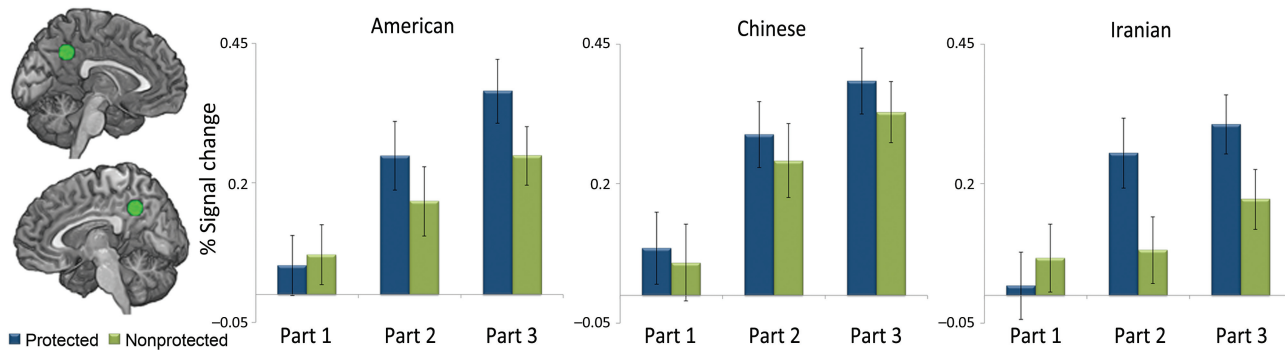


Figure 2. PMC activity increases over time as participants read stories.

In the PMC, there was a main effect of story segment ($F_{2,74} = 29.971$, $P = 2.92 \times 10^{-10}$), with signal increasing from the beginning to the end of the story. There was also a main effect of value type of the story ($F_{1,75} = 8.277$, $P = 0.005$) reflecting greater signal for stories that the subject identified as containing protected values. Additionally, there was an interaction between story segment and value type ($F_{2,74} = 11.514$, $P < 0.00005$). Visual inspection suggests that differences due to the value type were largest in the third segment of the story and were not present in the first. There was also a three-way interaction between story segment, value type, and culture ($F_{4,150} = 4.189$, $P = 0.018$; Fig. 2).

In the left TPJ, there were main effects of story segment ($F_{2,74} = 35.173$, $P = 1.83 \times 10^{-11}$) and value type ($F_{1,75} = 9.362$, $P = 0.003$), again with signal increasing from the beginning to the end of the story and greater signal for stories that the subject identified as containing protected values. Like in the PMC, there was an interaction between story segment and value type ($F_{2,74} = 3.197$, $P = 0.047$), and additionally there was an interaction between story segment and culture ($F_{4,150} = 3.878$, $P = 0.005$). There was also a three-way interaction between story segment, value type, and culture ($F_{4,150} = 4.948$, $P = 0.001$; see [Supplementary Fig. 5B](#)).

As in the PMC and left TPJ, in the right TPJ, there was a main effect of story segment ($F_{2,74} = 34.796$, $P = 2.23 \times 10^{-11}$), with signal increasing from the beginning to the end of the story. Additionally, there was an interaction between story segment and value type ($F_{2,74} = 10.130$, $P < 0.0005$; see [Supplementary Fig. 5C](#)). There was no three-way interaction ($F_{4,150} = 1.920$, $P = 0.110$). The MPFC also showed an interaction between story segment and value type ($F_{2,74} = 9.330$, $P < 0.0005$), and additionally showed an interaction between story segment and culture ($F_{4,150} = 2.860$, $P = 0.025$; see [Supplementary Fig. 5D](#)), but no three-way interaction ($F_{4,150} = 1.421$, $P = 0.230$).

We next analyzed the BOLD signal during the question-answering period as a function of the participants' responses. When participants answered that the story did not involve a protected value (i.e., they indicated that the protagonist would accept money to change their action), there was increased signal in the MPFC, orbitofrontal cortex, anterior insula, right caudate, right lateral occipital cortex, and left cerebellum. However, we also found that participants took significantly longer to answer that the story did not contain protected values.

Discussion

Neural Systems for Processing Narratives

In this study, participants inside the fMRI scanner read a series of short personal narratives culled from a large collection of

Internet weblogs, a feature that makes our study unique in its ecological validity. The stories read inside the scanner described real events and were written by the people who experienced them. We did not predetermine how the values in the stories should be interpreted by the participants; rather, we analyzed our data based on how each individual participant reported perceiving the values of the protagonist. After each story, participants indicated whether or not they thought that the protagonist could be paid any amount of money to make a choice different than the one they had made in the story, which was a measure of whether the participant thought that the protagonist held a protected value. When participants indicated that the values in the story were non-negotiable (i.e., protected), we found that activation in the PMC, MPFC, the inferior parietal lobes around the TPJ, and the anterior temporal lobes was increased relative to stories in which protected values were not attributed to the protagonist. The ensemble of these regions forms what is often called the default mode network ([Raichle et al. 2001](#); [Raichle and Snyder 2007](#); [Buckner et al. 2008](#)). In addition to showing greater signal for stories with protected values, all of the nodes mentioned showed significant increases in activity during story-reading compared with resting baseline. Furthermore, engagement of the network grew from the beginning of the story to the end of the story, as the story unfolded and the participant should be able to reach a more complete understanding.

While in the past this network has been conceived of as a "resting" network, since it shows high levels of activity during undirected rest conditions, lately it has been implicated in a range of active cognitive tasks ([Immordino-Yang et al. 2012](#); [Spreng 2012](#)). In attempting to characterize the kind of psychological operations that appear to engage this network, researchers have described them as related to social cognition ([Mars et al. 2012](#)), internally directed processing ([Immordino-Yang et al. 2012](#)), mental time travel ([Ostby et al. 2012](#)), or self-related processing ([Qin and Northoff 2011](#)). Interestingly, all of these operations are either involved in the processing of narratives or rely on a narrative organization of information. For example, the majority of studies that have shown cortical midline activations for self-related processing have focused on aspects of the autobiographical self such as personality trait judgment, rather than transient present-moment aspects of the self ([Northoff et al. 2006](#)). The autobiographical self is, in essence, a process of generating fragmentary narratives of our personal lives built from a multitude of recorded experiences ([Damasio 1998](#)). These same midline structures are activated just as much or more when we think about the biographies of other people ([Araujo et al. 2013, 2014](#)), suggesting that the processing of narratives may be more important for activating these structures than self-relatedness.

The role of this network in social cognition is also relevant to story comprehension, which involves both understanding the intentions and motivations of the characters and empathizing with them. Mar and Oatley (2008) have argued that one of the primary purposes of fiction is to provide models of the social world to facilitate social understanding. As such, many studies aimed at investigating the neural basis for understanding other people's mental states have used short stories as stimuli, and these studies tend to find activations in similar brain structures (2011). However, in our study, the differential activity in this network for stories that are perceived to contain protected values does not appear to be explained by differences in story content relating to theory of mind. Each participant rated a different set of stories as containing protected values, so the contrast between protected and nonprotected stories does not compare one specific set of stories to another; rather, it is a comparison based on each participant's perception of the values in the stories. Furthermore, an analysis of the stories that were most often rated as containing protected values did not show an increased amount of subjective content describing the private mental states of the characters in those stories.

A growing body of work on language comprehension points to the same network being involved in aspects of comprehending text, specifically in inferring coherent meaning from context. Ferstl and von Cramon (2001) created pairs of sentences that either created a coherent "microstory" or were unrelated to each other. Reading the coherent pairs led to increased activation in MPFC and in posterior medial regions around the inferior precuneus. The MPFC responds more to coherent versus incoherent sentence pairs even when the sentences refer only to inanimate objects and thus have no theory of mind content (Ferstl and von Cramon 2002). Its activity also varies parametrically with the degree of sentence relatedness (Sieborger et al. 2007). A meta-analysis of studies that compare processing of coherent and incoherent language found activation in the MPFC, PMC, the posterior superior temporal sulcus, and the anterior temporal lobes (Ferstl et al. 2008). These data suggest that these regions are important for building a higher level of meaning that depends on context and extends beyond the information in individual sentences. Further support for this view comes from a study in which stories were scrambled at varied levels of temporal specificity. Lerner et al. (2011) played subjects a spoken story that was scrambled at the level of words, sentences, or paragraphs, and measured intersubject correlations in the timecourse of each voxel. The intersubject correlation technique identifies brain activity that is common across individuals while they listen to the stimuli and therefore must be driven by processing of the stimulus. Intersubject correlations in the precuneus and MPFC were absent when meaning was scrambled at the level of words or sentences, but began to appear with paragraph or story-level coherence, confirming the involvement of these structures in comprehending coherent global meaning. The same intersubject correlation technique has shown that some network nodes (PMC, MPFC, and inferior parietal lobes) are correlated across subjects during an audio or audiovisual narrative (Wilson et al. 2008). A recent study also found shared intersubject correlations across time-locked spoken and written versions of the same narrative (Regev et al. 2013). In other words, this network responded not to specific sensory events, which were different in auditory and visual version of the story, but instead to the abstract meaning of the narrative, which was the same across both versions. In our own data, we saw that activity in this network increased as participants read through the stages of the story, with the highest activity occurring in the final segment of the story when the

actions of the protagonist tended to be integrated and the participant could build coherent meaning.

The anatomy of this network is ideal for it to function as a high-level coordinator of information across sensory, motor, and memory domains in order to generate coherent meaning. The PMC and the lateral inferior parietal cortices are highly interconnected with the rest of the brain, acting as hubs in the brain's densely interconnected network structure (Hagmann et al. 2008; van den Heuvel and Sporns 2013). The PMC, in particular, is connected bi-directionally to association cortices throughout the brain as well as to subcortical structures (Parvizi et al. 2006). The ability to coordinate the activity of distant brain regions is likely to be central to the cognitive capacity for integrating information (Shanahan 2012), a process essential to the understanding of stories and of the deep culturally situated values they hold. The complex emotions evoked by stories likely require coordination of multiple brain systems involved in different aspects of affective processing (Koelsch et al. 2015). Importantly, the architecture of the brain is one in which information flows in multiple directions, converging as it flows from low-level sensory cortices up to increasingly more integrative association cortices, but also diverging as information and influence flows from the top of the hierarchy back to lower-level regions (Damasio 1989; Meyer and Damasio 2009; Man et al. 2013). In this view, there is a multilevel hierarchy of "convergence-divergence zones" (CDZs), at the bottom of which are mapped sensory cortices that represent specific sensory features. These sensory features are fed up the hierarchy to CDZs that register the associations among them, and through top-down connections this circuitry can reinstantiate the lower-level patterns, as during mental imagery or memory (Stokes et al. 2009; Meyer et al. 2010; Reddy et al. 2010; Man et al. 2012; Johnson and Johnson 2014). At the highest level of the hierarchy are CDZs that combine signals across sensory domains and thus represent the highest levels of abstraction and semantic integration. Thus, in conceptualizing the network as a network of interconnected high-level CDZs, we note that these brain regions would not simply be collecting incoming information from other parts of the brain, but instead are likely to be coordinators of lower-level CDZs that represent and can reinstantiate disparate aspects of the information contained in a story. In the context of comprehending a story, we would expect the network to be involved in orchestrating the activation of various brain regions. For example, the network may stimulate association cortices that represent abstract concepts, in turn activating mental images in various early sensory cortices. It may also evoke related feeling states from subcortical brain regions that represent the internal state of the body, and connect to brain networks that participate in the recall of associated memories and knowledge.

The Role of Protected Values

Our stories described protagonists who performed morally questionable acts and justified those acts by appealing to deeply held values. In some cases, the participants indicated that they perceived these values as protected values for the protagonist in the story. When reading those particular stories, participants in all 3 cultural groups showed increased fMRI signal in the nodes of a specific and consistent network compared with when they were reading stories where they did not perceive the protagonist to be acting on a protected value.

In contrast to reasoning based on values that evoke utilitarian cost-benefit calculations, processing protected values relies on deontic or rule-based cognition (Tetlock et al. 2000; Tetlock

2003). Adherence to such values can sometimes lead people to prefer counterintuitive choices that do not maximize utilitarian value (Dehghani, Iliev, et al. 2009; Dehghani et al. 2010; Ginges et al. 2011). This commitment to normative principles is associated with certain feelings caused by social emotions, such as outrage or disgust (Tetlock 2003). In fact, recent investigations in moral psychology have emphasized the role of “gut feelings” in moral decision-making (Haidt 2001; Haidt and Kerebir 2010), and neuroimaging and lesion studies have confirmed the involvement of emotional brain systems in moral cognition (Anderson et al. 1999; Moll et al. 2001; Moll, de Oliveira-Souza, Bramati, et al. 2002; Moll, de Oliveira-Souza, Eslinger, et al. 2002; Heekeren et al. 2005). Importantly, the activation of brain systems for social emotion depends on the type of moral stimuli participants are exposed to. For example, moral dilemmas that involve “personal” elements tend to activate MPFC, PMC, and the TPJ more than “impersonal” moral dilemmas (Greene et al. 2001, 2004; Greene 2009). The “personal” dilemmas in these studies may invoke more deontic cognition compared with utilitarian analysis, a view which is consistent with reports that damage to the ventral MPFC leads to an increase in utilitarian judgments (Koenigs et al. 2007). This brain region, in particular, may be crucial for “moral affects,” the representation of complex emotions that depend on knowledge of social conventions and norms (Koelsch et al. 2015).

In our study, interpreting a story in terms of protected, principle-based values was associated with increased signal in the same brain regions activated by these kinds of moral judgments and social emotions. Our participants also reported having stronger “gut reactions” while reading the stories that were commonly rated as appealing to protected values, underscoring the role of emotion in the perception of these moral values. Importantly, however, this network of brain regions does not appear to respond nonspecifically to emotion in stories. For instance, Lehne et al. (2015) investigated the brain regions that responded when people experienced feelings of suspense while reading a story. While some of the regions that responded to suspense overlap with the network found in our study (including parts of the medial frontal cortex and inferior parietal lobes), the overall pattern of suspense-related activity does not match that reported here and notably does not include the PMC.

There are few neuroimaging studies aimed directly at understanding the psychology of protected values (Vilarroya and Hilferty 2013). In one study, Berns et al. (2012) asked people to passively read statements that described various values such as “You are a dog person” or “You believe in god.” Later, participants were offered money to disavow those values. Values that people were unwilling to sell were considered protected, and were associated with increased activity in the left TPJ, the ventrolateral prefrontal cortex, and the amygdala. The inferior parietal regions showed greater activity for reading values that were not protected. The only brain region shared between our study and this one is the left TPJ, which was more active in our study for narratives with perceived protected values, and in the Berns study when people read value statements, they were unwilling to sell. The differences between the Berns results and ours highlight the importance of context and social cognition. Reading a single sentence out of context is likely to engage different psychological processes than reading a narrative that puts protected values in context. In another study, Duc et al. (2013) investigated the neural response to different kinds of tradeoffs between protected and nonprotected values. In that experiment, brain activity was measured while subjects decided between conflicting pairs of values. Several brain structures, including the amygdala and the anterior

temporal cortices, showed increased activation when subjects were confronted with “taboo tradeoffs” that pitted protected values against mundane values. This specific kind of tradeoff is known to provoke moral outrage and disgust (Tetlock et al. 2000), and subjects’ ratings of moral disgust correlated with signal in the right amygdala. The other important difference between our study and that of Berns et al. is the increased role of social cognition in our study. We note the difference between making a difficult decision about one’s own values compared with reading stories and interpreting the actions of others. Highlighting this difference, we found in our data that a different set of brain regions were active when people were reading the stories compared with when they were making decisions about the values in those stories. Our work differs from both of the previous studies because (1) we study the effect of perceiving a protected value as motivating someone else’s actions and (2) the values in our study are situated within the context of a meaningful narrative.

Individual and Cultural Differences

Meaning and value are inherently embedded within cultural context, and neuroscience is beginning to appreciate how culture can shape the functioning of the human brain (Chiao 2009; Chiao and Immordino-Yang 2013; Han et al. 2013). Our goal was not to characterize the three specific cultures that took part in our experiment, but rather to measure the impact that culture might have on functional brain activation during a task that evokes social values. Our sample was drawn from recent immigrants to the Los Angeles area. The fact that they spent most of their lives in different countries leads to the reasonable expectation of group-level differences in cultural norms and values, even if the individuals may not be representative of their countries’ populations at large. We note that while each group read the stories in a different language, our primary contrast of interest was within-language; for each participant, we compared stories in which protected values were perceived with other stories in the same language in which protected values were not perceived. However, since the original stories were written in English, even though they were professionally translated and back-translated, we cannot exclude that some cultural differences may be due to cultural differences in storytelling style that might not be natural to Iranian or Chinese readers.

We found evidence both for universality of functional brain activation across cultures and also indication of cultural differences. Interestingly, cultural differences did not manifest in different brain regions responding to the task across groups; instead, the same brain regions responded to the task in all 3 groups, but with varying levels of intensity. Across all 3 cultural groups, activation of PMC, MPFC, and TPJ regions was greater when participants indicated that the protagonist was acting on the basis of a non-negotiable value. However, the magnitude of this difference interacted with cultural group membership in the precuneus and left TPJ. It is notable that the interaction between protected values and culture in the fMRI signal follows the same pattern across groups as responses on the PVQ and the Moral Foundations Questionnaire. Iranian participants indicated that they were less likely to trade their values for money and had higher moral concern in general compared with the other 2 groups. The Iranian subjects showed the greatest differentiation between protected and mundane stories in the precuneus and left TPJ. This suggests that cultural concern for protected values may be reflected in differential activity in this network. It has been suggested that the DMN may be a prime

candidate network to exhibit cultural differences (Ames and Fiske 2010); our work provides support for that hypothesis.

Values that vary within groups can be responsible for measured group-level differences. For example, concern for individualism versus collectivism varies within both European and Asian people, and may mediate group-level differences in measured brain activity (Lewis et al. 2008; Na and Kitayama 2011; Ma et al. 2014). On the other hand, group-level cultural differences do not always reduce to individual differences (Na et al. 2010). In our data, individual measures of protected values or moral concern did not correlate with neural differences in the PMC, yet group-level interactions were found. Iranian subjects were less likely to indicate that they would trade their values for money, and reported higher levels of moral concern on the MFQ compared with the other cultural groups. Correspondingly, they showed the greatest neural differences between protected and mundane stories in the PMC and left TPJ.

Evidence for differences in functional brain activations between East Asian and American people has been accumulating. For example, there are differences related to visual perception (Goh et al. 2007, 2010), causal attribution (Han et al. 2011), attention (Hedden et al. 2008), the experience of feelings (Immordino-Yang et al. 2014), and self-concept (Zhu et al. 2007; Chiao et al. 2010). A common theme in this research is the role of independent versus interdependent styles of self-construal (Markus and Kitayama 1991), which appears related to cultural differences in brain activity in the MPFC. Asians, who tend to have a more contextualized self-concept, show smaller differences between self and other in the MPFC (Sui and Han 2007; Zhu et al. 2007; Chiao et al. 2009, 2010; Ng et al. 2010). In addition to culture, the religious background of subjects can also modulate self-related MPFC activity (Han et al. 2008; Wu et al. 2010). We did not measure collectivism within our subjects, but our idea of this network as a generator of contextualized meaning is consistent with the finding that Asians, who tend to see themselves as part of a context, show smaller differences in the MPFC when thinking about the self as opposed to the other. In our data, the Chinese subjects also showed the smallest differences in brain activity between protected and mundane stories, even though the proportion of stories in which they indicated perceiving protected values was not different from that of the other groups. We also note that both protected and mundane stories activated nodes of the network in question. It may be that Chinese subjects processed both deontic and utilitarian values using a more intuitive, holistic process. Work in cultural psychology has established that people from East Asian cultures tend to be more focused on global context compared with Americans (Nisbett and Miyamoto 2005; Miyamoto et al. 2006).

Iranian culture is comparatively understudied in neuroscience; we are unaware of any previous fMRI study that compared Iranian and American participants. However, Iranians appear to fall in between people from the United States of America and people from China on the continuum of independence/interdependence (Fernández et al. 2005). Iranian subjects showed the greatest difference between protected and mundane values in brain activity, but did not differ from the other groups in terms of the number of stories in which they perceived protected values.

In contrast to the issue of self-construal, moral cognition has rarely been studied across cultures from a neuroscience perspective. Recently, Han et al. (2014) compared Koreans with Americans in a moral decision-making task based on Greene's et al. (2001) "personal" versus "impersonal" moral dilemma task. Replicating the earlier study, both groups showed increased activity

in PMC and MPFC during personal moral dilemmas. Consistent with our study, there was an interaction between culture and dilemma type in the MPFC, such that Asian subjects showed a smaller difference between personal and impersonal dilemmas compared with Americans.

Conclusions

Our finding that the PMC, MPFC, and TPJ are recruited above resting baseline during reading of our selection of value-laden narratives is compatible with the idea that this network supports intense search, coordination, and integration of knowledge. The differential recruitment of these structures during stories, in which strong non-negotiable values are perceived, highlights their participation in the building of meanings dependent on complex contexts.

Supplementary Material

Supplementary material can be found at: <http://www.cercor.oxfordjournals.org/>.

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Notes

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