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Interactivity of Neural Representations for Perceiving Shared Social Memory

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Abstract

Although the concept of "common sense" is often taken for granted, judging whether behavior or knowledge is common sense requires a complex series of mental processes. Additionally, different perceptions of common sense can lead to social conflicts. Thus, it is important to understand how we perceive common sense and make relevant judgments. The present study investigated the dynamics of neural representations underlying judgments of what common sense is. During functional magnetic resonance imaging, participants indicated the extent to which they thought that a given sentence corresponded to common sense under the given perspective. We incorporated two different decision contexts involving different cultural perspectives to account for social variability of the judgments, an important feature of common sense judgments apart from logical true/false judgments. Our findings demonstrated that common sense versus non-common sense perceptions involve the amygdala and a brain network for episodic memory recollection, including the hippocampus, angular gyrus, posterior cingulate cortex, and ventromedial prefrontal cortex, suggesting integrated affective, mnemonic, and social functioning in common sense processing. Furthermore, functional connectivity multivariate pattern analysis revealed that interactivity among the amygdala, angular gyrus, and parahippocampal cortex reflected representational features of common sense perception and not those of non-common sense perception. Our study demonstrated that the social memory network is exclusively involved in processing common sense and not non-common sense. These results suggest that intergroup exclusion and misunderstanding can be reduced by experiencing and encoding long-term social memories about behavioral norms and knowledge that act as common sense of the outgroup.

Key words: Common Sense, Neuroimaging, fcMVPA, Amygdala, MTL

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1. Introduction

Common sense /kam:ən sens/

The basic level of practical knowledge and judgment that we all need to help us live in a reasonable and safe way. - The Cambridge Dictionary

Common sense is a set of basic human faculties that perceive, understand, and judge situation rules and is expected to be naturally shared by nearly everyone, allowing them to adapt in social situations (De Marzio, 2010; Rosenfeld, 2011). Being equally accessible to ordinary people, common sense has provided a basis for several social principles, such as general public judgments, egalitarian mindsets, democratic politics, and opposition to elitism (Snir, 2015). Recently, the concept has also been adopted in artificial intelligence to recognize and model human intelligence and behaviors (Simonite, 2015a, 2015b). This seemingly selfexplanatory and ubiquitous concept may actually involve a complex series of social learning processes gleaned from a lifetime of experiences such as perceiving how other people usually behave and what they normally know, drawing generalizations on a societal level based on one's experiences and memories, and finally using these criteria to make relevant judgments on a specific social scenario or semantic information. Therefore, it is plausible to assume that recognition of social relevance and successful recollection of relevant social memory characterizes the psychological mechanism underlying common sense perception. To date, the neural representations and dynamic features to support this idea are still underspecified.

The core concept of common sense usually comprises two main social components: social behavioral norms and social knowledge. Social behavioral norm refers to generalized behavioral patterns that people believe humans normally possess, such as etiquette; this leads to social judgment (Bicchieri, 2005). social knowledge means the basic level of practical social information that

people normally believe they already possess in a given society (Stangor et al., 2014). Based on these components, a decade of neuroimaging studies on social - affective processes have established the roles of a consistent group of brain regions implicated in higher social abilities, such as making moral decisions, mentalizing (i.e., "theory of mind"), social simulating, imitating; the implicated brain regions include the amygdala, ventromedial prefrontal cortex (vmPFC), posterior cingulate cortex (PCC), superior temporal sulcus, and temporal parietal junction (TPJ) (Blair, 2007; Greene & Haidt, 2002; Raine & Yang, 2006). In this study, we aimed to explore the role of the social mnemonic process in perceiving commonsensical social norms and knowledge and to identify and characterize functional connectivity networks using multivariate pattern analysis to represent how brain regions implicated in social - affective processes interact in common sense processing. We focused on the general understanding that common sense encompasses social behavioral norms and social knowledge rather than disentangling these two components.

Social memory is a shared autobiographic, episodic, as well as semantic memory relevant to social schema that internalizes group and cultural identities and bonds diverse people into members of a group (French, 1995; Olick & Robbins, 1998). As people go through socialization and developmental processes in a certain society, their own cultural and social values are encoded and ingrained as social memories as much as they can be automatically retrieved in everyday decision-making situations. As these self-initiated social memories are retrieved, they may elicit autonomic responses that give a sense of inclusion, conformity, and relevance to ingroup members with whom people share the same common sense. On the other hand, meeting people who do not comply with one's own perception of common sense, such as outgroup members who behave based on a different commonsensical perspective, may elicit a sense of violation and irrelevance.

Brain regions such as the TPJ, PCC, and superior

temporal gyrus have been implicated in social processes such as recalling coherent social narratives and "theory of mind" processing (Fletcher et al., 1995; Frith & Frith, 2001; Gallagher et al., 2000). In addition, the amygdala has been proposed as a primary neural substrate that processes social and emotional learning and mediates social influence on memory (Edelson et al., 2011; LaBar & Cabeza, 2006; Richardson et al., 2004). Specifically, in the social domain, the amygdala or specific neurons within it show selectivity for social stimuli with a high relevance for the perceiver (Sander et al., 2003). The amygdala also interacts with the hippocampus and parahippocampal cortex in the medial temporal lobe (MTL) to modulate memory encoding and emotional response retrieval (Phelps, 2004; Richardson et al., 2004). Furthermore, PFC areas are recruited to construct autobiographical memories and modulate them according to emotional arousal (R. Cabeza et al., 2004; Cabeza & St Jacques, 2007). Based on these findings, we aimed to explore how these brain regions, as primary regions of interest, interactively represent the neural mechanisms underlying common sense perception as shared social memory. Given the various cognitive processes involved, it is probable that the most efficient way for the brain to achieve commonsensical perspective would be via macro-scale functional interactions.

In the current study, participants were shown sentences describing social information during functional magnetic resonance imaging (fMRI) and asked them to judge how the sentences complied with their common sense. Beyond exploring differences in the magnitude of neural activity during common sense versus non common-sense perception using the classical massunivariate approach, we hypothesized that processing common sense statements would require more interconnectivity between personal episodic and semantic memories, as well as relevant social schema relative to logical or non common-sense statements. We investigated the synchrony between brain regions

involved in these functions, including the amygdala, hippocampus, vmPFC, temporal lobe, and lateral parietal cortices (i.e., TPJ) using bivariate seed-based functional connectivity. More importantly, we identified conjoint patterns of large-scale functional connectivity during common sense judgment using functional connectivity multivariate pattern analysis (fcMVPA) based on machine-learning classification (Pantazatos et al., 2012a; Pantazatos et al., 2014). This was to measure differences in the functional network that differentiate between processing common sense stimuli and non commonsense stimuli. We expected to identify the interconnectivity of the social memory network, which encompasses regions such as the amygdala, angular gyrus, and parahippocampal cortex, as the neural representation of common sense processing. Our findings would further the understanding of how the interactivity among brain regions leads to social cognition processing.

Frequently, intergroup and interpersonal conflicts in society are aroused by small differences in common sense perceptions. In contrast to true/false judgments, which have less variability across different societies, common sense judgments vary substantially according to the society in which the judgment is made. In other words, there exists a discrete body of common sense beliefs that applies only to a specific society, and the same act/fact can be evaluated differently according to the society in which the evaluation is made. As a first step toward mutual understanding, it is important to investigate the manner in which the brain perceives common sense and responds when perceiving social information that does not comply with one's own perception of common sense. To reflect this flexibility, we incorporated experimental stimuli and common sense judgment tasks in the perspectives of two different cultures: South Korean and US American. This enabled us to understand whether the effects of common sense that emerge from the two independent perspectives are not solely due to familiarity responses but more likely due to the evaluation of social relevance.

2. Materials and Methods

2.1. Participants

Fifteen (7 women, 8men, mean age = 23.67 years) healthy individuals (all native Koreans) participated in our study and were compensated approximately \$13 per hour (approximately 15,000 KRW) for the fMRI experiment. Before the study commenced, participants provided written informed consent as directed by the Institutional Review Board of Yonsei University (Seoul, South Korea; 1040917-201312-HRBR-02-03). Before scanning, participants completed a screening form to declare any significant medical conditions they had.

2.2. Experiments and Procedures

There were four stimulus conditions regarding common sense judgments (common sense vs non common-sense × Korean vs US perspective) as well as two types of control conditions for logical judgments (true vs false). As the participants were all Korean, Korean and American perspective were selected to represent the social and cultural standards of ingroups and outgroups, respectively. Specifically, the six stimulus conditions included 1) common sense under both ingroup and outgroup perspectives, 2) common sense under the ingroup perspective and non common-sense under the outgroup perspective, 3) common sense under the outgroup perspective and non common-sense under the ingroup perspective, 4) non common-sense under both perspectives, 5) factually true regardless of perspective, and 6) factually false regardless of perspective. Twenty statements were presented for each type of condition, and the number of statements regarding social behavioral norms and social knowledge were equally balanced and included in the common sense judgment task. Unlike common sense statements, non common-sense stimuli consisted of social etiquette

or knowledge that is not commonly used or naturally shared in a certain society so that no pressure is imposed upon members of that society even when they do not conform. In fact, stimulus conditions 1 and 4 represented common or non common-sense for two different societies, and stimulus conditions 2 and 3 represented common sense for only one society, which is less relevant to members of the other society. For example, "King Sejong invented Hangul" is commonsensical social knowledge for Koreans but noncommonsense for Americans, which corresponds to stimulus condition 2. In contrast, "Pay a tip for the services you get at a restaurant" corresponds to stimulus condition 3 because it is a commonsensical behavioral norm in the USA but non common-sense in Korea. In addition, "Do not throw away trash anywhere" is an example of common sense for both Koreans and Americans, whereas "Both men and women generally wear a skirt" illustrates non common-sense for both societies. Participants rated how each stimulus corresponded to common sense according to the given cultural perspective during fMRI scanning. Common sense and non common-sense stimuli were successfully manipulated as participant ratings of common sense statements corresponded more often to common sense rather than to non common-sense stimuli (M common sense = 6.06, M non common-sense = 2.62, P < .001). Furthermore, interpretation of statements that were common sense to either only Americans or Koreans was well-distinguished as stimulus condition 2 was more often rated as only common sense under the Korean perspective and not under the American perspective (M ingroup perspective = 6.2, M outgroup perspective = 2.57, P < .001). Similarly, stimulus condition 3 was rated as common sense only under the American perspective and not under the Korean perspective (M ingroup perspective = 3.33, Moutgroup perspective = 5.54, P < 0.001). Moreover, for the true/false factual judgment task, participants reported the extent to which they thought the given sentence was "true" regardless of perspective using a 7-point

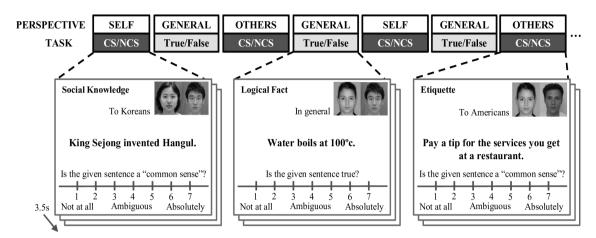


Fig. 1. Experimental design and task

For the common sense judgment task (both for social behavioral norms and social knowledge), participants were asked to indicate the extent to which they thought a given sentence corresponded to common sense under a given perspective (Korean or American) using a 7-point scale (1 = not at all, 7 = absolutely). For the true/false judgment task, participants reported the extent to which they thought the given sentence was true regardless of the perspective for judgment using the same scale.

scale (1 = not at all, 7 = absolutely). Unlike common sense and non common-sense stimuli, logical facts that do not require a retrieval of social context were used as stimuli. For example, "Water boils at 100°C" can be evaluated as true without considering a social context.

For each trial, a set of condition stimuli (task type, perspective cue, sentence for judgment, and reporting scale) was displayed vertically on-screen for 3500 ms followed by a fixation screen for 500 ms. The procedure and sample trials are illustrated in Fig. 1. For the common sense judgment task, participants were asked to indicate the extent to which they thought a given sentence corresponded to common sense under the given social perspective cue using a 7-point scale (1 = not at all, 4 = ambiguous, 7 = absolutely). To indicate which perspective participants needed to make a judgment, both text (e.g., "to Koreans" or "to Americans") and graphics (e.g., images of 1 Korean male and 1 Korean female in the ingroup-perspective condition and images of 1 American male and 1 American female in the outgroup-perspective condition) were provided as perspective cues. Along with the words "in general" in the instructions, two pictures of individuals of different sex and ethnicity (e.g., 1 Korean male and 1 American female) were presented

to participants to indicate that they were to make a decision without any regard for cultural perspective. We employed a block design considering the difficulty of switching perspectives for each trial to make decisions. We compiled 20 trials of common sense judgment tasks and 10 trials of true/false judgments into a set. After 20 trials of common sense judgment tasks from one perspective, 10 trials of true/false judgment tasks followed. The participants then proceeded with another 20 trials of common sense judgment tasks with the same set of sentence stimuli under the other perspective and another 10 trials of true/false judgments. Participants performed 8 sets of judgment tasks; 240 trials in total. A 20-trial common sense judgment block comprised four 5-trial sub-blocks for each common sense stimulus type (conditions 1 -4). True/false judgment tasks comprised two 5-trial sub-blocks for true and false stimuli (conditions 5 and 6). The order of the presented stimuli and perspective for judgment was counterbalanced across participants.

2.3. fMRI Data Acquisition and Analyses

fMRI was conducted using a 3-T Siemens Magnetom Trio MRI scanner. Functional data were acquired

using a gradient-echo planar pulse sequence (repetition time (TR) = 2000 ms, echo time = 30 ms, $3\times3\times4$ -mm resolution, 33 axial slices tilted 30° to the AC - PC plane, no gap, interleaved collection). High-resolution whole-brain T1-weighted anatomical scans (1×1×1-mm resolution, 192 axial slices) were also acquired. The first four volumes of each session were discarded to allow T1 equilibration effects. Stimuli were presented with MRI-compatible goggles, and responses were given with two MRI-compatible button boxes with four buttons each. fMRI data were analyzed using SPM8 (Wellcome Department of Cognitive Neurology, London, UK). Slice acquisition timing was corrected by resampling all slices in time relative to the middle slice. Functional images were realigned to correct for head movement and coregistered with each participant's anatomical scan. After the segmentation coregistered images, further preprocessing included spatial normalization of the coregistered structural image to a Montreal Neurological Institute template provided in SPM8, and spatial smoothing was conducted with an 8-mm full-width at half-maximum isotropic Gaussian kernel. To minimize the effect of signal changes due to movement, we used the robust-weighted least squares algorithm, which weighs each observation with the inverse of its variance (Diedrichsen & Shadmehr, 2005). Each scanning session was rescaled so that the mean global signal was 100 across the volumes.

2.4. Univariate General Linear Model Analysis

For general linear model (GLM) analyses, volumes were treated as a temporally correlated time series and modeled by convolving a canonical hemodynamic response function and its temporal derivative with a delta function marking the onset of each trial. The resulting hemodynamic functions were used as covariates in a GLM along with a basis set of cosine functions that were used to high-pass filter the data,

along with a covariate representing session effects. Least squares parameter estimates of the best-fitting synthetic hemodynamic response function for each condition of interest (averaged across scans) were used in pairwise contrasts and stored as a separate image for each participant. These different images were then tested using one-tailed t-tests against the null hypothesis of no difference between contrast conditions. The data were statistically analyzed by treating participants as a random effect at the group level. All the GLMs treated each trial as an event with zero duration. For the first-level analysis, imaging data were modeled to the onset of the six different stimulus conditions and two different perspectives taken: common sense for both societies and judged under the ingroup perspective, common sense for both societies and judged under the outgroup perspective, common sense only for the ingroup and judged under the ingroup perspective, common sense only for the ingroup and judged under the outgroup perspective, common sense only for the outgroup and judged under the ingroup perspective, common sense only for outgroup and judged under the outgroup perspective, non common-sense for both societies and judged under the ingroup perspective, non common-sense for both societies and judged under the outgroup perspective, factually true, and factually false. Group-level t maps were thresholded at P < .005, with the cluster extent threshold of 18 contiguous voxels (3-mm isotropic), which corresponds to an alpha level of P < .05 (Slotnick et al., 2003).

2.5. Bivariate Connectivity-Psychophysiological Interaction Analysis

To investigate how activities in different brain regions correlate with a defined region of interest along task conditions, we used a psychophysiological interaction (PPI) analysis (Friston et al., 1997). PPI analysis was performed by extracting time series within volumes of interest (VOI) as a physiological variable and using

experimental stimulus onset time as a psychological variable. Two variables were convolved into an interaction variable to identify brain regions with time series that are highly correlated with seed VOI in performing a certain cognitive function, such as common sense processing. The amygdala, vmPFC, and hippocampus were selected as a priori VOI based on their well-known representative functions in the social - affective system, social valuation, and social memory (Blair, 2007; Phelps, 2004). The coordinates of seed VOI were derived from the peak voxels from the GLM analyses (common sense vs non commonsense) of the left amygdala [-24 -4 -14], right vmPFC [6 41 -5], and right hippocampus [24 -22 -20]. Next, the 4-mm-radius sphere-shaped VOI was created, centering these three selected voxels. The voxel-by-voxel physiological variable was estimated by deconvolving the blood oxygen level-dependent (BOLD) signal of 674 TRs into neuronal time course with a parametric Bayesian formulation and extracting the first eigenvariate from principle component analysis. Any linear or nonlinear trend was removed. The psychological variable was generated from the onset time points of a condition of interest, such as the common sense judgment or non common-sense judgment conditions (i.e., 1 for the common sense judgment condition and 0 for others or 1 for the non common-sense judgment condition and 0 for others). Finally, the interaction variable was calculated for each condition of interest by multiplying the physiological and psychological variables. The resulting time series was convolved with a canonical hemodynamic response function and detrended again to more correctly represent BOLD signals acquired by MRI. Resulting images that show interaction between VOI and other whole-brain regions were entered into random effect analysis (P < .005/18). This approach made it possible to detect the interactions among the social - affective and memoryrelated regions during common sense processing. This also allowed the documentation of the brain network

discriminating common sense judgment from non common-sense processing. This was more investigated in the pattern analysis described below.

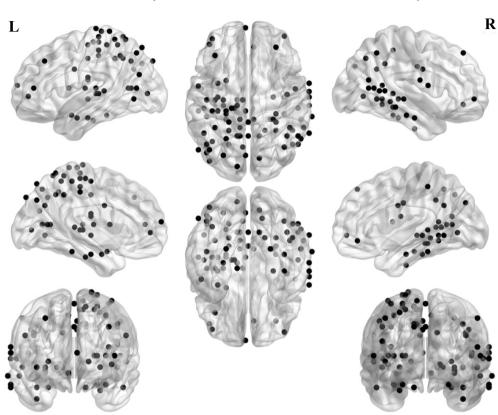
2.6. fcMVPA

2.6.1. Node Definitions and Task-Dependent Connectivity

While PPI analyses revealed connectivity from the individual seed voxel to other regions, fcMVPA addressed the whole-brain cross-correlation pattern. The GLM analysis revealed 86 subpeak voxels within the cerebrum that are more involved with common sense judgment than with non common-sense judgment (Fig. 2). The cube-shaped nodes centered on each peak voxel were created, including the surrounding 27 voxels (3×3×3). Any peak voxels outside of the gray matter or image boundary were excluded, and the Euclidean distance was measured between the peak voxel coordinates to ensure no overlap within 8 mm of each other. To obtain a task-dependent time series representing common sense or non common-sense processing, the interaction variable resulting from PPI analysis was extracted and averaged within 27 voxels of each cube-shaped node. As a result, a single mean time series with 674 time points reflecting the experimental conditions was obtained for each node. These time series of entire nodes were pairwise cross-correlated and z-transformed. Since the obtained connectivity matrices were diagonally symmetric, only the half was used as features in fcMVPA ($86 \times 85/2 =$ 3655 links).

2.6.2. Pattern Classification of Functional Connectivity in Different Conditions

fcMVPA was conducted using the functional connectivity link as a classifying feature. This analysis aimed to investigate whether the pattern of link strengths between the nodes could effectively classify common sense processing and explore features that



All Nodes (Common Sense vs. Non-Common Sense)

Fig. 2. Node definitions and task-dependent connectivity A total of 86 nodes defined from common sense vs non common-sense GLM results

were potentially informative. For proper feature selection, the paired t-test of correlation coefficients between the two experimental conditions within each link was performed. The features were ranked by absolute t-score values. The pattern classification was conducted with a support vector machine (SVM) algorithm using Spider v1.71 Matlab toolbox (http://people.kyb.tuebingen.mpg.de/ spider/) with default parameters (linear kernel SVM, regularization parameter C = 1). Leave-one-out crossvalidation (LOOCV) was applied so that one participant's link was removed from the training set and used as test data. Because there were 15 participants, 15 samples representing common sense processing and the same number of samples representing non common-sense processing were used as input data. Thirty accuracies were generated from 30 rounds of LOOCV iterations, which were then averaged to obtain a single representative figure for accuracy.

To find optimal features that maximize classification efficiency, features were cumulatively added in order of t-score rank in each round of cross-validation. Thus, the Nth SVM classification accuracy was obtained using the top N features whose t-score values were from the highest to the Nth, and (N+1)th accuracy was calculated by adding the feature with the next higher t-score value to the feature already included. This process was iterated until the classification used whole features, from the top to the last feature, with the smallest t-score value, so that this method resulted in 3655 accuracies. In this manner, we explored the optimal composition of the most informative features (i.e., those inducing peak accuracy) that classified common sense processing with non common-sense processing. No adjustments were needed for multiple comparisons

as fcMVPA is the process of determining how groups of functional connections simultaneously contributed to distinguish large-scale functional connectivity of two cognitive processes (Pantazatos et al., 2012b). Permutation tests were then independently conducted to test whether pattern classification accuracies were significantly above the chance level. Class label (i.e., common or non common-sense) was randomly assigned to classifying features, and pattern classification was performed using LOOCV. This process was repeated 1000 times using top features, which have significant t-score values at the simple t-comparison level of P < .05 and generated a chance accuracy (50%) null distribution.

3. Results

3.1. Behavioral Results

To ensure that the presented common sense sentences were perceived as such in the given perspective and non common-sense sentences were seen as violating the society's conventional meaning of common sense, we conducted a priori t-tests comparing patient ratings of common sense and non common- sense sentences for both the Korean and American perspectives. The results indicated that common sense manipulation was successful for both judging perspectives. In the common sense judgment task, common sense sentences were consistently rated as more likely to correspond to common sense (M common sense = 6.06) than non common-sense sentences (M non common-sense = 2.62, P< .0001). The results further showed that participants successfully switched their judgment criteria according to the perspective cues that they were instructed to assume. Half the sentences we used as stimuli corresponded to common sense under one perspective but not under the other (conditions 2 and 3). Participants correctly evaluated the sentences of condition 2 as common sense only under the Korean perspective (M

ingroup perspective = 6.2). The same sentences were perceived as non common-sense when evaluated under the American perspective (M outgroup perspective = 2.57, P<.001). Participants also correctly judged stimulus condition 3 as common sense under the American perspective (M outgroup perspective = 5.54). These same sentences were judged as non common-sense under the Korean perspective (M ingroup perspective = 3.33, P <.001). No significant difference was observed in participant reaction times by condition. These behavioral results show that participants not only judged the familiar ingroup as common sense based on their activated social memory but also successfully judged less familiar social norms or knowledge of the outgroup by assuming that perspective and evaluating relevance perhaps based on social experiences they have directly or indirectly accumulated.

3.2. fMRI Results

3.2.1. Univariate Whole-Brain GLM Results

First, we were interested in the different neural substrates involved in common sense judgment compared with the factual true/false judgment. Significantly increased activation was identified in the inferior temporal lobe (BA 20), superior middle frontal gyrus (BA 8), PCC, and precuneus when evaluating common sense but not factual information (see GLM results in S1 Table). The precuneus is known to be involved in the social cognition system (Fletcher, Frith, et al., 1995; Zerubavel, Bearman, Weber & Ochsner, 2015) and self-referential functions (Vanderwal et al., 2008), and the inferior temporal gyrus plays a role in the integration of semantic memory (Chan et al., 2001). These initial GLM results illustrate that perceiving common sense is different from simply processing factual information and it demands more of a social perspective on episodic and semantic memories.

We next sought to investigate regions showing greater activation during judgment of a sentence corresponding to common sense based on activated social perspective than during judgment of a non common-sense sentence. Several regions, including the amygdala, angular gyrus, hippocampus, parahippocampal cortex, and vmPFC, were found to be more engaged when participants perceived common sense. The reverse contrast only yielded suprathreshold clusters in the right lingual gyrus, cerebellum, and left precentral cortex (see GLM results in S1 Table). Personal episodic memory of social schema seems to be recruited more to process common sense than non common-sense stimuli, which results in increased simultaneous activation of the hippocampus, parahippocampal cortex, and angular gyrus. Furthermore, these findings may reflect that common sense perception requires more involvement of the amygdala and final integration and decision making in the vmPFC.

Lastly, we focused on finding brain regions that were specifically involved in common sense processing in the ingroup. Brain regions that showed exclusive activation in perceiving common sense stimuli for the ingroup were explored by contrasting them with regions recruited to process common sense of outgroups and non common-sense of both groups. The bilateral precuneus, right angular gyrus, hippocampus, and middle temporal gyrus were shown to be exclusively involved in the common sense processing of the self-relevant group (see GLM results in S1 Table).

3.2.2. Bivariate PPI Results

When perceiving common sense, the brain regions involving affective, episodic, and semantic memory and social schema were recruited more compared with non common-sense conditions. To investigate how activities in these regions are functionally synchronized with other brain regions along task conditions, we conducted PPI analysis. The left amygdala, right hippocampus, and vmPFC regions, which were found to be heavily involved in common sense processing, were chosen as functional seed regions from the preceding GLM results. In relation to common vs non common-sense

task conditions, left amygdala seed activity showed robust connectivity with the left PCC, right middle orbito frontal cortex, middle frontal cortex, and left middle cingulate cortex. Links between the amygdala -PCC and amygdala - PFC show that affective function is actively gathered with other cognitive regions during common sense processing. Next, the right hippocampus seed showed connectivity with the inferior parietal lobule, including the left supramarginal gyrus and right angular gyrus, precuneus, inferior orbitofrontal cortex, middle frontal gyrus, and superior temporal pole. The connection between the hippocampus and inferior parietal lobule supports the integration of memory and social schematic knowledge which is highly required in common sense processing. Finally, the right vmPFC showed synchronized activation with the MTL region, fusiform gyrus, lingual gyrus, inferior temporal gyrus, superior and middle frontal gyrus, right superior medial prefrontal gyrus, ventrolateral PFC (BA 44), visual cortices, etc. (Fig. 3 and S2 Table). This vmPFC-MTL link again shows that semantic and episodic memory are acquired during common sense processing. The functional connectivity between these regions suggests integrated affective, mnemonic, and social functioning in common sense processing, which is further investigated in the following pattern analysis.

3.2.3. Multivariate Pattern Analysis of Functional Connectivity Networks Discriminating Between Common Sense and Non Common-Sense

To examine how each region revealed in the GLM analyses was collectively involved in common sense judgment, we conducted fcMVPA. Specifically, we extracted a task-based time series of 86 nodes predefined from the GLM results. Next, we investigated patterns of condition-dependent functional connectivity that sensitively categorize the dynamic of common sense perception from the perspective of multivariate machinelearning classification. For common vs non commonsense discrimination, peak accuracy reached 96% when

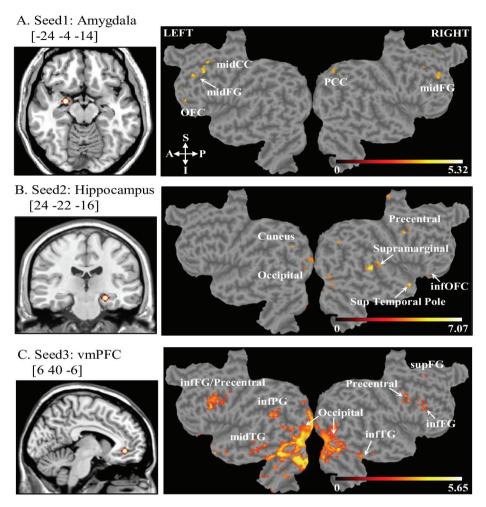


Fig. 3. PPI results

(A) Cortical regions covaried with the left amygdala seed region (left) while perceiving common sense sentences are demonstrated in flattened brain images. The posterior cingulate cortex (PCC), orbitofrontal cortex (OFC), middle frontal gyrus (midFG), and middle cingulum cortex (midCC) were functionally synchronized with the left amygdala along task conditions. (B) The right hippocampal seed region was synchronized with the supramarginal gyrus, inferior orbitofrontal cortex (infOFC), precentral gyrus, and occipital lobe. (C) The ventromedial prefrontal cortex (vmPFC) seed region showed synchronization with the parahippocampal cortex, posterior hippocampus, infFG, precentral gyrus, superior frontal gyrus (supFG), inferior parietal gyrus (infPG), middle temporal gyrus (midTG), and occipital lobe.

72 functional connectivity features were included in the iterative classification methods; the accuracy gradually decreased to 23% when all features were included. That is, the inclusion of irrelevant features decreased classification performance. The functional links mainly included the following brain region pairs: left angular gyrus - left amygdala, left precuneus - left superior parietal gyrus, and left amygdala - right middle temporal gyrus (see S3 Table). Classification accuracy results are shown in Fig. 4. A permutation test was also performed to determine if the obtained accuracies statistically

differed from the null distribution. The results of the permutation test are also plotted in Fig. 4. The 1000 iterations of permutation accuracies remained at chance level, verifying that the original data applied two distinct patterns of functional connectivity.

To identify brain regions that most importantly classified common sense and non common-sense perception networks, we measured betweenness centrality, representing how many times a node plays a role as the shortest path between two nodes (Freeman, 1977; Rubinov & Sporns, 2010). The centrality of 72 features

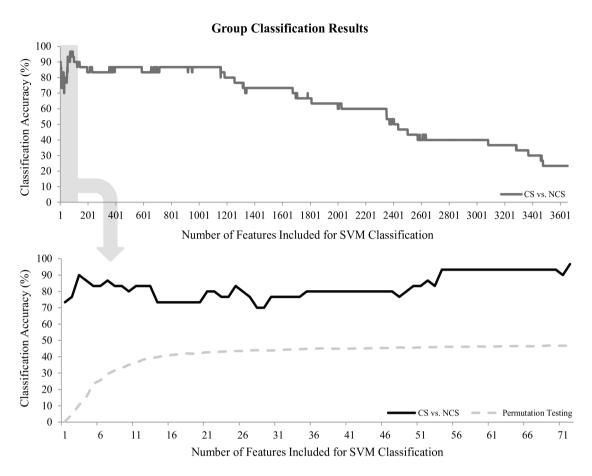


Fig. 4. fcMVPA accuracy graph

Common vs non common-sense classification accuracy (y-axis) changed by the number of features (x-axis) accumulated. The peak accuracy was 96% when 72 features were included. The results of permutation tests are demonstrated by the dashed bar.

that elicited peak classification accuracy was measured using GraphVar toolbox (Kruschwitz et al., 2015). Fig. 5 plots the network of links that best discriminated the two types of processing. The size of the nodes represents the degree of betweenness centrality, and the line between the nodes shows if there was a connection between the two nodes. The hub with the highest betweenness centrality was revealed in the left angular gyrus, which had a normalized value of 0.2. The left amygdala, cuneus, middle cingulate cortex, superior parietal lobule, and right middle temporal gyrus were the next top five regions, showing normalized betweenness centrality values of 0.122, 0.09, 0.048, 0.042, and 0.036, respectively. The right parahippocampal cortex also showed a high centrality value of 0.03 (Fig. 5). Aside

from the betweenness centrality, binary degree centrality of the top 72 features was also measured, which represents the number of links between each node (Rubinov & Sporns, 2010). The left angular gyrus again acted as a hub for the network and showed a normalized centrality value of 0.188, followed by the left amygdala, middle cingulate gyrus, calcarine, cuneus, inferior frontal gyrus, and superior parietal lobule (normalized values = 0.094, 0.082, 0.705, 0.047, and 0.047, respectively). Although betweenness and degree centrality are two independent indices, they showed almost identical interconnectivity results, demonstrating that common sense perception requires memory retrieval of social schema in the parahippocampal cortex and angular gyrus, as well as immediate social - affective processing in the amygdala.

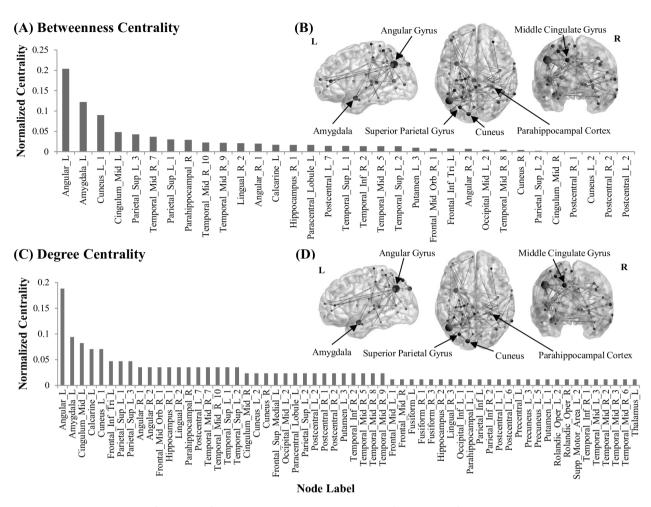


Fig. 5. Centrality of nodes included in the production of peak classification accuracy

(A) Normalized betweenness centrality values of nodes that discriminated common vs non common-sense with the highest accuracy are visualized in circles. The size of each circle is proportional to the centrality value (bigger size = bigger value). The line refers to whether a connection existed between two nodes. Node labels are named after the AAL: the brain region (i.e., angular, middle temporal gyrus, superior parietal gyrus), laterality [left (L) or right (R)], and assigned number of nodes in case there is more than one in the same region (i.e., 1, 2, 3...) (i.e., Angular L 2). (B) The bar graph shows normalized betweenness centrality values of nodes in the descending order. (C) Normalized degree centrality values of nodes are visualized in circles. The almost identical pattern of two independent centrality networks is shown. (D) Normalized degree centrality values are summarized in the bar graph in the descending order

4. Discussion

Using uni-, bi-, and multivariate statistical analyses, our findings consistently indicated that common sense perception is subserved by the neural synchrony of a general memory retrieval network in ensembles of social - affective regions, such as the amygdala and vmPFC. While participants perceived common sense sentences, we observed increased BOLD signals in the amygdala, MTL, angular gyrus, and vmPFC. The hippocampus was especially recruited in judging common sense shared by the highly relevant ingroup society. The functional

connectivity networks between regions that were identified in the univariate analysis were further investigated using bivariate and multivariate connectivity analyses. These regions showed functional connectivity with each other as well as with other brain regions, such as the PCC and right TPJ. Furthermore, nodes created in whole-brain large-scale networks showed representational patterns of functional interactivity that reflected critical features of common sense perception, with the majority of links involving the amygdala, parahippocampal cortex, angular gyrus, and middle frontal gyrus. Taken together, the current study demonstrated that processing social judgment, as in common sense, requires the recruitment of neural interactions between regions underlying mnemonic, affective, and social systems supporting the notion of social memory.

4.1. Large-Scale Interactivity-Connectivity as a Tool for Exploring Neural Representation of Common Sense Processing

Beyond mass uni- or bivariate approaches to analyzing neuroimaging data, pattern-based multivariate analysis has recently received increased attention. The conventional approaches are relatively insensitive to signal loss as analyses are performed within one location, and very stringent corrections for multiple comparisons are necessary (Haynes & Rees, 2006; O'Toole et al., 2007). The multivariate approach has advantages over conventional ones in terms of sensitivity as spatial patterns of several brain regions are jointly entered into the analysis.

In the present study, we adopted the fcMVPA method to identify large-scale brain interactivity underlying common sense processing. We also applied a novel fcMVPA approach by gradually increasing the number of included features with iteration of SVM classification processes, which allowed us to track changes in classification accuracies to identify optimal brain networks that most powerfully represent underlying mechanisms of common sense vs non common-sense processing (Pantazatos et al., 2012; S. P. Pantazatos et al., 2012b). We could also check reproducibility and reduce falsepositive results from the SVM classifier using LOOCV, which validated that the classifier could be applied to independent test data.

4.2. The Amygdala's Role in Understanding Social Relevance

The findings on amygdala involvement during common sense perception support and further expand its role in

social perception. In our study, the amygdala showed strong activation during common sense perception and also functioned as a key node linking other brain regions in the general memory recollection network for distinguishing common sense from non common-sense perceptions. Historically, the amygdala was viewed as responsible for processing emotional stimuli (Adolphs et al., 1995; Loughead et al., 2008; Phillips & LeDoux, 1992); this traditional view is shifting to a more abstract and broadly ecological role: processing "relevance" even after stimuli's level of arousal and valence is matched (Ewbank et al., 2009). Specifically in the social domain, the amygdala or neurons within it show selectivity for social stimuli with high relevance for the perceiver (Cunningham et al., 2008). For example, the amygdala was significantly more recruited to process social information that was relevant with subsequent impression evaluation (Schiller et al., 2009). In an fMRI study by Knutson et al. (2006), the amygdala was significantly more responsive to the faces of candidates who agreed with participants' political opinions than to those of candidates who did not agree with them (Knutson et al., 2006). Also, the amygdala was significantly more responsive to the faces of candidates whom they voted for than those of candidates they did not vote for (Rule et al., 2009). These findings indicate that the amygdala is recruited in processing the relevance of stimuli and differentially responds to social information that is subjectively more valued and therefore more salient. Furthermore, people tend to trust and conform to the judgment of the social group, and this tendency is modulated by heightened activation of the amygdala and its enhanced functional connectivity with the hippocampus (Edelson et al., 2011). Interestingly, the authors showed that the amygdala mediated long-lasting conformity effects only in contexts involving social influence (such as presenting other people's answers) but not in nonsocial contexts (such as providing computer-generated answers). The current data are consistent with these previous findings, showing that social relevance, which

is represented by ingroup or outgroup perspective, modulates amygdala involvement in social perception and decision-making processes regarding common sense. It is particularly worth noting that in our work, the subjective value participants found from the social stimuli was not personal per se (e.g., personal preferences for candidates to vote). Rather, the amygdala's response observed in our study reflects a more generalized value of the stimuli thought to be shared by a certain society at large, a finding that elucidates the amygdala's role in relevance representation.

4.3. Common Sense and Self-Initiated Memory Retrieval Network

In addition to the extensive involvement of the amygdala in common sense perception, the current data showed increased MTL region activity and interconnectivity patterns with several cortical regions, including the PCC, angular gyrus, and vmPFC. This suggests that common sense judgment involves a self-initiated memory retrieval process without explicit demand from the judgment task. The MTL region, which includes the hippocampus and the surrounding parahippocampal, peripheral, and entorhinal cortices, has been implicated as a critical component supporting memory formation and retrieval (Roberto Cabeza et al., 2004; Eichenbaum et al., 1999; Prince et al., 2005). In particular, the importance of the hippocampus in successful memory retrieval has been widely accepted. An fMRI study comparing patterns of functional connectivity demonstrated that the hippocampus commonly engages in episodic, autobiographical, and semantic retrieval processes (Burianova et al., 2010). Recent animal studies have also revealed the specific role of hippocampal neurons in social memory, especially in social recognition, such as encountering familiar social others (Hitti & Siegelbaum, 2014; Okuyama et al., 2016). Our findings showed that the hippocampus is also involved with more broad and

abstract concepts of social memory, such as semantic and autobiographical memory. Moreover, connectivity analyses have revealed that hippocampal activity positively correlated with numerous other cortical areas, including the PCC and TPJ, comprising a common functional network underlying general memory retrieval. These findings are consistent with the idea of a general (episodic memory) recollection network, as proposed by Rugg and Vilberg (2013) (Rugg & Vilberg, 2013). Recollection-sensitive brain activities, independent of memory content, have been consistently observed in the hippocampus and the parahippocampal, medial PFC, PCC, and lateral parietal cortices, including the angular gyrus (Duarte et al., 2011; Hayama et al., 2012). Evidence, especially from anatomic and functional topography studies in the MTL, indicates that these regions are functionally interconnected and constitute a broader network system for declarative memory processing (Aggleton, 2012).

Our data also revealed higher interactivity between the MTL regions and angular gyrus when the stimulus was evaluated as reflecting common sense. The functional contribution of the lateral parietal cortex to memory recollection is less understood than that of the other regions of the right PCC or medial PFC. However, recent studies exploring resting-state functional and structural connectivity using diffusion tensor imaging have demonstrated that the angular gyrus is strongly linked to the hippocampus, parahippocampal cortex, PCC, and vmPFC. Previous fMRI findings have indicated that the angular gyrus mediates memory detection processes in concert with the hippocampus (Cabeza et al., 2011; Hutchinson et al., 2009). Enhanced activation in the angular gyrus has been associated with successful memory retrieval and higher functional connectivity between regions (specifically, effective connectivity from the angular gyrus to the hippocampus) that characterized the retrieval process (Daselaar et al., 2009; McCormick et al., 2010). Lesion studies have also suggested the functional significance of the

parietal cortex, especially in self-initiated memory recollection, showing a free recall deficit in patients with bilateral parietal lobe damage (Berryhill et al., 2007). Therefore, stronger interactivity of the angular gyrus and hippocampus when perceiving common sense might reflect a self-initiated memory searching process and successful retrieval of the relevant declarative memories. Moreover, the specificity of the neural synchrony pattern between the amygdala and regions of the memory recollection network (parahippocampal cortex and angular gyrus) suggests that social relevance detection and successful recollection of relevant social memory characterize the psychological mechanism underlying common sense perception.

As a potential limitation to this study, we only included 15 samples in the analysis, which is a relatively small sample size. This small sample size and small number of trials per each condition limited us from performing some analyses that necessitate strong statistical power, such as multi-way factorial analysis of variance. However, we did not simply focus on finding voxel-by-voxel location-based activation in common sense processing, but we also explored the large-scale functional connectivity patterns of brain regions. We argue that this multivariate analytical approach increased statistical sensitivity and reduced concerns regarding potential false-positive results. Indeed, 15 or a similar number of subjects had been shown to hold enough statistical power (Desmond & Glover, 2002; Pajula & Tohka, 2016). Another limitation of the current study is that we did not measure affective responses elicited by each stimulus. Emotional discomfort might have automatically been evoked, unlike commonsensical stimuli, by perceiving behaviors and knowledge that did not comply with one's own common sense. It is possible that differences in neural activities between common sense perception and other stimuli were modulated by different affective responses. Further studies are needed to separate the effect of social memory and emotions in processing common

sense using affective valence and arousal ratings of common or non common-sense stimuli.

Herein, we discovered that a distinct neural network is recruited for common sense judgment, and common sense perception is a consequence of harmonious functional interactions between brain regions, including the amygdala, MTL, and lateral parietal cortices. Our study thereby suggests that common sense processing requires recollecting semantic/episodic memories shared with relevant social groups. In addition, the present study suggests that different neural activities are involved in processing common sense and non commonsense. This difference perhaps can be the neural basis of cultural ostracism. If we can manifest similar patterns of neural activities in perceiving ingroup common sense and those of outgroups, which are perceived as non common-sense for ingroup members, it seems plausible that we can reduce intergroup or interpersonal exclusion, hostility, and ostracism and enhance mutual understanding and empathy toward others. Further work is needed to determine if experiencing and learning common norms and knowledge only shared by outgroup members can yield this effect.

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Supporting information

S1 Table. GLM analysis results.

S2 Table. PPI analyses results: Common vs non common-sense.

S3 Table. List of fcMVPA features in peak accuracy. The black and white colors of columns 4 and 5 show the direction of the edge; black cells demonstrate a stronger connectivity between two conditions. For example, in the first row, the edge between two nodes in the left angular gyrus showed a stronger connectivity during common sense perception rather than non common-sense perception.

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