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Concepts in context: Processing mental state concepts with internal or external focus involves different neural systems

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Abstract

According to embodied cognition theories concepts are contextually-situated and grounded in neural systems that produce experiential states. This view predicts that processing mental state concepts recruits neural regions associated with *different* aspects of experience depending on the context in which people understand a concept. This neuroimaging study tested this prediction using a set of sentences that described emotional (e.g., fear, joy) and non-emotional (e.g., thinking, hunger) mental states with internal focus (i.e. focusing on bodily sensations and introspection) or external focus (i.e. focusing on expression and action). Consistent with our predictions, data suggested that the inferior frontal gyrus, a region associated with action representation, was engaged more by external than internal sentences. By contrast, the ventromedial prefrontal cortex, a region associated with the generation of internal states, was engaged more by internal emotion sentences than external sentence categories. Similar patterns emerged when we examined the relationship between neural activity and independent ratings of sentence focus. Furthermore, ratings of emotion were associated with activation in the medial prefrontal cortex, whereas ratings of activity were associated with activation in the inferior frontal gyrus. These results suggest that mental state concepts are represented in a dynamic way, using context-relevant interoceptive and sensorimotor resources.

Keywords

simulation; embodiment; emotion; mental states; vmPFC; IFG.

Introduction

It has long been argued that some of the most important human concepts refer to mental states. After all, understanding and predicting the self and others often requires conceptualizing behavior in mental state terms (Dennett, 1987; Frith & Frith, 2006). Unsurprisingly then, human language commonly communicates mental states, such as disgust, anger, doubt or hunger. An important question in psychology and cognitive

neuroscience is: how do people understand these references to mental states? Take for instance the sentence '*she was sick with disgust*'. How do we attach meaning to the internal sensations implied by this sentence? And how do we understand the sentence '*his nose wrinkled with disgust*' that implies a facial expression?

One account of this process is forwarded by theories of embodied cognition (e.g., Barsalou, 1999; 2009; Gallese & Lakoff, 2005). This account posits that neural systems for perception, action, interoception, and introspection engage in multimodal simulations to implement the concepts necessary to understand the world around us (we discuss alternatives to this simulation account later). Recently, it has been proposed that the pattern of simulation that represents a concept is not rigid, but dynamically shaped by the context at hand (Barsalou, 1999; 2009; Wilson-Mendenhall, Barrett, Simmons, & Barsalou, 2011). This dynamic view of simulation is specifically relevant to the understanding of complex, abstract concepts, such as mental states. To give a specific example, even though the sentences '*she was sick with disgust*' and '*his nose wrinkled with disgust*' are both about disgust, they may lead to different patterns of simulation, because they emphasize distinct aspects of experience. In the present study, we focus on the novel question whether activation in neural systems associated with action, interoception and introspection is flexibly modulated when people process descriptions of mental states that focus on internal or external aspects of experience.

Embodied cognition

Accumulating evidence suggests that processing conceptual references to mental states is associated with recruitment of embodied, multimodal resources. For example, several behavioral and psychophysiological studies show changes in sensorimotor states (e.g., facial expression, posture) during conceptual emotion tasks (Niedenthal, Winkielman, Mondillon, & Vermeulen, 2009; Oosterwijk, Rotteveel, Fischer, & Hess, 2009; Oosterwijk, Topper, Rotteveel, & Fischer, 2010; for a review, see Winkielman, Niedenthal, Wielgosz, Eelen, & Kavanagh, 2015). Furthermore, neuroimaging studies demonstrated that the brain's motor system is engaged by action-related language (Tettamanti, Buccino, Saccuman, Gallese, Danna, Scifo et al., 2005; for an overview, see Pulvermuller & Fadiga, 2010) *as well as* abstract emotion words (Mosely, Carota, Hauk, Mohr, & Pulvermuller, 2012).

It is surprising, however, that research on comprehension of mental state concepts mainly focuses on neural systems supporting sensorimotor states, since prominent embodiment theories explicitly argue for the importance of feelings, introspections and interoceptive changes in representing abstract concepts (e.g., Barsalou, 1999; 2009). This lack of attention to the simulation of internal aspects of mental states is even more surprising in view of the wealth of evidence showing that *inferring* mental states in other people is associated with internal simulation (e.g., for disgust, Wicker, Keysers, Plailly, Royet, Gallese & Rizzolatti, 2003; for pain, Lamm, Decety & Singer, 2011; for empathy, Decety, 2011). This raises the question whether core regions involved in the generation of internal experiences, such as the insula and the ventromedial prefrontal cortex (vmPFC), are also involved in understanding abstract mental state concepts while processing language.

Another critical question regarding mental state concepts, is to what extent people access *different* aspects of experience depending on the context in which they process a mental

state. According to embodied cognition models, people do not represent concepts in isolation, but within the relevant situational context (Barsalou, 2009; Wilson-Mendenhall et al., 2011). One way in which context may shape access (or simulation) is by making different aspects of experience salient. Although abstract concepts tend to integrate experiences across different modalities (Barsalou, 1999; Van Dantzig, Cowell, Zeelenberg, & Pecher, 2011), the relative weight of a modality may differ depending on which experience is most relevant for understanding a particular instance of a mental state.

Initial support for this idea comes from a recent behavioral study that explicitly manipulated a focus on certain aspects of experience when people read unrelated sentences containing mental state concepts (Oosterwijk, Winkelman, Pecher, Zeelenberg, Rotteveel & Fischer, 2012). We found greater processing costs (slower RTs) when consecutive sentences switched between a focus on internal and external aspects as compared to when consecutive sentences shared the same focus. Although this behavioral finding is consistent with the theoretical proposal that understanding internally- vs. externally-focused mental states involves different simulations, stronger and more mechanistic evidence would be offered by direct exploration of the neural resources that presumably underlie such simulations. Therefore, we adapted our paradigm and used functional magnetic resonance imaging to directly test whether neural systems associated with the representation of internal and external states are indeed modulated by manipulating focus in mental state language.

The current study

Our first hypothesis is that sentences describing a mental state in terms of internal sensations (internal focus) will engage regions associated with representing interoceptive and introspective states more strongly than processing sentences focusing on external aspects of experience. To test this hypothesis, we focused on the insula, and sub-regions of the vmPFC (i.e., rostral anterior cingulate cortex and medial orbitofrontal cortex), because previous work has shown that these regions are associated with the generation of internal sensations (Craig, 2009; Medford & Critchley, 2010; Etkin, Egner, & Kalisch, 2011), self-reflection (Northoff, Heinzel, De Greck, Bermpohl, Dobrowolny, & Panksepp, 2006; Wagner, Haxby & Heatherton, 2012) the processing of internal states in others (Gallese, Keysers & Rizzolatti, 2004) and mentalizing in general (Amodio & Frith, 2006). Our second hypothesis is that processing sentences describing mental states in terms of external, expressive manifestations (external focus) will engage regions associated with representing action and expression more strongly than processing sentences focusing on internal aspects of experience. We focused on the inferior frontal gyrus when testing this hypothesis, because previous work has shown that this region is associated with understanding actions and behavioral expressions of emotion (De Gelder, Snyder, Greve, Gerard, Hadjikhani, 2004; Gallese et al., 2004; Jabbi & Keysers, 2008; Kilner, Neal, Weiskopf, Friston, & Frith, 2009) and action-language (Tettamanti et al., 2005; Pulvermuller & Fadiga, 2010).

Because internal changes not only characterize emotions, but also visceral states (e.g., hunger, dizziness) and cognitive states (e.g., familiarity, thinking) (cf. Barrett & Bliss-Moreau, 2009; Craig, 2009), we included sentences describing both emotional *and* non-emotional mental states (as in Oosterwijk et al., 2012). This manipulation allowed us to test

whether internal and external focus produces similar patterns of neural activity across emotion and non-emotion sentences (cf. Oosterwijk et al., 2012). This is important in the context of debates about the degree of overlap in neural mechanisms underlying cognition and emotion (Pessoa, 2008; Barrett & Satpute, 2013) and the potentially greater role of internal qualities in the representation of emotional content.

As a further test of our hypotheses, we collected ratings of internal focus, external focus, and several other dimensions from an independent sample of participants. In addition to providing a manipulation check of our sentence category classification, these ratings allowed us to investigate if similar patterns emerged when examining the correlation between trial-by-trial ratings of internal/external focus and neural activity. Hence, this analysis allows us to link patterns of brain activity to internal and external focus while taking into account the possible variability among sentences with regard to these dimensions across the different sentence categories.

Method

Participants

Eighteen right-handed individuals (8M, 10F, $M_{\text{age}} = 34.2$, $SD_{\text{age}} = 11.3$) participated in the experiment. Two individuals were excluded because their response pattern indicated that they did not adequately understand the task instructions (incorrect > 20%). We also excluded corrupted data from a third individual. All procedures were performed in accordance with the Declaration of Helsinki.

Materials

The mental state sentences used in this study were taken from an existing set of materials (cf. Oosterwijk et al., 2012). The non-mental state sentences (e.g., *'the jungle was full of life'*) were specifically written for the present study (the full list of sentences is available upon request). Mental state sentences differed in the *state* described (emotion vs. non-emotion) and in *focus* (internal vs. external). Emotion sentences described both positive and negative emotional states, namely fear, nervousness, anger, rage, hate, disgust, disappointment, despair, sorrow, regret, shame, guilt, embarrassment, happiness, love, and pride. Non-emotion sentences described both positive, neutral and negative non-emotional states, namely doubt, confusion, hunger, tiredness, exhaustion, dizziness, thinking, knowing, meditation, visualization, understanding, imagining, remembering, wonder, intuition, and bewilderment. Internal sentences described mental states with a focus on interoceptive sensations, feelings and introspections (e.g., *'her mouth went dry with fear'*, *'he was lost in thought'*). External sentences described mental states with a focus on actions and expressions (e.g., *'his chest swelled with pride'*, *'she shook her head in doubt'*). Importantly, mental state concepts were held constant across internal and external categories, such that *the same* emotional and non-emotional mental states were described both with internal and with external focus. The full list of sentences can be found in the Supplementary Materials. The number of words did not differ between mental state sentences and non-mental state sentences, $F(1, 158) = .04$, *ns.*, nor between different mental state categories, $F(3, 76) = .63$, *ns.* Furthermore, half of the sentences had a male subject, the other half a female subject.

To ensure that the sentences indeed described our dimensions of interest, we asked two independent groups of participants to rate the sentences. One group was asked to rate on a scale from 1 (*'not at all'*) to 5 (*'extremely well'*) to what extent the target sentences described an action (activity, $n = 51$), and to what extent the sentences described internal (internal focus, $n = 23$) or external aspects of experience (external focus, $n = 28$). Further details on this procedure can be found in Oosterwijk and colleagues (2012). Another group of participants rated the target sentences and the control sentences in an online rating study ($n = 22$). These participants were asked to rate on a scale from 1 (*'not at all'*) to 5 (*'extremely well'*) to what extent the sentences described a bodily sensation, an emotion and a mental state.

Task

All participants performed a short training-session with feedback prior to scanning. The experimental task was programmed in Eprime (version 2.0, Psychology Software Tools) and presented 80 mental state sentences (20 in each category) and 80 non-mental state sentences in two runs. To ensure deep processing, we instructed participants to judge whether each sentence described a mental state or not (cf. Niedenthal, et al., 2009). Responses were made on an MRI compatible button-box. Each trial started with a 500-millisecond fixation cross. Subsequently, the sentence appeared in the center of the screen for a fixed period of 2500 milliseconds during which the participants could respond. Any response made after 2500 milliseconds was logged as incorrect. Analyses of the response times are presented in the Supplementary Materials. The inter-stimulus-interval was variable with a range between 1000 and 5000 milliseconds. Since we presented our task in two runs, we created different sentence-lists presented in each run that were counterbalanced to control for possible order effects. Within each run, sentences were randomly presented.

Imaging details

Preprocessing and imaging analysis.—Two ~8 minute blood oxygenation level-dependent (BOLD) sensitive fMRI scans were acquired with a Signa EXCITE (GE Healthcare, USA) 3.0 Tesla scanner (T2*-weighted echo planar imaging (EPI) scans, TR = 2500 ms, TE = 22 ms, FOV = 19.2 cm², 64 × 64 matrix, X 2.9 mm axial slices, flip angle = 70 degrees, and 192 whole-brain acquisitions). For anatomical reference we acquired a high-resolution T1-weighted image [spoiled gradient recalled (SPGR), TR=8 ms, TE=3 ms, FOV=25 cm, approximately 1 mm³ voxels].

Functional and structural neuroimaging data were preprocessed with the Analysis of Functional Neuroimages (AFNI) software library (Cox, 1996). Standardized AFNI commands are noted in square brackets. GE x-y slices were reconstructed into AFNI BRIK format. EPI images were co-registered using a 3D-coregistration algorithm developed to minimize the amount of image translation and rotation relative to all other images [3dvolreg]. Voxels with abnormally large amplitudes were replaced by interpolation [3dDespike]. We included two example EPI images in the Supplementary Materials to illustrate the extent of signal dropout in the orbitofrontal and anterior temporal regions. Six motion parameters were used as nuisance regressors to accommodate EPI intensity changes due to motion artifacts. The functional echoplanar dataset was co-registered to the

anatomical images [3dAllineate] and an outlier file was generated to determine if additional time points should be censored based on whether a given time point greatly exceeded the mean number of voxel outliers for the time series [3dToutcount].

The preprocessed images were analyzed using a multiple regression model. Since we did not assume that concept processing effects were dependent on whether a sentence was categorized as describing a mental state or not, we included all trials in our model irrespective of whether participants gave a correct or incorrect answer. Nevertheless, it is important to note that when we performed our analyses while excluding erroneous trials we found highly similar results, which provides evidence that accuracy rates did not drive our effects. Furthermore, to control for the influence of reaction times, we applied the variable-epoch method delimiting the length of trials in each of the five conditions (internal emotion, external emotion, internal non-emotion, external non-emotion, non-mental state) by reaction time (see Grinband, Wager, Lindquist, Ferrera, & Hirsch, 2008; Yarkoni, Barch, Gray, Conturo, & Braver, 2009).

Regressors of interest were generated by convolving [3dDeconvolve] the time series of the individual conditions with a gamma function (Boynton, Engel, Glover & Heeger, 1996) which models the delay and temporal dynamics of a prototypical hemodynamic response (Friston, Frith, Turner, & Frackowiak, 1995; Cohen, 1997). Baseline and motion regressors representing small head movements and linear drift were included in the model. To account for individual anatomical differences, the contrast images were spatially blurred with a Gaussian blur (4mm FWHM) before automated transformation to Talairach space. Significance in pairwise linear contrasts between sentence conditions was determined by voxelwise *t*-tests [3dttest].

In addition to the calculation of contrasts, we also performed separate parametric modulation analyses to examine the relationship between neural activity during mental state trials and the subjective ratings of internal focus, external focus, mental state, emotion, activity, and body sensation. For the individual-level regression analyses, onset times were specified for mental state trials (collapsing across the internal emotion, external emotion, internal non-emotion, external non-emotion conditions) and for non-mental state trials. In each analysis, the rating data consisted of the mean rating for each mental state sentence from the independent sample (e.g., the mean internal focus rating for each sentence). The rating data were mean centered and entered into the regression analysis as auxiliary behavioral covariates associated with the mental state trials. This procedure creates an additional regressor in the model that scales the predicted BOLD response for each trial by the rating data. At the group level, each participant's beta resulting from the parametric modulation regressor was entered into a one-sample *t*-test, which indicated if the mean across subjects differed significantly from zero (zero indicating no correlation between brain activity and the ratings).

Hypotheses testing—To test our hypothesis that processing internal and external sentences involves different patterns of neural activation, we focused on three structurally defined regions of interest (ROIs) that have been previously associated in the literature with the representation of internal and external sensations. ROIs were based on labels identified

by the labeling system created by Desikan, Segonne, Fischl, Quinn, Dickerson, Blacker and colleagues (2006). To examine the recruitment of regions associated with internal states we examined percent signal change in the ventromedial prefrontal cortex (vmPFC), which consisted of the medial orbitofrontal cortex (mOFC) label and the rostral anterior cingulate cortex (rACC) label. The vmPFC ROI corresponds to the ventral part of areas 24, 32, and 14m, the medial part of areas 10, 11m, 14r, and 14c, and the entirety of area 25 (Mackey & Petrides, 2010; 2014). Our second ROI to examine access to internal states was the insula, as defined by Desikan et al.'s insula label. To examine the recruitment of regions associated with external states we examined percent signal change in the inferior frontal gyrus (IFG), which consisted of the pars opercularis (BA44) and the pars triangularis (BA45) label. For each ROI, we extracted percent signal change in the four different mental state vs. non-mental state contrasts. We then performed a repeated measures ANOVA with *region* (vmPFC, insula, IFG), *state* (emotion vs. non-emotion), *focus* (internal vs. external) and *hemisphere* (left vs. right) as repeated factors. Because we found no two-way or three-way interactions between *hemisphere* and *focus* and/or *state*, we performed follow-up repeated measures ANOVA's for each ROI separately on the percent signal change averaged across hemispheres. To correct for multiple comparisons, we performed the three separate ROI analyses and the planned comparisons at an adjusted significance level of .015.

In addition to the ROI analyses, we performed an exploratory whole brain analysis to examine all pairwise linear contrasts between the experimental sentences. To minimize Type I error we used the AFNI command AlphaSim, which estimates on the basis of Monte-Carlo simulations the probability of discovering a cluster of a certain number of contiguous voxels in a field of random noise after the field has been thresholded. With the voxelwise threshold set at $p < 0.005$, clusters must be 8 voxels or larger to be considered significant at a probability of $p < 0.01$.

As a second test of our hypotheses, we performed parametric modulation analyses on the whole brain to examine the relationship between neural activity and subjective ratings of internal and external focus. In further exploration, we also analyzed the mental state, emotion, activity, and body sensation ratings. We applied a threshold of $p < .005$; $k = 8$ as identified by AlphaSim.

Results

Analysis of behavioral data

Manipulation checks—Analysis of the independently-obtained subjective ratings confirmed our categorization of the sentences (see Table 1 for an overview of the means and standard deviations per sentence category). As expected, internal sentences had higher internal focus than external sentences, $M = 4.1$ vs. $M = 3.3$, $F(1, 22) = 27.11$, $p < .001$, $\eta^2_{\text{partial}} = .55$, and external sentences had higher external focus than internal sentences, $M = 3.7$ vs. $M = 2.0$, $F(1, 27) = 84.90$, $p < .001$, $\eta^2_{\text{partial}} = .76$. Participants also rated emotion sentences with higher internal focus than non-emotion sentences, $M = 4.1$ vs. $M = 3.3$, $F(1, 22) = 33.59$, $p < .001$, $\eta^2_{\text{partial}} = .60$, and with higher external focus than non-emotion sentences, $M = 2.99$ vs. $M = 2.73$, $F(1, 27) = 24.43$, $p < .001$, $\eta^2_{\text{partial}} = .48$. Notably, for internal focus we found an interaction between *state* and *focus*, $F(1, 22) = 4.99$, $p < .05$,

$\eta^2_{\text{partial}} = .19$, driven by higher internal focus ratings for internal emotion sentences than all other sentence categories (all p 's < .001). For external focus we also found an interaction between *state* and *focus*, $F(1, 27) = 11.04$, $p < .01$, $\eta^2_{\text{partial}} = .29$. Follow-up t -tests demonstrated that internal emotion and non-emotion sentences differed significantly in external focus ($p < .001$), whereas external emotion and non-emotion sentences did not.

As expected, participants gave emotion sentences a higher emotion rating than non-emotion sentences $M = 4.2$ vs. $M = 2.5$, $F(1, 21) = 79.95$, $p < .001$, $\eta^2_{\text{partial}} = .79$. Furthermore, a main effect of *focus*, $F(1, 21) = 6.53$, $p < .05$, $\eta^2_{\text{partial}} = .24$, indicated that external sentences had a higher emotion rating than internal sentences. This main effect was qualified by an interaction between *state* and *focus*, $F(1, 21) = 11.50$, $p < .01$, $\eta^2_{\text{partial}} = .35$. Importantly, follow-up t -tests demonstrated that internal and external emotion sentences did not differ in emotion rating. The interaction was driven by higher emotion ratings for external non-emotion sentences than internal non-emotion sentences ($p < .01$). In terms of activity, participants gave external sentences a higher rating than internal sentences, $M = 3.8$ vs. $M = 2.5$, $F(1, 50) = 158.46$, $p < .001$, $\eta^2_{\text{partial}} = .76$, and non-emotion sentences a higher rating than emotion sentences, $M = 3.3$ vs. $M = 3.0$, $F(1, 50) = 20.77$, $p < .001$, $\eta^2_{\text{partial}} = .29$. There was no interaction. In terms of bodily sensation, participants gave external sentences a higher rating than internal sentences, ($M = 3.7$ vs. $M = 2.8$), $F(1, 24) = 36.43$, $p < .001$, $\eta^2_{\text{partial}} = .63$, and emotion sentences a higher rating than non-emotion sentences. ($M = 3.5$ vs. $M = 3.1$), $F(1, 21) = 20.31$, $p < .001$, $\eta^2_{\text{partial}} = .49$.

Finally, concerning the mental state rating, the absence of a main effect of *state*, *focus* or an interaction between *state* and *focus* (all $F < 1.24$) indicated that the mental state sentence categories described mental states equally well. Furthermore, all mental state sentences were significantly different from the non-mental state sentences on the mental state, emotion and bodily sensation ratings (all p 's < .001).

Analysis of imaging data

ROI analyses—A 3 (*region*) \times 2 (*state*) \times 2 (*focus*) \times 2 (*hemisphere*) repeated measures ANOVA tested whether brain regions associated with internal and external experiences were engaged differently when people processed sentences with internal and external focus. As predicted, this analysis demonstrated a significant interaction between *region* and *focus*, $F(2, 28) = 4.62$, $p = .018$, $\eta^2_{\text{partial}} = .25$. Furthermore, the analysis demonstrated a significant interaction between *region* and *state*, $F(2, 28) = 9.90$, $p = .001$, $\eta^2_{\text{partial}} = .41$. This analysis was followed by separate ANOVAs for each ROI to discern the interactions in more detail.

Our first hypothesis was that the vmPFC and insula, regions associated with the representation and generation of internal states, would be relatively more active for internal than for external sentences. For the vmPFC, we did not find a main effect of *focus*, $F < 1$, but we did find a significant interaction between *state* and *focus*, $F(1, 14) = 7.80$, $p = .014$, $\eta^2_{\text{partial}} = .36$ (see for a graphical display Figure 1). As expected, planned comparisons demonstrated that internal emotion sentences ($M = .035$; $SE = .040$) engaged the vmPFC significantly more ($p = .002$) than external non-emotion sentences ($M = -.066$; $SE = .024$). The planned comparison between internal emotion sentences and external emotion sentences

approached our adjusted level of significance ($M = .035$; $SE = .040$ vs. $M = -.023$; $SE = .030$; $p = .022$). Internal non-emotion sentences and external non-emotion sentences ($M = -.099$; $SE = .038$ vs. $M = -.066$; $SE = .024$; $p = .25$) did not differ significantly. Finally, although the comparison between internal non-emotion sentences and external emotion sentences did approach significance, the difference was such that external emotion sentences showed more vmPFC activation as compared to internal non-emotion sentences ($M = -.023$; $SE = .030$ vs. $M = -.099$; $SE = .038$; $p = .029$). A significant effect of *state*, $F(1, 14) = 16.75$, $p = .001$, $\eta^2_{\text{partial}} = .55$, further indicated generally stronger engagement of the vmPFC for emotion as compared to non-emotion sentences ($M = .006$; $SE = .033$ vs. $M = -.083$; $SE = .029$). This latter finding is consistent with the hypothesis that emotion sentences are more prone to be represented in terms of their internal quality than non-emotion sentences.

The insula did not show a main effect of *focus*, $F < 1$, nor a main effect of *state*, $F(1, 14) = 1.47$, $p = .26$. We only found a marginally significant interaction between *state* and *focus*, $F(1, 14) = 4.08$, $p = .063$, $\eta^2_{\text{partial}} = .23$. Nevertheless, since none of the planned comparisons approached significance (all p 's $> .2$), we do not further elaborate on this finding.

Our second hypothesis was that the inferior frontal gyrus (IFG), a region associated with action and expression, would be relatively more active for external than for internal sentences. Consistent with this hypothesis, we found a main effect of *focus* that approached significance, $F(1, 14) = 3.54$, $p = .081$, $\eta^2_{\text{partial}} = .20$, suggesting that external sentences indeed engaged the IFG more than internal sentences ($M = .171$; $SE = .029$ vs. $M = .125$; $SE = .031$).

In order to exclude the possibility that our results could be explained by reaction time differences between sentence categories we ran three additional ANCOVA analyses for each region separately. As per the recommendation of Thomas, Annaz, Ansari, Serif, Jarrold and Karmiloff-Smith (2009), we included mean-centered RTs for each condition as covariates in these analyses. Importantly, the analyses for the vmPFC and the IFG did not forward significant interactions between the covariates and the effects of interest (all p 's $< .084$), suggesting that RT differences are not driving our findings. For the insula we did find a significant interaction between *state* and *focus* and one RT covariate, but since none of the planned comparisons in the main analysis for the insula were significant, we do not discuss this finding further.

Whole brain contrasts—The results of the exploratory whole brain contrasts were highly consistent with the ROI analyses. As shown in Figure 2, contrasts comparing internal emotion sentences to each of the other sentence categories revealed clusters in bilateral vmPFC, including the rACC (see also Table 2). The contrast comparing external non-emotion to internal emotion sentences revealed a significant cluster in the anterior insula and the left IFG, including parts of the pars opercularis. None of the other contrasts produced significant clusters.

Parametric modulation analyses—As a further test of our hypotheses, we performed parametric modulation analyses to examine whether ratings of internal and external focus

(produced by an independent sample of participants) correlated with neural activity during sentence processing. The results were highly consistent with the ROI and whole brain analyses. Ratings of external focus were positively correlated with neural activity in the right IFG, middle frontal gyrus (MFG) and superior frontal gyrus (SFG), whereas ratings of internal focus were negatively correlated with neural activity in bilateral IFG, MFG and left supplementary motor area(SMA)/SFG (see Table 3 and Figure 3). At a more liberal threshold ($p < .01$; $k = 6$), predicted clusters of activation in the left rACC and the right posterior insula emerged that positively correlated with ratings of internal focus.

Exploratively, we also performed parametric modulation analyses on the other rating dimensions. As shown in Figure 3, ratings of emotion were positively correlated with neural activity in bilateral ventromedial prefrontal cortex (vmPFC), including the rACC, and in bilateral posterior cingulate cortex (PCC), right paracentral lobule, left parahippocampal gyrus, and amygdala. Ratings of activity were positively correlated with bilateral IFG and the left SMA and MFG. The bodily sensation and mental state rating did not show any significant modulation effects.

Discussion

This study provides evidence for a flexible representation of mental state concepts. Our findings indicate that different patterns of brain activation can represent the same mental state concepts depending on the focus provided by the surrounding linguistic context. These findings are consistent with embodied cognition proposals that argue that simulations are multimodal and dynamic, and depend on the situational context in which a mental state, or any other category, is processed (Wilson-Mendenhall et al., 2011; Barsalou, 2009).

Our first finding was that processing emotion sentences with internal focus engaged the vmPFC (i.e., rACC and mOFC) significantly more than external sentences. This result was both evident from our ROI analysis, and from our explorative whole brain contrasts. Furthermore, a parametric modulation analysis demonstrated that when ratings of internal focus increased, activity in the vmPFC also increased. Because the vmPFC plays an important role in the representation and the generation of internal states (Etkin, et al., 2011; Medford & Critchley, 2010), this finding supports our prediction that representing internal aspects of mental state concepts involves internal simulation. It is important to note, however, that we only found a significant effect for emotion sentences. Thus, even though the difference is subtle, reading sentences such as “*she is sick with disgust*” may lead to a relatively stronger engagement of the ‘internal modality’ (Barsalou, 1999) than reading sentences such as “*she is wrinkling her nose in disgust*”.

This finding supports embodied cognition views that argue for the importance of simulated feelings, introspections and interoceptive changes in representing mental state concepts (Barsalou, 1999; 2009). We believe that a simulation explanation of our findings is most fitting, in particular because the vmPFC is also commonly active during self-relevant processes (Wagner, et al., 2012), including when people process self-relevant emotion words (Herbert, Herbert, & Pauli 2011). Thus, even though our internal emotion sentences described the mental states of other people, the understanding of these sentences involved a

pattern of activation associated with an embodied, first-person perspective (see also Barrett & Satpute, 2013). With this, our findings are consistent with work that shows a role for the vmPFC in “emotion mentalizing”, in which people focus on the affective feelings of the observed (Atique, Erb, Gharabaghi, Grodd, & Anders, 2011), and with work that demonstrates a role for the vmPFC in the integration of embodied information during mentalizing (Lombardo, Chakrabarti, Bullmore, Wheelwright, Sadek, Suckling et al., 2009). Furthermore, our findings connect to suggestions in the literature that the vmPFC plays a central role in the affective significance of concepts (Binder, Desai, Graves & Conant, 2009; Roy, Shohamy, & Wager, 2012).

Our second finding, reflected by a trend, suggested that sentences describing mental states with a focus on external aspects of experience engaged the IFG (i.e., pars triangularis and pars opercularis) more strongly than internal sentences, irrespective of whether the sentences described emotional or non-emotional mental states. A parametric modulation analysis further demonstrated that IFG and SMA activation was correlated with ratings of external focus and activity. Although our ROI analysis did not reach significance, possibly because of limited power due to the number of participants, we do think these results are informative, in particular because they replicate previous work on the understanding of action-related language (Tettamanti et al., 2005; Pulvermüller & Fadiga, 2010). Furthermore, our results are consistent with embodied cognition views that argue for the importance of sensorimotor representations in language understanding (Glenberg & Gallese, 2012) and social cognition (Gallese, et al., 2004).

Situated Conceptualizations

Together our findings are in agreement with the proposal that “*situated conceptualizations*” underlie abstract concepts (Barsalou, 1999; Wilson-Mendenhall et al., 2011; Wilson-Mendenhall, Simmons, Martin & Barsalou, 2013). In this view, a concept -- such as disgust -- includes many different instantiations of disgust, each of which is grounded in a relevant situation. The focal properties of these situated conceptualizations often differ between instances. For example, “*she is sick with disgust*” grounds disgust in a situated conceptualization in which internal sensations play a central role, whereas “*she is wrinkling her nose in disgust*” grounds disgust in a situated conceptualization in which actions and expressions play a central role. Our finding that these different situated conceptualizations resulted in different patterns of activation in the IFG and vmPFC, is consistent with the idea that situated conceptualizations emerge from distributed patterns of brain activation in multimodal systems associated with perception, action, interoception and mentalizing (see also Wilson-Mendenhall et al., 2011; Wilson-Mendenhall et al., 2013).

Although all our sentences described abstract concepts (i.e., mental states), it is important to note that our manipulation of focus could have produced different levels of abstractness at the sentence level. We believe, however, that these differences on a concrete-abstract dimension are an intrinsic property of our sentences. Sentences with external focus may be inherently more concrete than sentences with internal focus, since external aspects of experience (e.g., actions, movements and expressions) can be *seen* on the outside of a person. Thus, referencing the behavioral aspects of a mental event may generate a more

concrete situated conceptualization that grounds the concept in neural systems associated with actions and expressions. Sentences with internal focus, by contrast, may be inherently more abstract than sentences with external focus, since they emphasize internal aspects of experience (e.g., feelings, bodily sensations and introspections) that someone can only access from the *inside*. Thus, referencing the internal aspects of a mental event may generate a more abstract situated conceptualization that grounds the concept in neural systems associated with internal experience (Barsalou, 1999; Barsalou & Wiemer-Hastings, 2005; see for a discussion Wilson-Mendenhall, Simmons, Martin & Barsalou, 2013; see for a similar view Baetens, Ma, Steen & Van Overwalle, 2013). This latter point is consistent with recent work proposing that neural systems associated with “emotional processing” or affective/internal states, including the rACC, play a central role in the processing of abstract words (Vigliocco, Kousta, Della Rosa, Vinson, Tettamatti, Devlin & Cappa, 2013).

Modal vs. amodal accounts

Although we rely on a modal account of concept representation as the framework to explain our results, it is important to mention that our results can be accommodated by accounts of concept representation that emphasize both modal *and* amodal components. First of all, it should be noted that our study aimed to investigate the flexible engagement of frontal areas associated with internal and external states, as a result of processing *the same* concepts in different contexts. Thus, our results do not allow us to draw conclusions about the possibility of context-independent concept meaning, because the activity pattern associated with the “core” meaning of a mental state concept was subtracted out (for arguments against conceptual cores see LeBois, Wilson-Mendenhall & Barsalou, in press). This can explain why we did not find patterns of activation in the anterior temporal lobe, a region reliably found in studies that investigate social concepts (Zahn, Moll, Kreuger, Huey, Garrido, & Grafman, 2007; Ross & Olson, 2010).

Moreover, because our study only assessed the context-dependent meaning of concepts, it cannot differentiate between a theoretical model that argues for a fully distributed and situated representation of concepts (Barsalou, 1999; Wilson-Mendenhall et al., 2011; 2013) and theoretical models that argue for a combination between distributed representation and “core” conceptual content (e.g., Mahon & Caramazza, 2008; Patterson, Nestor & Rogers, 2007). In these latter models the assumption is that although context-dependent representations of meaning (as investigated in our study) may be supported by activation in sensory-motor systems, concepts have context-independent “conceptual cores” that are represented in an amodal way. When we interpret our results along these lines, this would mean that the sentence “*she is sick with disgust*” integrates a context-dependent representation of the concept disgust, supported by modal simulation in the vmPFC, with the “core” conceptual meaning of disgust, possibly supported by an amodal “hub” such as the anterior temporal lobe (Patterson, Nestor & Rogers, 2007). In short, although our results are in agreement with accounts that posit modal simulations as the main process underlying concepts, our findings are also consistent with amodal accounts that incorporate some access to modalities and emphasize contextual flexibility when processing conceptual information.

Emotion vs. non-emotion

Concerning the distinction between emotion and non-emotion sentences, our data showed that although the IFG was only modulated by focus, the vmPFC demonstrated a main effect for emotion and an interaction between focus and emotion. Moreover, parametric modulation analyses demonstrated a correlation between engagement of vmPFC and emotion ratings. These findings are consistent with recent demonstrations that the medial prefrontal cortex (mPFC) plays an important role in emotion experience (e.g., Lindquist, Wager, Kober, Bliss-Moreau & Barrett, 2012) and in other forms of internal mentation (Andrews-Hanna, Reidler, Sepulcre, Poulin, Buckner, 2010; Northoff, et al., 2006; cf. Oosterwijk, Lindquist, Anderson, Dautoff, Moriguchi, & Barrett, 2012). Taken together with the behavioral result of higher internal focus ratings for emotion than non-emotion sentences, these findings imply that people draw more on internal resources when processing emotion sentences as compared to non-emotion sentences. Note, however, that this difference likely reflects a matter of degree, and not a matter of neural separation (see also Pessoa, 2008; Barrett & Satpute, 2013).

One explanation for this finding is that the emotion sentences seem to be more polarized in terms of valence than the non-emotion sentences. Thus, vmPFC activity may reflect affective simulation in order to represent this positive or negative content. Another explanation, although speculative, is that this difference may be explained by a stronger motivation to understand internal aspects of emotions in other people, or by the richer personal experiences that people have with the internal aspects of emotional as compared to non-emotional states. In other words, internal simulation may be a relatively strong “ingredient” in the situated conceptualizations that underlie the understanding of emotions of other people, including when we understand those through language (Barrett, 2012; Oosterwijk & Barrett, 2014).

Mentalizing vs. mirror system

The results of the present study shed new light on recent developments in social neuroscience that propose a dissociation between two neural systems that support social cognition, namely the “mirror system” (IFG, IPL, insula) for vicariously experiencing actions and sensations and a “mentalizing system” (mPFC, PCC/precuneus, temporoparietal junction) for simulation of reflective states (e.g., Waytz & Mitchell, 2011; Spunt & Lieberman, 2011; Zaki & Ochsner, 2012; Keysers & Gazzola, 2007; Van Overwalle & Baetens, 2009). Interestingly, dissociations between these systems are often found when comparing processing of perceptual stimuli portraying action or expression with processing of abstract or verbal stimuli (Lamm, et al., 2011; see also Spunt, Satpute & Lieberman, 2010). In experiments that compared identical stimuli, dissociations were found when participants were instructed to identify actions or to make mental state attributions (Spunt et al., 2010; Spunt & Lieberman, 2011). In our paradigm, however, different involvement of regions in the “mirror system” and “mentalizing” system was solely directed by internal or external focus, while holding instructions constant. Given this, our study not only supports the idea that mental state concepts are embodied, but also for the idea that the brain represents other people’s minds in a flexible fashion depending on the information available in the situational context.

Conclusion

The present study offers novel insights into the contextual modulation of embodied processing. Our findings suggest that in contexts where cues about expressions or actions are a dominant source of information, as in external sentences, simulations of actions are most relevant for understanding. In contexts where cues about internal states are a dominant source of information, as in internal sentences, interoceptive or introspective simulations are most relevant for understanding (see also Oosterwijk & Barrett, 2014; Winkielman et al., 2015; Van Overwalle & Baetens, 2009). These insights fine-tune our understanding of the role of embodied simulation in conceptual processing.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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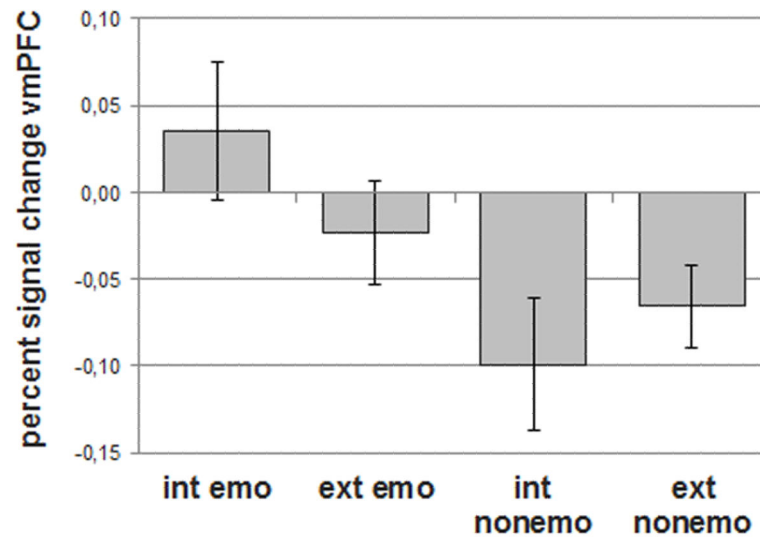


Figure 1.

Extracted percent signal change for the ventromedial prefrontal cortex (vmPFC) in each sentence category. Bars represent standard errors. Int emo = internal emotion sentences; ext emo = external emotion sentences; int nonemo = internal nonemotion sentences; ext nonemo = external non-emotion sentences.

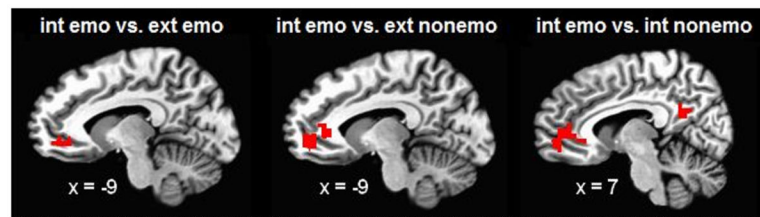


Figure 2.

Visual representation of significant clusters ($p < .005$, corrected) for the internal emotion sentences against all three other mental state sentences.

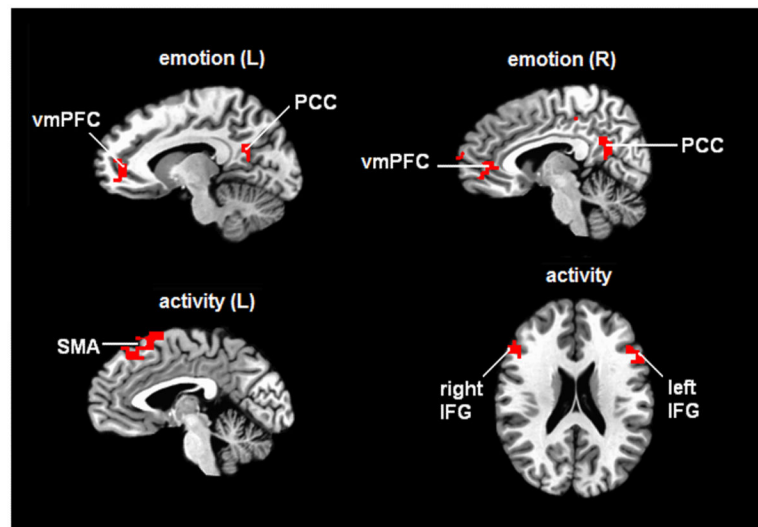


Figure 3.

Visual representation of patterns of neural activity that correlate with ratings of emotion and activity ($p < .005$, corrected). vmPFC = ventromedial prefrontal cortex; SMA = supplementary motor area; IFG = inferior frontal gyrus; PCC = posterior cingulate gyrus; L = left hemisphere; R = right hemisphere.

Table 1

Overview of mean ratings per sentence category.

Rating dimension	Emotion		Non-emotion		Non-mental
	Internal	External	Internal	External	
Internal focus	4.47 ^a (.44)	3.66 ^b (.82)	3.65 ^b (.71)	3.02 ^c (.81)	--
External focus	2.19 ^a (.72)	3.78 ^b (.64)	1.79 ^c (.59)	3.67 ^b (.75)	--
Activity	2.37 ^a (.76)	3.70 ^b (.58)	2.64 ^c (.74)	3.92 ^d (.61)	--
Mental state	3.76 ^a (.88)	3.71 ^a (.94)	3.79 ^a (.60)	3.73 ^a (.68)	1.47 ^b (.56)
Emotion	4.22 ^a (.71)	4.23 ^a (.75)	2.41 ^b (.79)	2.64 ^c (.82)	1.34 ^d (.49)
Bodily	3.00 ^a (.66)	3.90 ^b (.77)	2.67 ^c (.47)	3.58 ^d (.74)	1.54 ^e (.48)

Note. Means (standard deviation in parentheses) with different superscripts differ significantly ($p < .01$). Internal focus, external focus and activity ratings were not collected for non-mental state sentences.

Table 2

Significant clusters in whole brain contrast analyses.

Contrast	size	x	y	z	region
emo int vs emo ext	13	-10	39	-4	left anterior cingulate gyrus
emo int vs nonemo int	134	-10	35	4	left/right mPFC/ACC
	22	10	-53	24	left PCC
emo int vs nonemo ext	67	6	39	4	left/right mPFC/ACC
nonemo ext vs emo int	16	-30	27	4	left IFG/insula
emo ext vs nonemo int	no clusters				
emo ext vs nonemo ext	no clusters				
nonemo int vs nonemo ext	no clusters				

Note. Table shows significant clusters ($p < .005$, corrected) within whole brain contrast analyses, comparing the four different sentences categories to each other. Coordinates are in Talairach space.

Table 3

Significant clusters in parametric modulation analyses.

Rating	size	x	y	Z	Region	direction
external focus	16	42	27	16	right inferior frontal gyrus	ac.
	8	-2	39	52	left superior frontal gyrus	ac.
internal focus	103	-42	31	24	left inferior frontal gyrus/middle frontal gyrus	deac.
	25	-2	27	52	left superior frontal gyrus	deac.
	23	46	27	20	right inferior frontal gyrus/middle frontal gyrus	deac.
	13	-2	11	60	left supplementary motor area	deac.
	9	-58	-41	0	left middle temporal gyrus	deac.
	9	30	23	4	right anterior insula	deac.
	9	-42	11	32	left middle frontal gyrus	deac.
	14*	46	-33	20	right posterior insula	ac.
	6*	-10	43	-4	left anterior cingulate gyrus	ac.
	6*	50	-21	12	right transverse temporal gyrus	ac.
	6*	-34	-33	20	left posterior insula	ac.
emotion rating	46	-10	-57	20	left/right posterior cingulate gyrus	ac.
	42	-10	47	4	left/right medial prefrontal cortex/anterior cingulate gyrus	ac.
	15	-30	23	4	left anterior insula	deac.
	12	-2	63	12	left/right medial prefrontal cortex	ac.
	10	18	31	4	right anterior cingulate gyrus	ac.
	10	2	-29	44	right paracentral lobule	ac.
	9	-18	-9	-16	left parahippocampal gyrus/amygdala	ac.
Activity	47	-42	31	24	left inferior frontal gyrus/middle frontal gyrus	ac.
	47	-2	15	60	left inferior frontal gyrus/ supplementary motor area	ac.
	30	-42	35	0	left inferior frontal gyrus	ac.
	16	50	31	12	right inferior frontal gyrus	ac.
mental state	no clusters					
bodily sensation	no clusters					

Note. Table shows significant clusters ($p < .005$, corrected) within parametric modulation analyses that model the following ratings produced by an independent sample of participants: extent to which the sentences have internal and external focus; extent to which the sentences describe an emotion, an activity, a mental state and a bodily sensation. Coordinates are in Talarairach space.

* Cluster is significant at $p < .01$; $k = 6$.