Dissociation of a trait and a valence representation in the mPFC

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A previous functional MRI adaptation study on trait inference indicated that a trait code is located in the ventral medial prefrontal cortex (vmPFC), but could not rule out that this adaptation effect is due to the trait’s underlying valence. To address this issue, we presented sentences describing positive and negative valences of either a human trait or object characteristic, and manipulated whether the human trait or object characteristic was repeated or not, either with the same or opposite valence. In two trait conditions, a behavioral trait-implying sentence was preceded by a prime sentence that implied the same or the opposite trait. The results confirmed the earlier finding of robust trait adaptation from prime to target in the vmPFC, and also found adaptation in the precuneus and right mid-occipital cortex. In contrast, no valence adaptation was found in two novel object conditions, in which the target sentence again implied a positive or negative trait, but was preceded by a prime sentence that described an object with the same or the opposite valence. Together with the previous study, this indicates that a specific trait code, but not a generalized valence code, is represented in the vmPFC.

Keywords: trait; valence; mPFC; fMRI adaptation

INTRODUCTION
Recent neuroimaging studies have investigated brain regions crucial for forming enduring trait impression of others based on behavioral information. The primary region associated with such tasks is the medial prefrontal cortex (mPFC) (Mitchell, et al., 2004, 2005, 2006; Harris et al., 2005; Schiller, et al., 2009; Baron, et al., 2011; Ma, et al., 2011, 2012a,b; for a review, Van Overwalle, 2009). However, it is still not clear whether the mPFC only processes traits or whether it is also a repository of trait representations, and to what extent trait valence plays a role in this?

According to a simulation account, knowledge about the self is used as an anchor to mentally simulate the traits and preferences of other people (see Tamir and Mitchell, 2010). Support for this account comes from studies showing that the activity of the dorsal part of the mPFC increases linearly with the dissimilarity between self and other (Mitchell et al., 2006; Tamir and Mitchell, 2010). Other studies have demonstrated that when the self is judged first, a subsequent judgment of similar others on the same trait results in a reduction of the functional MRI (fMRI) signal (fMRI adaptation) as if judging the self and similar others rest on the same process. This was not the case for dissimilar others (Jenkins et al., 2008).

An alternative view is that brain activation in the mPFC does not only reflect trait-relevant information processing, but that the mPFC also stores the neural representation or memory code of traits. In other words, the representational approach suggests that trait information is stored in the mPFC and represented by a distributed population of neurons, and investigates in which location this occurs. This idea is in line with the structured event complex framework by Krueger et al., (2009) who argued that the mPFC represents abstract dynamic summary representations that give rise to social event knowledge.

To investigate the existence of a memory code in the brain, neuroscientific researchers often apply an fMRI adaptation paradigm. Adaptation refers to the observation that repeated presentations of a novel stimulus or stimulus characteristics that are variable and irrelevant (Grill-Spector et al., 2006). The adaptation effect has been demonstrated in many perceptual domains, including the perception of colors, shapes and objects and occurs in both lower- and higher-level visual areas (Grill-Spector et al., 1999; Thompson-Schill et al., 1999; Kourtzi and Kanwisher, 2000; Engel and Furmanski, 2001; Grill-Spector and Malach, 2001; Krekelberg et al., 2006; Bedny et al., 2008; Devauchelle et al., 2009; Roggeman et al., 2011; Diana et al., 2012; Josse et al., 2012). Moreover, fMRI adaptation has also been found during action observation (Ramsey and Hamilton, 2010a,b) and trait inferences of similar others as described above (Jenkins et al., 2008).

Recently, Ma et al. (2013) applied an fMRI adaptation paradigm to explore whether the trait concept is represented in the mPFC or not. They presented two sentences in which different actors engaged in different behaviors that either implied the same trait, an opposite trait, or no trait at all in a given context. If fMRI adaptation is found in the mPFC for the non-presented, but implied trait, irrespective of variations in behaviors and actors, this would provide strong support for a trait code. And indeed, these researchers found robust suppression of activation in the ventral mPFC (vmPFC) when a critical trait-implying sentence was preceded by a sentence that implied the same or opposite trait, but not when the preceding sentence did not imply any trait. This suppression effect was found nowhere else in the brain. This seems to indicate that trait concepts are not only processed but also represented by an ensemble of neurons in the vmPFC.

However, this adaptation effect in the vmPFC might not be exclusively due to trait representation. An alternative explanation is that the stimuli used in this study included a set of social behaviors with positive, negative or neutral valence. Hence, the observed adaptation effect might possibly be due to the repetition of valences. In fact, human social behaviors are always highly intertwined with affective connotations and this study did not disentangle the contribution of specific traits vs their underlying valences on the adaptation effect in the mPFC. The aim of this study is to disentangle the contribution of trait and valence.

To verify whether the vmPFC does represent a trait code or responds to the magnitude of valence, this study modified the previous fMRI adaptation paradigm for exploring trait codes (Ma et al., 2013). Like in the earlier trait-adaptation study (Ma et al., 2013), a behavioral trait-implying sentence (the target) was preceded by another sentence.
read a prime sentence involving an object followed by a target sentence involving an agent’s trait-implying behavior that had the same or opposite valence. The target sentence (e.g. ‘Jun gave his brother a hug’ to induce the trait with positive valence) was preceded by a prime sentence that described an object with the same valence (Object-Similar condition, e.g. ‘The photo is nice’) or the opposite valence (Object-Opposite condition, e.g. ‘The soup is sour’). The positive or negative trait or object sentences were counterbalanced across participants, so that each set of prime and target sentences was used in different conditions for different participants. To avoid that participants would ignore the (first) prime sentence and pay attention only on the (second) target sentence, we added a Singleton condition consisting of a single trait-implying behavioral sentence, immediately followed by a trait question. There were 16 trials in each condition.

The trait sentences were borrowed from earlier studies on trait inference using fMRI (Ma et al., 2011, 2012) and event-related potential (ERP, by Van Duynslaeger et al., 2007), while the object sentences were created anew. All the trait sentences were originally created in Dutch and consisted of six words (except 10 sentences with seven words) and most of the object sentences consisted of four words (except three sentences with five words and one sentence with six words). Importantly, a pilot study (n = 55) showed that the mean valence of the trait sentences (M = 6.04 and M = 1.97 for positive and negative traits, respectively) was equivalent to the mean valence of the object sentences (M = 6.01 and M = 2.15, respectively; t(15) < 1, ps > 0.49).

Participants were instructed to infer the agent’s trait from the target sentence and indicated by button press after each trial whether or not a given trait applied to the target description. To avoid associations with a familiar and/or existing name, fictitious ‘Star Trek’-like names were used (Ma et al., 2011, 2012a,b). To exclude any possible adaptation effect resulting from the agent, the agents’ names differed in all the trait-implied sentences. All the sentences were presented at once in the middle of the screen for a duration of 5.5 s. To optimize estimation of the event-related fMRI response, each prime and target sentence was separated by a variable interstimulus interval of 2.5–4.5 s randomly drawn from a uniform distribution, during which participants passively viewed a fixation crosshair. We presented one of four pseudo-randomized versions of the material, counterbalanced between conditions and participants.

**Images procedure**

Images were collected with a 3 Tesla Magnetom Trio MRI scanner system (Siemens medical Systems, Erlangen, Germany), using an eight-channel radiofrequency head coil. Stimuli were projected onto a screen at the end of the magnet bore that participants viewed by way of a mirror mounted on the head coil. Stimulus presentation was controlled by E-Prime 2.0 (www.pstnet.com/eprime; Psychology Software Tools) under Windows XP. Immediately prior to the experiment, participants completed a brief practice session. Foam cushions were placed within the head coil to minimize head movements. We first collected a high-resolution T1-weighted structural scan (MP-RAGE) followed by one functional run (30 axial slices; 4 mm thick; 1 mm skip). Functional scanning used a gradient-echo echoplanar pulse sequence (TR = 2 s; TE = 33 ms; 3.5 × 3.5 × 4.0 mm in-plane resolution).

**Image processing and statistical analysis**

The fMRI data were preprocessed and analyzed using SPM8 (Wellcome Department of Cognitive Neurology, London, UK). For each functional run, data were preprocessed to remove sources of noise and artifacts. Functional data were corrected for differences in acquisition time between slices for each whole-brain volume, realigned...
within and across runs to correct for head movement, and coregistered with each participant’s anatomical data. Functional data were then transformed into a standard anatomical space (2 mm isotropic voxels) based on the ICBM 152 brain template [Montreal Neurological Institute (MNI)], which approximates Talairach and Tournoux atlas space. Normalized data were then spatially smoothed (6 mm full-width-at-half-maximum) using a Gaussian kernel. Afterwards, realigned data were examined, using the Artifact Detection Tool software package (ART; http://web.mit.edu/swg/art/ art.pdf; http://www.nitrc.org/projects/artifact_detect), for excessive motion artifacts and for correlations between motion and experimental design and between global mean signal and the experimental design. Outliers where identified in temporal difference series by assessing between-scan differences (Z-threshold: 3.0, scan to scan movement threshold 0.45 mm; rotation threshold: 0.02 radians). These outliers were omitted in the analysis by including a single regressor for each outlier (bad scan). The ART software did not detect substantial correlations between motion and experimental design or global signal and experimental design.

Next, single participant (first level) analyses were conducted. Statistical analyses were performed using the general linear model of SPM8 of which the event-related design was modeled with one regressor for each condition, time-locked at the presentation of the prime and target sentences and convolved with a canonical hemodynamic response function (with event duration assumed to be 0 for all conditions). Six motion parameters from the realignment as well as outlier time points (identified by ART) were included as nuisance regressors. The response of the participants was not modeled. We used a default high-pass filter of 128 s and serial correlations were accounted for by the default autoregressive AR(1) model.

For the group (second level) analyses, we conducted a whole-brain analysis with a voxel-based statistical threshold of $P < 0.001$ (uncorrected) with a minimum cluster extent of 10 voxels. Statistical comparisons between conditions were conducted using t-tests on the parameter estimates associated with each trial type for each subject, $P < 0.05$ (FWE corrected). We defined adaptation as the contrast (i.e. decrease in activation) between prime and target sentences (i.e. prime > target). This adaptation contrast was further analyzed in conjunction analyses (combining all trait or object conditions) to identify the brain areas commonly involved in the processes of trait inference or evaluation, respectively. More critically, an interaction analysis of the adaptation effect with a trait > objects contrast was conducted to isolate the brain areas involved in a trait code. Likewise, an interaction analysis of the adaptation effect with an object > trait contrast was conducted to isolate the brain areas involved in a non-social valence code. To further verify that the brain areas identified in the previous analysis showed the hypothesized adaptation pattern, we computed the percentage signal change. This was done in two steps. First, we identified a region of interest (ROI) as a sphere of 8 mm around the peak coordinates from the whole-brain interaction as described above. Second, we extracted the percentage signal change in this ROI from each participant using the MarsBar toolbox (http://marsbar.sourceforge.net). We also calculated an adaptation index as the percentage signal change of prime minus target condition. These data were analyzed using ANOVA and t-tests with a threshold of $P < 0.05$. The same strategy was applied for a possible valence code as well.

**RESULTS**

**Behavioral results**

A repeated-measure ANOVA was conducted on the reaction times (RT) and accuracy rates from the five conditions (Table 1). The RT data revealed a significant effect, $F(1, 16) = 36.46$, $P < 0.001$.

<table>
<thead>
<tr>
<th>Condition</th>
<th>Trait-similar</th>
<th>Trait-opposite</th>
<th>Object-similar</th>
<th>Object-opposite</th>
<th>Singleton</th>
</tr>
</thead>
<tbody>
<tr>
<td>RT (ms)</td>
<td>1287</td>
<td>1252</td>
<td>1286</td>
<td>1249</td>
<td>1486</td>
</tr>
<tr>
<td>Accuracy rate (%)</td>
<td>97.8</td>
<td>95.8</td>
<td>96.2</td>
<td>98.5</td>
<td>95.1</td>
</tr>
</tbody>
</table>

Means in a row sharing the same subscript do not differ significantly from each other according to a Fisher LSD test, $P < 0.05$.

Participants responded almost equally fast in the four experimental conditions, and much faster as compared to the Singleton condition. The faster RT in all the four conditions reflect a significant amount of priming across the experimental trials, and so provide behavioral confirmation for the priming manipulation that produces the fMRI adaptation effect. The accuracy rate data revealed significant differences among conditions, $F(1, 16) = 6.60$, $P < 0.001$. Participants responded with higher accuracy in the Trait-Similar and Object-Opposite conditions as compared to the Trait-Opposite, Object-Similar and Singleton conditions.

**fMRI results**

Our analytic strategy for detecting an adaptation effect during trait and valence processing was based on a similar strategy by Ma et al. (2013). First, to identify a common process of trait inference and object–trait evaluation across the Similar and Opposite conditions, we conducted a whole-brain, random-effects analysis contrasting prime > target trials in the Similar and Opposite conditions for traits and objects, followed by a conjunction analysis. Next and more importantly, we conducted a number of Prime > Target interactions to isolate the specific areas involved in trait and valence codes, respectively (Table 2). Second, to verify that the areas isolating the trait and valence code showed the hypothesized adaptation pattern, we defined ROIs centered on the peak values from the whole-brain interaction and extracted the % signal change. From this, we calculated an adaptation index which was submitted to a significance test.

We begin with the trait conditions to isolate a trait code. The whole-brain analysis of the prime > target adaptation contrast revealed significant adaptation effects ($P < 0.05$, FWE corrected) in the mPFC for the Trait-Similar and Trait-Opposite conditions. This adaptation effect was also observed in other brain areas in the Trait-Similar condition, including the left insula, bilateral inferior parietal cortex, right cingulate, bilateral fusiform and bilateral mid-occipital cortex and some of these areas were also significant in the Trait-Opposite condition (Table 2). The conjunction analysis of the Trait-Similar and Trait-Opposite conditions confirmed a common adaptation effect in the vmPFC, bilateral precuneus, bilateral fusiform and right mid-occipital cortex, irrespective of valence.

To identify the brain areas involved in the trait code, we conducted a number of whole-brain interaction analyses with the prime > target adaptation contrast. Specifically, we explored interactions where this prime > target adaptation contrast was present for traits, but absent for objects (Table 2 for the contrast weights, where object conditions receive a uniform ‘1’ weight indicating that this adaptation contrast is absent). We conducted these adaptation contrasts for the Trait-Similar condition, for the Trait-Opposite conditions, and finally for the theoretically most interesting Trait-Similar > Trait-Opposite contrast. This latter contrast gives somewhat more weight to adaptation for similar than for opposite traits. These three interactions showed a consistent pattern of active brain areas that included the vmPFC, left insula, right postcentral cortex, left inferior parietal cortex, cingulate, bilateral fusiform, bilateral pSTS, bilateral precuneus and bilateral
Trait adaptation: interaction of prime > target contrast with traits only (not objects)

Coordinates refer to the MNI stereotaxic space. All clusters thresholded at \( P < 0.01 \) with at least 10 voxels. Only significant clusters are listed. The contrasts between parentheses refer to the prime and target in the Trait-Similar, Trait-Opposite, Object-Similar, Object-Opposite conditions, respectively. *Predicted trait-adaptation pattern in a % signal change analysis was significant according to a t-test (\( P < 0.05 \)); the predicted valence adaptation pattern was nowhere significant. **\( P < 0.05 \), ***\( P < 0.01 \), ****\( P < 0.001 \) (FWE corrected).

mid-occipital cortex. However, it is possible that the results of these interactions are driven by some difference between trait and object conditions, but not necessarily by the predicted adaptation pattern. To verify which of these brain areas would reveal the predicted adaptation effect for traits but not for objects, we defined ROIs centered at the peak value of the clusters identified by latter whole-brain interaction (i.e. prime > target contrast in interaction with Trait-Similar > Trait-Opposite; Table 2). We then calculated an adaptation index by subtracting the percentage signal change in the target sentence from the prime sentence (Figure 1). Statistically, a trait code would be revealed when adaptation is present for traits, and less so for objects, that is, when the adaptation index is significantly larger for traits than for objects. This difference was largest for the vmPFC (\( P < 0.001 \)) as predicted, followed by the bilateral precuneus (\( P < 0.01 \)) and right mid-occipital cortex (\( P < 0.05 \); all \( \Delta f > 17 \)). No other brain area showed this predicted adaptation pattern.

To ensure that these areas (including the vmPFC) were involved only in adaptation (i.e. decrease of activation and no increase of adaptation for objects) revealed when adaptation is present for traits, and less so for objects, that is, when the adaptation index is significantly larger for traits than for objects. This difference was largest for the vmPFC (\( P < 0.001 \)) as predicted, followed by the bilateral precuneus (\( P < 0.01 \)) and right mid-occipital cortex (\( P < 0.05 \); all \( \Delta f > 17 \)). No other brain area showed this predicted adaptation pattern.

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activation), we also conducted a whole-brain analysis of the reverse target > prime contrast in the Trait-Similar and Trait-Opposite conditions (Table 3). The results revealed a series of brain areas that were more strongly recruited during the presence of the target sentence, including the left mid-orbital frontal cortex, right insula, supplementary motor cortex, bilateral inferior parietal cortex and lingual gyrus. Importantly, there was no activation of the mPFC, precuneus or mid-occipital.

We applied a similar set of analyses using the same logic to detect a potential adaptation effect for valence. The whole-brain analysis of the prime > target adaptation contrast for object conditions (i.e. object–trait pairs with similar or opposite valance) revealed significant adaptation effects ($P<.05$, FWE corrected) in the fusiform and left mid-occipital areas for the Object-Similar and Object-Opposite conditions (Table 2). The left fusiform and left mid-occipital cortex were also involved in a conjunction analysis. We then tested for a stronger (prime > target) adaptation effect for similarly as compared to oppositely valenced stimuli. Specifically, we conducted a whole-brain interaction analysis of the adaptation contrast on the prime > target contrast and on the Similar > Opposite valence contrast. This analysis revealed a valence adaptation effect for traits, but not for object–trait pairs (Table 2), which runs against the idea of a generalized valence effect irrespective of stimulus type. Moreover, the adaptation index for the brain areas (also computed from ROIs centered around the whole-brain peak values in the same manner as before) failed to show significant differences between Similar and Opposite valences for object–trait pairs. Because these differences are essential for a valence interpretation, this failure is very damaging for this hypothesis. The whole-brain analysis of the reverse target > prime contrast in the Object-Similar and Object-Opposite conditions revealed several brain areas (Table 3), but no mPFC activation.

Fig. 1 Percent signal change in the ventral prefrontal cortex, bilateral precuneus and right mid-occipital for the prime and target sentences in all conditions, and for the adaptation index (target–prime condition) based on four ROIs centered around the peak values in the interaction analysis (with MNI coordinates, vmPFC: $-6 48 -4$; left precuneus: $-12 -54 20$; right precuneus: $18 -54 20$; right mid-occipital: $44 -76 30$).
DISCUSSION
Numerous neuroimaging studies have revealed that the mPFC is involved in inferring traits of others or the self (Ma et al., 2012b; for a review, see Van Overwalle, 2009). Traits are not only processed but also represented in the vmPFC irrespective of specific behaviors, as revealed in a novel adaptation study by Ma et al. (2013). This is an important finding, because it sheds light on how exactly traits are represented in the brain, and how neural dysfunctions such as lesions might disrupt this process. However, because human social behaviors and traits are highly intertwined with affective meaning and feelings, and because the vmPFC is proposed to be critical in the generation of affective meaning (e.g. an aggressive agent) which follow from these goal interpretations (e.g. an aggressive act), whereas traits are secondary inferences (e.g. an aggressive act), whereas traits are secondary inferences, it is necessary to disentangle the role of valence in trait representation. This was the aim of this study.

Trait code only in the vmPFC
The results confirmed the previous study (Ma et al., 2013) that a trait code is represented in a distinct location of the vmPFC—and only the trait code. There is no coding of general valence. This conclusion was made possible by including two novel object conditions in this study, with a similar or opposite valence than the traits. We found that adaptation of general valence from object prime sentences to trait target sentences was absent. In contrast, adaptation from prime to target sentences for traits was robust, and was revealed in the same location as the earlier trait-adaptation study (Ma et al., 2013). It was further confirmed by the adaptation index, which showed a great amount of adaptation for similar and opposite traits, but not for object–trait pairs. Interestingly, the finding that similar and opposite traits show approximately the same amount of adaptation was also demonstrated in the earlier Ma et al. (2013) study, and demonstrates that a trait and its opposite seem to be represented by a highly similar and overlapping neural population in the mPFC. Presumably, it is mainly the trait content itself that is represented in the trait code, and less so the extent to which the trait is expressed. For instance, stating that a person is not romantic often makes one think of romantic behaviors and then negates them. This is in line with the schema-plus-tag model, in which a negated trait is represented as the original (true) trait with a negation tag (Mayo et al., 2004).

Our finding that the vmPFC houses the neural substrate of a trait code is consistent with the claim that one of the primary functions of PFC is the representation of action and guidance of behavior (Barbey et al., 2009; Forbes and Grafman, 2010). According to these authors, series of events form a script that represents a set of goal-oriented actions, that is sequentially ordered and guides perceptions and behavior. These scripts—also referred to as structured event complexes—are represented as memory codes in the brain, and upon activation, can guide the interpretation of observed behavior and the execution of behaviors (Grafman, 2002; Wood and Grafman, 2003; Barbey et al., 2009). This is in line with the social psychology literature that conceives traits as abstracted instances of goal-directed behaviors (see also Read, 1987; Read et al., 1990, Reeder et al., 2004; Reeder, 2009). Recent behavioral and neural evidence confirms that goals are primary inferencies (e.g. an aggressive act), whereas traits are secondary inferencies (e.g. an aggressive agent) which follow from these goal interpretations (Van Duytslaeger et al., 2007; Van der Cruyssen et al. 2009; Ma et al., 2012b; Malle and Holbrook, 2012; Van Overwalle et al., 2012). Neuroimaging studies confirm that trait inferences involve a high-level form of abstraction of agent characteristics on the basis of lower-level actions (Spunt et al., 2010; Baetens et al., 2013; Gilead et al., 2013).

Table 3 The target > prime contrast from the whole brain analysis

<table>
<thead>
<tr>
<th>Anatomical label</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Voxels</th>
<th>Max t</th>
<th>Similar traits</th>
<th>Opposite traits</th>
<th>Conjunction: Similar and Opposite traits</th>
</tr>
</thead>
<tbody>
<tr>
<td>Target &gt; prime contrasts for traits</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L mid-orbital frontal</td>
<td>42</td>
<td>48</td>
<td>-4</td>
<td>872</td>
<td>5.96***</td>
<td>-42</td>
<td>48</td>
<td>-2 795 5.95***</td>
</tr>
<tr>
<td>R insula</td>
<td>34</td>
<td>22</td>
<td>-6</td>
<td>3949</td>
<td>8.05***</td>
<td>32</td>
<td>24</td>
<td>-4 3857 8.03***</td>
</tr>
<tr>
<td>Supplementary motor</td>
<td>-4</td>
<td>18</td>
<td>48</td>
<td>7009</td>
<td>8.21***</td>
<td>-4</td>
<td>18</td>
<td>48 6337 8.21***</td>
</tr>
<tr>
<td>R parahippocampal</td>
<td>12</td>
<td>2</td>
<td>-8</td>
<td>340</td>
<td>5.20***</td>
<td>-32</td>
<td>50</td>
<td>-50 4229 7.90***</td>
</tr>
<tr>
<td>L inferior parietal</td>
<td>-32</td>
<td>-50</td>
<td>48</td>
<td>2467</td>
<td>7.90***</td>
<td>-32</td>
<td>-50</td>
<td>48 2253 7.90***</td>
</tr>
<tr>
<td>R inferior parietal</td>
<td>36</td>
<td>-50</td>
<td>44</td>
<td>1696</td>
<td>6.69***</td>
<td>36</td>
<td>-50</td>
<td>44 1579 6.69***</td>
</tr>
<tr>
<td>R fusiform</td>
<td>30</td>
<td>-60</td>
<td>-22</td>
<td>611</td>
<td>6.01***</td>
<td>30</td>
<td>-22</td>
<td>611 5.16*</td>
</tr>
<tr>
<td>L fusiform</td>
<td>-8</td>
<td>76</td>
<td>24</td>
<td>937</td>
<td>5.83</td>
<td>-8</td>
<td>76</td>
<td>24 5.83</td>
</tr>
<tr>
<td>Lingual gyrus</td>
<td>-6</td>
<td>-74</td>
<td>-24</td>
<td>937</td>
<td>5.83</td>
<td>-6</td>
<td>-74</td>
<td>-24 850 5.83</td>
</tr>
</tbody>
</table>

Coordinates refer to the MNI stereotaxic space. All clusters thresholded at P < 0.001 with at least 10 voxels. Only significant clusters are listed. The contrasts between parentheses refer to the prime and target in the Trait-Similar, Trait-Opposite, Object-Similar, Object-Opposite conditions, respectively. *P < 0.05, **P < 0.01, ***P < 0.001 (FWE corrected also).
A role for the precuneus?

This study also revealed that the bilateral precuneus was involved in trait adaptation. At first sight, this might seem to confirm findings from the previous fMRI adaptation study (Ma et al., 2013). This study found that the precuneus was involved in adaptation of trait-relevant sentences (Trait-Similar and Trait-Opposite conditions) as well as trait-irrelevant sentences. However, the precuneus showed no adaptation when the trait-irrelevant condition served as control (i.e. trait-relevant > trait-irrelevant contrast). Ma et al. (2013) explained the activation of the precuneus by assuming that some minimal amount of a trait inference process takes place even for irrelevant control sentences, due to the explicit instructions to infer a trait. Thus, participants might have attempted to infer a trait even when the behavior was non-diagnostic. This study adds another explanation. It starts from the observation that the trait-irrelevant sentences which served as control in the previous study (Ma et al., 2013) were similar to the trait-relevant sentences in all respects, except for the fact that a trait was not implied. However, in this study, there were more differences in the object sentences which served as control. Object sentences had no two interacting agents but only an object and the verb did not represent an intentional action but rather an unintentional state or observation (e.g. ‘is’, ‘smells’), hence rendering the overall scene completely different. Given that the precuneus is strongly involved in scene construction (Hassabis and Maguire, 2007; Speer et al., 2007), we presume that its activation in this study is due to these larger differences between the trait sentences in comparison with the object sentences. That is, the larger difference between the trait and the object conditions may have increased the perceived similarity within the trait conditions, increasing adaptation not only for traits but also for scenes and so may have activated the precuneus. We found additional activation in the occipital cortex that survived a significant test of the adaptation index, and which—using the same logic—may be related to the greater complexity of and consequently increased attention to the trait sentences in comparison with the object control sentences.

Nevertheless, it is possible that the precuneus serves a role in trait representation, albeit at a more indirect level. In support of this idea, it has been suggested that the precuneus may be associated with mentalizing to some extent (see meta-analyses by Carrington and Bailey, 2009; Mar, 2011; Schilbach et al., 2012), the situational structure and context or construction of a scene, which includes the integration of relevant behavioral information into a coherent spatial context (Hassabis and Maguire, 2007; Speer et al., 2007), and the retrieval of episodic context information including autobiographic memory (Spreng et al., 2009). This may indicate that the precuneus reflects episodic information, such as a scene or situational background with prospective social intention, linked to the abstract trait concept represented in the vmPFC. This is also consistent with the simulation account proposed by Mitchell (2009; see also Tamir and Mitchell, 2010) which states that perceivers attribute mental states to another person by using their own mind as a model of the other mind. Mitchell (2009) suggested that individuals can use their previous knowledge and experience (by retrieving episodic or autobiographic memory which recruits the precuneus, e.g. Spreng et al., 2009) or their own mental traits (self-referential processing which recruits the mPFC) as proxies for understanding other minds (Mitchell et al., 2005; Jenkins et al., 2008). Nevertheless, so far several studies failed to find functional connectivity between the vmPFC and the precuneus during trait processing of others (Lombardo et al., 2010) and self-processing (Schmitz and Johnson, 2006; Sajonz et al., 2010; Van Buuren et al., 2010; Whitfield-Gabrieli et al., 2011). Future studies should further investigate this functional connectivity during trait judgments of others.

Limitations

This study attempted to dissociate trait and valence representations based on the previous fMRI study on trait adaptation (Ma et al., 2013). To address this issue, we replaced the trait-irrelevant condition in the previous study with two objects conditions. To control for the total scanning time and to keep the participants attentive, we decreased the number of trials to 16 for each condition. This lowered the statistical power and reliability of this study (Button et al., 2013). Moreover, the creation of two new object-conditions may have induced confounding factors, such as imaging the objects described in the
sentences, which activated the fusiform and other brain areas (Simons et al., 2003; Grill-Spector et al., 2004). Nevertheless, even under these less ideal circumstances, the peak coordinates in the vmPFC (−6 48 −4) of this study were very close to the previous fMRI findings on trait adaptation (−6 42 −14; Ma et al., 2013). This suggests that the current findings are quite robust, and confirms that a trait code is represented in vmPFC.

CONCLUSION
We demonstrate here that the vmPFC houses a trait code, independently from the valence that comprises this trait. This study was set up to detect a valence code, but we found no adaptation effect for it, only for traits. Although this finding awaits further confirmation, it is important because it indicates that a full trait meaning and valence is achieved after the appropriate trait code is activated upon receiving a stimulus input, and so allows further processing in the brain. Whether valence is first extracted upon activating the trait code, followed by a fuller trait meaning, or vice versa, is not clear from the present findings. In general, the results are in line with the social brain hypothesis (Dunbar 1992, 2003) which states that during human evolution, the frontal brain has been expanded greatly among humans compared with non-human primates because of evolutionary pressures to live and collaborate in increasingly larger groups, and to store interpersonal trait knowledge in the brain. The present results also suggest that neural dysfunction in this particular area of the vmPFC may severely disrupt trait identification and processing, as patients lose the capacity to form a deep trait meaning, rendering any interpretation of human action superficial and incapable of integration with concrete behavior (Milne and Grafman, 2001; Young et al., 2010). We suggest that they lack an essential key to do so fluently and adequately: the trait code.

REFERENCES


