Imaging tactile imagery: Changes in brain connectivity support perceptual grounding of mental images in primary sensory cortices

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ARTICLE INFO

Article history:
Accepted 6 May 2014
Available online 13 May 2014

Keywords:
Mental imagery
Vibrotactile
Perceptual grounding
Core construction system
fMRI
Psychophysiological interaction (PPI)
Connectivity

ABSTRACT

Constructing mental representations in the absence of sensory stimulation is a fundamental ability of the human mind and has been investigated in numerous brain imaging studies. However, it is still unclear how brain areas facilitating mental construction processes interact with brain regions related to specific sensory representations. In this fMRI study subjects formed mental representations of tactile stimuli either from memory (imagery) or from presentation of actual corresponding vibrotactile patterned stimuli. First our analysis addressed the question of whether tactile imagery recruits primary somatosensory cortex (SI), because the activation of early perceptual areas is classically interpreted as perceptual grounding of the mental image. We also tested whether a network, referred to as ‘core construction system’, is involved in the generation of mental representations in the somatosensory domain. In fact, we observed imagery-induced activation of SI. We further found support for the notion of a modality independent construction network with the retrosplenial cortices and the precuneus as core components, which were supplemented with the left inferior frontal gyrus (IFG). Finally, psychophysiological interaction (PPI) analyses revealed robust imagery-modulated changes in the connectivity of these construction related areas, which suggests that they orchestrate the assembly of an abstract mental representation. Interestingly, we found increased coupling between prefrontal cortex (left IFG) and SI during mental imagery, indicating the augmentation of an abstract mental representation by reactivating perceptually grounded sensory details.

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Introduction

The cognitive process of forming mental images in the absence of perceptual stimuli is a fundamental aspect of human cognition. It underlies future thinking and thereby enables planning and supports decision-making. Mental imagery has therefore always attracted cognitive neuroscientists (e.g. Shepard and Metzler (1971)) and Kosslyn (1973) and research has broadened to all sensory modalities and content of diverse complexity (Albright, 2012; Hassabis and Maguire, 2007, 2009; McNorgan, 2012; Schacter et al., 2012).

Initial neuroimaging work was dominated by the question of whether mental imagery activates early sensory cortices, a phenomenon we refer to as perceptual grounding (Barsalou, 2008; Kosslyn et al., 2001). Overlap in neural activation during imagery and perception strengthened the view that the nature of mental representations is formed by our perceptual apparatus and experience. Evidence for such early sensory activation has now accumulated across different modalities, where activation of early sensory cortices appears dependent on how fine-grained the mental image is (Kosslyn and Thompson, 2003; McNorgan, 2012; Thompson et al., 2009). The imagery literature is dominated by work on “the mind’s eye”, while other sensory modalities are underrepresented, such as the somatosensory domain (Newman et al., 2005; Olivetti Belardinelli et al., 2009; Yoo et al., 2003). To fill this gap and to facilitate the identification of modality independent principles, our study focused on tactile imagery.

The construction process of mental image generation involves memory retrieval, forming and maintenance of a mental representation, and finally a conscious experience similar to perception (Moulton and Kosslyn, 2009; Schacter, 2012; Schacter et al., 2012). On the neural level, a “core construction network” is activated during the assembly of mental representations independently of content and modality (Hassabis and Maguire, 2009; Summerfield et al., 2009, 2010). The few initial reports on network properties, such as changes in connectivity during imagery, leave the question open of how the construction network interacts with the brain areas related to perceptual grounding (Chen et al., 2009; Deshpande et al., 2010; Gao et al., 2011; Kasess et al., 2008; Mechelli et al., 2004; Schlegel et al., 2013). It has been suggested that the modality independent core network couples to task specific regions including sensory areas (Schacter et al., 2012). Here we employed...
a novel tactile imagery recall task that necessitated to actively form a mental representation to test if changes in connectivity can reveal new insights into the construction process of mental representations.

Our paradigm was inspired by a classic visual imagery task of letters in a grid (Podgorny and Shepard, 1978). Analogously, we used a 16-pin Braille display to present vibrotactile bar-patterns. Subjects either perceived or imagined tactile stimuli and reported whether a probe-pin was included in a pattern or not. This demanding discrimination task compelled subjects to form mental representations of fine-sensory detail and allowed the behavioral assessment of their performance.

We hypothesized that this task necessitates perceptual grounding in SI and involves the activation of the core construction network. We then tested for modulations of functional interaction between the construction network and brain areas associated with the content of the mental representation and provide new evidence for the role of the prefrontal cortex in interacting with early perceptual areas.

Materials and methods

Participants

Fourteen healthy volunteers (age range: 22–30 years; 8 males, one left-handed) without any neurological or psychiatric disorder completed the study after giving written informed consent. The study corresponded to the Human Subject Guidelines of the Declaration of Helsinki and was approved by the Ethics Committee of the Charité University Hospital Berlin.

Experimental stimuli and conditions

To test for perceptual grounding and the involvement of the construction system in tactile imagery, we designed a vibrotactile imagery task inspired by classical investigation of visual imagery (Podgorny and Shepard, 1978) with three experimental conditions: (1) PERCEPTION, (2) IMAGERY, and (3) CONTROL (Fig. 1A). In short, subjects indicated whether a probe stimulus was covered by a particular vibrotactile pattern or not, where this pattern stimulus was either perceived or imagined. In the control condition subjects detected a hardly detectable gap within the probe stimulus.

Vibrotactile stimuli (1.5 s duration) were delivered to the left index finger using a 16-dot piezoelectric Braille display (4 × 4 matrix with 2.5 mm spacing) controlled by a programmable stimulator (Piezostimulator, QuaeroSys, St. Johann, Germany). Four vibrotactile patterns were defined consisting of eight pattern pins and eight background pins (Fig. 1B). Pattern pins were driven by a 120 Hz sinusoidal carrier signal, which was amplitude-modulated by a half sine wave to smooth stimulus on- and offsets while the background pins were retracted during stimulus presentation. Prior to the experiment, participants were trained to associate a set of four color cues with the four vibrotactile patterns.

The trials in the fMRI paradigm were constituted as follows: (1) In the PERCEPTION condition, subjects were presented with one of the four vibrotactile pattern stimuli. In addition to the pattern pins a probe pin was applied with 8 Hz oscillatory amplitude modulation around half a sine wave. On each trial the participant’s task was to decide whether or not the probe pin was included in the pattern and indicate this by a right-hand button-press response. The mapping between yes/no answers and fingers was counterbalanced over subjects. The probe was part of the pattern in 50% of the trials. A color cue was presented to match the low-level visual stimulation to the IMAGERY condition. Subjects were intensively trained on the cue-pattern association, the cue was meaningless (different color set) to avoid automatic imagery upon cue presentation. Thereby the meaningless cue prevented any interaction of imagery and perceptual processes in the PERCEPTION condition. (2) On each trial of the IMAGERY condition, participants were cued with one of the learned color displays to imagine the corresponding vibrotactile pattern and as in the PERCEPTION condition to indicate via button press, whether a probe pin was included in the (mentally represented) pattern or not. (3) In the CONTROL condition, no vibrotactile pattern was presented. Instead, only the probe pin was presented together with a meaningless color cue. The participant’s task was to indicate whether the probe pin vibration was briefly interrupted or not. In 25% of the trials it was paused for half of an 8 Hz sinusoidal oscillation (i.e. 62.5 ms) either 375 ms after stimulus onset or 375 ms before stimulus offset. Both temporal positions of the interruption were equally probable to ensure the participant’s continuing...
attention throughout the probe pin presentation. In all conditions, trials lasted 3 s comprising a 1.5 s stimulus presentation and a 1.5 s response window.

We employed simple visual stimuli to cue the recall of tactile perceptions. Visual stimuli were simple color patches to be used only as a recall cue without any further visual processing demands to foster the modality-specificity of the imagery processes to the tactile domain. To render visual strategies unlikely, our task was designed to require detailed spatial resolution of the tactile percept. Additionally, subjects were instructed to mentally reactivate how the percept of the vibrotactile stimulus had felt on their finger. Debriefing of the subjects after the experiment did not reveal the use of visual strategies.

fMRI experimental design and data acquisition

fmri data acquisition

Functional imaging was performed on a 1.5 Tesla Siemens Sonata MRI scanner (Siemens Medical Solutions, Erlangen, Germany) equipped with a standard circular polarized head coil. T2*-weighted images were acquired with a gradient-echo planar image sequence (TR = 2010 ms, TE = 40 ms, flip angle = 90°). Each EPI volume consisted of 36 axial slices covering the whole brain in an interleaved slice ordering (voxel size 3 × 3 × 3 mm³, matrix size 64 × 64).

fmri data analysis

The fMRI data were pre-processed with SPM8 (Wellcome Trust Centre for Neuroimaging, Institute for Neurology, University College London, London, UK). To minimize movement-induced image artifacts each data set was realigned to its mean image. Next, masks defining gray and white matter were generated for each subject by segmenting each data set was realigned to its mean image. Next, masks defining gray and white matter were generated for each data set was realigned to its mean image. After estimating the inter-subject alignment by matching tissue class images together, the warping parameters were used to transform each subject's fMRI volumes into MNI space. Finally, the EPI images were re-interpolated to 2 × 2 × 2 mm³ voxel size and spatially smoothed with an 8 mm FWHM Gaussian kernel.

fMRI statistical analysis was performed according to a standard general linear model (GLM) approach using a two-level mixed-effects analysis in SPM8. At the subject level, regressors were specified for the event related design as trial onset regressors separately for: PERCEPTION, IMAGERY, CONTROL and CONTROL interrupted where the last regressor refers to those trials with interrupted presentation of the probe pin. To account for potential confounds of response time differences between conditions, we included an additional regressor with the button-press onset of each trial. Further the movement parameters were modeled as regressors of no interest. After the model was fitted to the experimental data contrast images were first evaluated at the single-subject level and then passed to second-level one-sample t-tests. For one subject the data of two runs was excluded as the subject reported to have confused the task conditions.

We also sought to identify the network that underpins the mental representation of vibrotactile patterns, shared by PERCEPTION and IMAGERY. We tested the respective contrasts to the CONTROL condition against the conjunction null hypothesis (Friston et al., 1999; Nichols et al., 2005). Specifically, the CONTROL condition trials were divided equally and arbitrarily into two distinct sets and modeled as separate regressors. This separation allowed for independent computation of the conjunction contrasts (PERCEPTION > CONTROL1 and IMAGERY > CONTROL2), which required separate trials for independent baselines. At the second level this modification resulted in a 2 × 2 within-subject ANOVA, with factors condition (PERCEPTION, IMAGERY) and control (CONTROL1, CONTROL2), which was assessed using a flexible factorial within-subject GLM including a between-subject factor.

To test for temporal aspects of BOLD responses, we computed peristimulus time histograms using the rfxplot second-level analysis toolbox (Glascher, 2009), where time-courses were only adjusted for block and nuisance effects.

Connectivity analysis

Task-dependent connectivity modulations were assessed using the psychophysiological interaction (PPI) approach as implemented in SPM8 (Friston, 2011; Friston et al., 1997; Gitelman et al., 2003). To identify how core regions of the construction system interact with perceptual areas during imagery, we defined four seed regions-of-interest within the core construction network based on our GLM analysis. For each seed region the first eigenvariate of the BOLD time-series was extracted from voxels within a 4 mm radius sphere around the subject-specific peak voxel in the contrast IMAGERY > PERCEPTION, individually thresholded: left retrosplenial cortex (RSC) (x = −14.0 ± 2.9, y = −60.1 ± 5.7, z = 21.3 ± 5.6), right RSC (x = 15.3 ± 3.7, y = −58.4 ± 4.5, z = 20.7 ± 6.5), precuneus (x = 20.0 ± 2.7, y = −58.9 ± 3.5, z = 47.9 ± 6.0), and left IFG (x = −41.7 ± 3.0, y = 22.4 ± 5.3, z = 24.7 ± 5.1). The deconvolved time-series were multiplied by the psychological variables (IMAGERY > PERCEPTION contrast, expressed as onset weights [1 −1], and reconvolved with the HRF to obtain the PPI interaction-terms (Gitelman et al., 2003). On the single-subject level our multi-run PPI design contained sets of three regressors per run: interaction-term, time-series and psychological factor supplemented with a run constant. PPIs were estimated and the interaction term parameter estimates were forward to second-level t-tests.

All reported coordinates correspond to MNI space. The SPM anatomy toolbox was used to establish cytoarchitectonical references where possible (Eickhoff et al., 2007, 2008). All activations are reported at p < 0.05, corrected for false discovery rate (FDR) at the cluster level, except if stated otherwise.

Results

Behavioral data

To test that the three task conditions were similarly demanding, we compared performance levels expressed as percentage of correct responses: PERCEPTION: 76.5 ± 11.8% (SD), IMAGERY: 73.7 ± 9.3%, CONTROL: 76.5 ± 12.3 (one-way ANOVA between conditions F(2,26) = 0.56, p = 0.577). This corresponds to a hit-rate for PERCEPTION of 61.3 ± 15.9%, for IMAGERY of 58.8 ± 12.4%, and for CONTROL of 46.1 ± 30.2% and a correct rejection-rate for PERCEPTION
of 84.1 ± 9.3%, for IMAGERY of 78.7 ± 8.2%, and for CONTROL of 91.9 ± 5.4%, resulting in mean d′ for PERCEPTION of 1.58 ± 0.70, for IMAGERY of 1.29 ± 0.59, and for CONTROL of 1.69 ± 1.59 and mean bias C for PERCEPTION of −0.12 ± 29.3, for IMAGERY of −0.04 ± 16, and for CONTROL of 0.13 ± 0.44. A repeated-measures ANOVA revealed no significant differences between the three conditions in d′ (F(2,26) = 1.407, p = .263) or in C (F(2,26) = 2.947, p = 0.70). Median response times (RTs), assessed as delay after onset of the response display, were compared in a one-way ANOVA (F(2,26) = 4.88, p = 0.016) and post-hoc paired t-tests revealed significantly elongated RTs in IMAGERY (666 ± 106 ms) as expected (Formisano et al., 2002; Kosslyn, 1976) when compared to PERCEPTION (578 ± 130 ms, t(13) = 4.68, p < 0.01) but not to CONTROL (595 ± 139 ms, t(13) = 1.99, p = 0.06). For one subject the RTs of two runs were lost due to computer failure.

fMRI data

The contrast PERCEPTION > CONTROL was evaluated to identify task-related network activation of processing a patterned vibrotactile stimulus when perceiving it. As expected, this contrast revealed increased activation in a tactile processing network comprising contralateral primary and secondary somatosensory cortex, intraparietal sulcus (IPS) and supplementary motor area (SMA; see Fig. 2A and Table 1A; Blankenburg et al., 2006; Bodegard et al., 2001; Burton and Sinclair, 2000; Francis et al., 2000; Moore et al., 2013; Wacker et al., 2011). The contrast also revealed activation in right lateral occipital complex (LOC) matching reports on visuo-haptic object-related clusters termed lateral occipital tactile–visual area (LOtv; Amedi et al., 2001, 2002, 2007).

Perceptual grounding and stimulus representation

To test for perceptual grounding of mental representations, we performed two analyses. First, we contrasted the IMAGERY and CONTROL conditions, where only the first required a mental representation of a tactile stimulus while both conditions were matched regarding physical stimulation. We found activation in IPS, superior parietal lobe (SPL), inferior parietal lobe (IPL), the frontal eye fields (FEF), inferior frontal gyrus (IFG) and bilateral LOtv. Crucially, this contrast also revealed activation of the right SI, supporting the concept that the mental image is grounded in perceptual areas. As the employed IMAGERY condition involves the recall of a previously learned stimulus, memory retrieval...
related activation was expected. Correspondingly, we found the right parahippocampal region activated. Fig. 2B and Table 1B summarize the corresponding activation pattern.

Second, we sought to identify brain regions related to the mental stimulus representation by means of a conjunction analysis. Because for both the PERCEPTION and IMAGERY conditions a mental representation of the tactile pattern had to be formed, we computed the conjunction of their contrasts to the CONTROL condition and tested against the conjunction null hypothesis (Nichols et al., 2005). As presented in Fig. 2C and Table 1C we found further support for perceptual grounding by means of SI activation (p < 0.001 uncorrected due to strong a priori assumptions). Additionally we found activation in bilateral IPS and IPL, and right SPL and LOtv.

Table 1

<table>
<thead>
<tr>
<th>Cluster size</th>
<th>Anatomical region</th>
<th>Peak MNI coordinates</th>
<th>z-Score peak</th>
</tr>
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<tbody>
<tr>
<td>A. PERCEPTION &gt; CONTROL</td>
<td>Right SPL</td>
<td>28</td>
<td>−62</td>
</tr>
<tr>
<td></td>
<td>Right IPS</td>
<td>34</td>
<td>−42</td>
</tr>
<tr>
<td></td>
<td>Right SI</td>
<td>56</td>
<td>−24</td>
</tr>
<tr>
<td></td>
<td>Left IPS/SI</td>
<td>−58</td>
<td>−24</td>
</tr>
<tr>
<td></td>
<td>Right SPL</td>
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<td>−40</td>
</tr>
<tr>
<td></td>
<td>Left IPL</td>
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<td>−72</td>
</tr>
<tr>
<td></td>
<td>Right LOtv</td>
<td>58</td>
<td>−60</td>
</tr>
<tr>
<td></td>
<td>Right precuneus</td>
<td>60</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>Left FEF</td>
<td>−30</td>
<td>−4</td>
</tr>
<tr>
<td>B. IMAGERY &gt; CONTROL</td>
<td>Right IPL</td>
<td>46</td>
<td>−70</td>
</tr>
<tr>
<td></td>
<td>Right SPL</td>
<td>20</td>
<td>−64</td>
</tr>
<tr>
<td></td>
<td>Left SPL</td>
<td>−32</td>
<td>−74</td>
</tr>
<tr>
<td></td>
<td>Left LOtv</td>
<td>56</td>
<td>−48</td>
</tr>
<tr>
<td></td>
<td>Right IFG</td>
<td>−44</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>Right FEF</td>
<td>26</td>
<td>10</td>
</tr>
<tr>
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<td>−6</td>
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<tr>
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<td>−34</td>
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<td></td>
<td>Right RSC</td>
<td>18</td>
<td>−62</td>
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<tr>
<td></td>
<td>Left LOtv</td>
<td>−58</td>
<td>−62</td>
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<tr>
<td></td>
<td>Right SI</td>
<td>56</td>
<td>−18</td>
</tr>
<tr>
<td></td>
<td>Left VI</td>
<td>−6</td>
<td>−84</td>
</tr>
<tr>
<td>C. (IMAGERY &gt; CONTROL) &amp; (PERCEPTION &gt; CONTROL)</td>
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<td></td>
<td>Right IPL</td>
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<td>−70</td>
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<tr>
<td></td>
<td>Left IPS</td>
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<td></td>
<td>Right SPL</td>
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<td></td>
<td>Right IPS</td>
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<td></td>
<td>Right LOtv</td>
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<td></td>
<td>Right SI (uncor.)</td>
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<tr>
<td></td>
<td>Left IPL</td>
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<td>−80</td>
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<tr>
<td>D. IMAGERY &gt; PERCEPTION</td>
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<td>Left IFG</td>
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<tr>
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<td>−58</td>
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<td>Left IPS</td>
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<td>Left VI</td>
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<td>Prec</td>
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<td>medIFS</td>
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<tr>
<td></td>
<td>Left PFC</td>
<td>−44</td>
<td>44</td>
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</table>

**Engagement of the core construction network in tactile imagery**

We next tested whether tactile imagery involves the recruitment of the construction system. We contrasted the IMAGERY against the PERCEPTION condition as in both conditions, subjects performed the same task, i.e. processing a bar-pattern stimulus and allocating a probe pin within this representation. In the PERCEPTION condition the stimulus was perceived; in the IMAGERY condition its representation was derived from memory. This contrast therefore reflects the construction related network without task-specific or representation-specific activations. In accordance with the description of the core construction system, this contrast revealed increased activations of bilateral retrosplenial cortices (RSC), the precuneus and also the left IFG (Hassabis and Maguire, 2009; McNorgan, 2012). We further observed activation of bilateral FEF, SPL, IPL and primary visual cortex (VI) and prefrontal cortex (PFC) as shown in Fig. 2D and Table 1D.

**BOLD time-courses**

To characterize the temporal dynamics of recorded BOLD responses we computed peri-stimulus time histograms (BOLD time-courses) as presented in Fig. 2E for right SI, left IFG, precuneus and bilateral RSC. Evoked responses follow the hemodynamic response function, where responses in SI for IMAGERY and PERCEPTION appear similar in their dynamics and amplitude while the CONTROL condition elicited weaker responses.

**Interaction between the core construction and the content representation system**

To identify the dynamic interaction of the construction system with the network related to the mental pattern representation, we implemented psychophysiological interaction (PPI) analyses. Seed regions for the PPI analyses were defined within the construction network and PPIs calculated for the contrast IMAGERY > PERCEPTION. Results are summarized in Fig. 3 and Table 2.

Increases in connectivity from the RSC and precuneus to a distributed network of areas indicate their prominent function of orchestrating the memory retrieval and (re)construction processes during mental imagery. Connectivity to bilateral IPS as representation-related areas was modulated from the precuneus and right RSC and to the right SI from bilateral RSCs and precuneus. In contrast, the analysis for the left IFG revealed a selective and substantial increase in coupling to the right SI. This connection had spatial specificity onto the BA1 sub-region of SI which was also activated during imagery (compare Figs. 2B and C). This finding indicates that the coupling of IFG and SI is crucial for augmenting an abstract mental image with perceptually grounded details when mentally reactivating perceptual processes.

**Discussion**

This article reports on an fMRI experiment during which subjects were required to form a mental representation of vibrotactile pattern stimuli. First, our report complements the imagery literature by presenting a stringently controlled study in the tactile domain. We found clear evidence for perceptual grounding of the mental image in primary somatosensory cortex, supplementing reports from other modalities (Kosslyn and Thompson, 2003; McNorgan, 2012). Secondly, our findings support the notion that tactile imagery involves the brain’s construction system, which can be distinguished from a network related to the mental content representation (Hassabis and Maguire, 2007, 2009). Finally our connectivity analysis revealed increased coupling between core elements of the construction network and content related brain areas during imagery including the modulation of connectivity between prefrontal cortex (left IFG) and right SI.
To our knowledge, and as reviewed by McNorgan (2012), there have only been three fMRI reports on imagery in the somatosensory domain. The studies of Newman et al. (2005) and Olivetti Belardinelli et al. (2009) investigated rather abstract aspects of somatosensory imagery by letting subjects compare haptic/form properties or by cueing the imagery of active touch. Yoo et al. (2003) reported the only study comparing tactile imagery to perception. Specifically, the authors used brushing stimuli in a block design and reported an initial indication of perceptual grounding. Our study substantially extends this work as our design allowed for investigating the mental construction process and required a mental representation of high granularity. Furthermore, the current study advances the study by Yoo et al. by providing a behavioral report for successful imagery and control conditions, which enable to differentiate between construction and representation-related activations, as well as the study of their interaction by means of PPI analyses.

Perceptual grounding of the mental representation

Previous work has focused on the activation of primary sensory cortices during mental imagery as an activation overlap in early sensory areas is interpreted as grounding of the mental representation in perception-specific neural processes (McNorgan, 2012). Such activation is seen to support the fact that mental representations are rather 'depictive' in their nature than propositional (Kosslyn and Thompson, 2003). Inclusion of a control condition allowed for testing whether SI is recruited during imagery by contrasting IMAGERY versus CONTROL. In addition, the computation of a conjunction analysis enabled us to identify the spatial overlap in the neural representations for imagery and perception, as the content to be mentally represented was matched between PERCEPTION and IMAGERY. In fact, we found activation of SI in both analyses and this activation topologically matched the SI activation during perception within the hand region of BA1. Considering the temporal aspects of the SI responses, we found indistinguishable dynamics and amplitude during IMAGERY and PERCEPTION while observing smaller responses in the CONTROL condition. This is particularly interesting as a recent visual imagery study by Albers et al. (2013) found temporally overlapping BOLD responses in early visual cortices

![Fig. 3. Psychophysiological interaction (PPI) analysis. Increases in functional connectivity for IMAGERY > PERCEPTION for seed regions placed within the construction system: A. left retrosplenial cortex (RSC), B. right RSC, C. precuneus, D. left inferior frontal gyrus (IFG). All p < 0.05 corrected for FDR on the cluster level. E. Summary of connectivity increases between the reported seed regions within the construction network and areas related to the mental representation as identified in the conjunction analysis (Fig. 2C). Bilateral RSCs and the precuneus show increased connectivity to a distributed network of brain areas, which emphasizes their role in orchestrating retrieval and construction of a mental representation. In contrast, the left IFG shows topologically specific coupling to BA1 hand region of SI, which indicates a mechanism to augment a mental representation with sensory details.]

![Table 2](https://example.com/table2.png)
when working memory content was derived from either imagery or perception. Taken together, our findings indicate bottom-up (perception) and top-down (imagery) induced activations in early sensory cortices to follow similar BOLD dynamics.

Additionally, we observed activation in a sub-region of the lateral occipital complex (referred to as LOtv; Amedi et al., 2001, 2002), which has been related to modality independent processing of object form (Amedi et al., 2007; Tal and Amedi, 2009) and also during visual imagery (Hassabis et al., 2007; Lacey et al., 2009). Lacey et al. (2010) addressed the controversy of whether haptic shape perception depends on visual imagery by investigating LOC activity and connectivity modulations by the familiarity of objects (Deshpande et al., 2010). Their fMRI study supports that shape representation in LOC can be assessed by either top-down (visual imagery) or bottom-up (haptic perception). This is in agreement with our results indicating LOtv as part of the content representing network shared by imagery and perception.

The brain’s construction network in imagery

Imagery is not the mere representation of mental content but rather an active construction process. The notion of ‘construction’ has been developed in the study of episodic memory and future thinking where complex mental assemblies are composed (Buckner and Carroll, 2007; Hassabis and Maguire, 2009; Schacter et al., 2012). It appears that a similar brain network supports episodic memory processing (Hassabis and Maguire, 2009; Hassabis et al., 2007; Summerfield et al., 2009), simulation of future events (Schacter et al., 2012), scene construction, perspective taking (Buckner and Carroll, 2007), or spatial imagery (Thompson et al., 2009). The common network is referred to as a ‘core’ construction system (Hassabis and Maguire, 2007, 2009) and comprises medial temporal lobe (MTL) regions (hippocampus and parahippocampal gyrus), retrosplenial and posterior parietal cortices, ventromedial prefrontal cortex and the precuneus (Hassabis and Maguire, 2009; Mullally and Maguire, in press; Schacter et al., 2012).

The observation that this network highly overlaps with the default mode network (Raichle et al., 2001) fostered the discussion on the functional specificity of its components. It has been suggested that construction-related regions flexibly couple with specific brain regions dependent on the imagery demands, such as perspective taking (Schacter et al., 2012). In line with this hypothesis our study focused on the imagery of sensory content to test for interactions of construction-related and grounding-related brain regions. The employed task compelled subjects to reactivate a sensory experience and thereby generate a vivid mental representation. Kosslyn (2005) also emphasizes the allocation of attention within a mental image as intrinsic to the imagination process. While visual imagery requires attentional shifting in a mental visuospatial representation, our tactile task necessitated allocating attention within (peri-)personal space towards the fingertip. These task differences need to be considered when discussing the functional interpretation of the core construction network structures.

The MTL regions are well known for their involvement in tasks such as spatial navigation and episodic memory. Schacter and Addis (2009) reviewed the potential dissociation of the contributions of the hippocampus and parahippocampal cortex to construction processes, suggesting that the latter allows access to contextual associations that are then combined with further details by the hippocampus (see also Addis and Schacter, 2012). In line with this, Mullally and Maguire (in press) suggest that the hippocampus mainly contributes to spatial coherence by binding together diverse temporal and spatial aspects. The cued recall imagery task that was employed here did not pose major binding demands and intense training minimized subjects’ recall efforts. The contrast IMAGERY > CONTROL revealed activation in the parahippocampal region and thereby provides further evidence for the modality independent involvement of MTL for mental imagery. Additionally, our results suggest that simple sensory representations can be constructed independently of the hippocampus.

The precuneus and the RSC are known to be highly connected to various brain sites relating to functional involvement in memory and construction processes. Together with the posterior cingulate cortex (BA23 and 31), the RSC (BA29 and 30) is described as part of the parieto-medial temporal pathway of visual information processing (Kavvatz et al., 2011). Although no unifying description of RSC’s functional role has yet been given, its activity has been related to perspective taking, shifting between viewpoints and reference frames (reviewed by Vann et al. (2009)).

A recent meta-analysis on mental imagery in different modalities reports modality-independent activation of the left IFG (McNorgan, 2012). While the IFG is not described as a core component of the construction network, it is part of the lateral prefrontal cortex (lPFC) and is known for its role in working memory (WM), including tactile WM (Aksztulewicz et al., 2011; Preuschhof et al., 2006; Spitzer et al., 2010, 2014). Conceptually an involvement of WM in imagery is plausible because the mental representation has to be maintained for conscious access and deliberate content processing (Baars and Franklin, 2003; Likova, 2012). Imagery can even be regarded as the active/dynamic component of WM in line with the view of construction-related areas to update/manipulate WM content (Albers et al., 2013; Likova, 2012; Tong, 2013). Evidence for information maintenance in IFPC during WM was recently given by Lee et al. (2013). The authors used a decoding approach to distinguish where different types of information are coded during a WM task. Their results indicated that information on rather abstract, non-perceptual properties appear to be maintained in IFPC, which is in line with reports on the prefrontal coding of analog stimulus properties during tactile WM (Spitzer et al., 2013). In our imagery study, such an abstract aspect could be the conceptual information of what should be imagined, such as the association of the color cue and the corresponding tactile percept. However, the IFG’s role for an abstract representation of stimulus properties or stimulus identity remains speculative and encourages future investigations, especially when considering it’s coupling to SI as revealed by our connectivity analysis.

While our paradigm was not designed to dissociate supramodal imagery processes from those specific for the tactile modality, the identified imagery network strikingly overlaps with the well described core construction network (Hassabis and Maguire, 2009). Also, Daselaar et al. (2010) and Zvyagintsev et al. (2013) specifically aimed to identify supramodal imagery networks when contrasting visual with auditory imagery and gave support for a network highly overlapping with the default mode network. Conceptually it appears difficult to depict construction processes as truly supramodal or amodal, as similarly discussed for mental representations to be either abstract/symbolic or modality-specific (perceptually ground) or both. While our subjects received visual cues, the construction process was directed to the tactile domain as subjects were necessitated to reactivate fine sensory details.

Together our results support the notion that parahippocampal cortex, retrosplenial cortices and precuneus contribute, independent of modality, to the initiation of mental content in WM. This content is augmented with perceptually grounded details via coupling to sensory areas, where SI might constitute as a dynamic sensory information ‘buffer’ (Albers et al., 2013; Kosslyn, 2005; Likova, 2012).

The interaction of construction and content networks

To date, few studies have investigated changes in connectivity for imagery (Gao et al., 2011; Mechelli et al., 2004; Schlegel et al., 2013; Szameit et al., 2012). We used PPI analyses to identify connectivity changes related to the construction of the mental representation. More specifically, we were interested in how the construction system interacts with areas related to the content-representation and
perceptual grounding and therefore defined seed regions within the construction network. Firstly, during imagery the precuneus and bilateral RSCs showed increased connectivity to a distributed network related to the processing of tactile stimuli (cf. Figs. 3A, B, C and Table 2A, B, C). This emphasizes their functional role for memory retrieval and the active reconstruction of the mental image. Supplemented with the IGF, they appear as the core of the construction network to assemble a mental representation by reactivation of early perceptual areas.

Interestingly, we found a substantial and selective increase in coupling of left IGF with right SI, i.e. the same BA1 sub-region activated by imagery. This interaction of IGF with SI may support perceptual grounding by augmenting an abstract mental representation with sensory details that are grounded in primary sensory cortices. These results are the first to indicate a direct involvement of prefrontal cortex interaction with primary sensory areas, related to the construction process of a mental image.

Conclusion

We presented an imagery task that stringently controlled for the content that had to be mentally represented. We found this mental representation to be perceptually grounded, as SI activation was shared by imagery and stimulus-driven perception. Furthermore, we found the core construction system to be involved in the active construction of the mental stimulus representation and the involvement of prefrontal cortex, specifically the left IGF. Most interestingly our analysis revealed increased connectivity between prefrontal cortex and SI during imagery, which is the first indication of a direct mechanism that augments an abstract mental representation with perceptually grounded sensory details.

Acknowledgments

TTS is supported by the Research Training Group GRK 1589/1 “Sensory Computation in Neural Systems” by the German Research Foundation (DFG). FB was supported by a grant from the German Federal Ministry of Education and Research (BMBF).

References


