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Crossmodal interactions of haptic and visual texture information in early sensory cortex

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ABSTRACT

Both visual and haptic information add to the perception of surface texture. While prior studies have reported crossmodal interactions of both sensory modalities at the behavioral level, neuroimaging studies primarily investigated texture perception in separate visual and haptic paradigms. These experimental designs, however, only allowed to identify overlap in both sensory processing streams but no interaction of visual and haptic texture processing. By varying texture characteristics in a bimodal task, the current study investigated how these crossmodal interactions are reflected at the cortical level. We used fMRI to compare cortical activation in response to matching versus non-matching visual–haptic texture information. We expected that passive simultaneous presentation of matching visual–haptic input would be sufficient to induce BOLD responses graded with varying texture characteristics. Since no cognitive evaluation of the stimuli was required, we expected to find changes primarily at a rather early processing stage. Our results confirmed our assumptions by showing crossmodal interactions of visual–haptic texture information in early somatosensory and visual cortex. However, the nature of the crossmodal effects was slightly different in both sensory cortices. In early visual cortex, matching visual–haptic information increased the average activation level and induced parametric BOLD signal variations with varying texture characteristics. In early somatosensory cortex only the latter was true. These results challenge the notion that visual and haptic texture information is processed independently and indicate a crossmodal interaction of sensory information already at an early cortical processing stage.

Introduction

Humans need to be able to differentiate surface qualities of objects not only by touch but also visually. This is important for object recognition (e.g. nectarine vs. peach) and for the interaction with objects in our environment (Fikes et al., 1994) (e.g. for goal-directed movement: grasping a slippery piece of soap vs. a splintering piece of wood). Behavioral studies showed that both haptic and visual informations add to texture perception (Lederman and Abbott, 1981) and that a crossmodal transfer of texture information between both sensory modalities occurs (Picard, 2006).

However, it is only in the last decade that the neural basis of texture perception and its multidimensional experience have received increased attention. Several neuroimaging studies focused on texture matching and discrimination (Cant and Goodale, 2007; Cavina-Pratesi et al., 2009; Kaas et al., 2012; Peuskens et al., 2004; Sathian et al., 2011; Stilla and Sathian, 2008) as well as on different dimensions of texture perception within the tactile and visual modality; examples include spatial density (Merabet et al., 2004; Zhang et al., 2005), spatial orientation (Kitada et al., 2006; Zhang et al., 2005) and roughness (Burton et al., 2008; Merabet et al., 2004; Kitada et al., 2005; Roland and Brendan, 1998; Simões-Franklin et al., 2011). Most of the tactile studies stress the importance of the parietal operculum and the posterior insula (Kaas et al., 2012; Kitada et al., 2005; Roland and Brendan, 1998; Simões-Franklin et al., 2011; Stilla and Sathian, 2008) for processing surface textures, while studies focusing on visual texture perception often report regions near the collateral sulcus, the lingual gyrus and areas in early visual cortex (Cant and Goodale, 2007, 2011; Cant and Xu, 2012; Cavina-Pratesi et al., 2010; Peuskens et al., 2004; Stilla and Sathian, 2008; Sathian et al., 2011).

Next to the identification of cortical key players in visual and haptic texture perception a recent approach by Hiramatsu et al. (2011) aimed at investigating how visual material properties are coded in the cortex along the ventral visual pathway. The authors reported that while both early and higher-order visual areas seem to contain information distinguishing material categories (including texture information), the neural representation shifts gradually from an image-based representation in early areas (V1/V2 and V3/V4) to a perceptual representation in

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areas around the fusiform gyrus and the collateral sulcus. Hence, physical and perceptual measures of visual material qualities seem to be processed in a spatially distributed network in the visual cortex, rather than in a single localized region. A similar distributed network was described by Sathian et al. (2011) for the processing of haptic texture information. In connectivity analyses Sathian and colleagues showed a flow of texture information from task-non-selective regions of the postcentral gyrus to texture-selective areas in the parietal operculum and further to regions of the middle occipital cortex. Despite the pure tactile stimulation in many paradigms, consistent visual cortex activation was reported in several of these studies (Merabet et al., 2007; Simões-Franklin et al., 2011; Stilla and Sathian, 2008). Some findings even indicate the existence of bisensory texture-selective regions in the posterior visual cortex and the lingual gyrus by comparing activations elicited by unimodal shape, location and texture matching in both the visual and haptic modality (Sathian et al., 2011; Stilla and Sathian, 2008).

All of the above-mentioned studies investigated texture perception in separate visual and haptic paradigms. The effect of simultaneous visual and haptic exploration of textures has been mostly neglected so far. Hence, we can only assume an overlap of visual and haptic texture representations in some brain areas, but we cannot infer from these studies whether visual and haptic information interacts in these cortical regions. The imaging study by Sathian et al. (2011) gives a first indication that this might indeed be the case. Behavioral studies also indicate the existence of such crossmodal interaction and matching effects in visuo-haptic tasks. It was shown that people consistently and absolutely match specific tactile vibration rates (simulating manual exploration of a textured surface) to visual spatial frequencies (Guzman-Martinez et al., 2012), indicating some kind of crossmodal association effect in visual and haptic texture perception. Furthermore, Lunghi et al. (2010) even showed that simultaneous tactile stimulation can disambiguate binocular rivalry, a process in which two equally salient but dissimilar monocular stimuli are presented to corresponding retinal locations. Both stimuli compete for perceptual dominance and at any instant only one is perceived consciously while the other image is suppressed. In this study subjects haptically explored a linear grating with a matching orientation to either one of two rival visual stimuli. Exploration of the haptic stimulus prolonged dominance or reduced suppression of the matching visual stimulus, indicating a crossmodal interaction. The authors infer from these results that haptic information can modulate visual processing already at a very early stage, probably in V1. This raises the question whether a change in cortical processing can be expected when matching as compared to non-matching visual–haptic texture information is provided, i.e. representing crossmodal interactions at the cortical level.

In a unimodal tactile fMRI study, Kitada et al. (2005) used a parametric stimulus set, i.e. linear gratings varying in spatial period, and demonstrated that differences in tactile roughness yield graded BOLD responses in the parietal operculum, insula and the lateral prefrontal cortex, but only when subjects actively judge rather than merely attend to roughness. Assuming that crossmodal interactions of texture information are not only presented at the behavioral but also at the cortical level, the question arises whether matching visual–haptic information is sufficient for the observation of graded BOLD responses with varying texture characteristics even without an active judgment task.

The main objective of the present study was to investigate texture perception in a paradigm that combines visual and haptic input in a single condition in order to explore crossmodal interactions at the cortical level. We propose differences in cortical processing of matching and non-matching visual–haptic texture information, representing the influence of one sensory modality on information processing in the other modality as indicated by earlier behavioral studies. Based on the studies mentioned above we would expect these crossmodal effects already in early sensory cortices, e.g. postcentral gyrus and posterior occipital cortex (Dionne et al., 2010; Hiramatsu et al., 2011; Merabet et al., 2007; Sathian et al., 2011; Stilla and Sathian, 2008), but perception-related differences rather in higher-order cortical regions, e.g. the collateral sulcus as well as the parietal operculum and the insula (Cavina-Pratesi et al., 2010; Hiramatsu et al., 2011; Kitada et al., 2005). The unfamiliar dot pattern textures used in this experiment varied only along a single texture dimension, i.e. the average center-to-center dot spacing, ensuring that changes in other surface properties like color and friction do not influence the results. Stimulus presentation was always bimodal, but the sensory information content differed as texture information was varied either in the haptic, visual or in both channels.

We analyzed the data in two different ways. First we were interested in the average difference of the BOLD signal between both unimodal and the bimodal texture variation conditions, disregarding dot pattern differences. As we did not ask subjects to perform a cognitive task with the presented textures, we would expect to find differences, if any, at a rather early sensory processing stage. Second we were interested in relative differences of the BOLD response within each of these three conditions, taking into account the parametric dot pattern variation. Is the BOLD response modulated by texture differences when texture characteristics are varied either unimodally or bimodally? Based on previous behavioral studies we expected perceived roughness by touch to be almost perfectly correlated with the inter-dot spacing (Connor et al., 1990; Dépeault et al., 2009; Eck et al., 2011), while visual spatial density estimates should be negatively correlated with average inter-dot distance. Hence, no difference in the parametric BOLD modulation was expected between the two subjective measures tactile roughness and visual spatial density and the objective texture characteristic inter-dot spacing. However, to account for possible subjective perceptual differences we used individual post-fMRI ratings of haptic roughness and visual spatial density as well as the physical inter-dot spacing of the textures in separate parametric models.

Material and methods

Participants

Seventeen right-handed, healthy volunteers (13 women, 4 men; 27 ± 5.9 years) with normal or corrected-to-normal vision participated in the study. Subjects with calluses or injuries to the hands were excluded from participation. All participants were graduate and undergraduate students at Maastricht University. They were naïve to the hypotheses and received course credit or monetary compensation for their participation in the experiment. In accordance with the Declaration of Helsinki, written informed consent was obtained from each participant and the study was approved by the local ethics committee.

Stimuli

Haptic stimuli consisted of seven 5×5 cm^2 plastic plates, six embossed with different dot patterns and one control stimulus without any dots. The dots were arranged non-periodically and were 0.8 mm in diameter and 0.6 mm in elevation. The only characteristic that varied between the textures was the mean center-to-center dot spacing of each stimulus and hence the number of texture elements (dots). The average inter-dot spacing ranged from 1.50 mm to 2.75 mm and increased in steps of 0.25 mm (see Table 1 for detailed information on the stimulus characteristics). Details about the algorithm used to produce these textures can be found in Eck et al. (2011). For each dot matrix a 3D wireframe model was created and computer-rendered in AutoCAD® 2010 (Autodesk Inc., San Rafael, CA, USA) in order to create a set of matching visual stimuli. Two distant light sources following the direction of the viewpoint provided the lighting of each stimulus in such a way that all faces of the model were illuminated (see Fig. 1).

Experimental setup

All textures were arranged on a circular wooden board which was covered by a second wooden plate with a rectangular cut out. The

Table 1
Texture characteristics of stimuli. Surface area of the stimuli = 25 cm^2.

Stimulus	Smooth control stimulus	1	2	3	4	5	6
Average inter-dot spacing in mm	–	1.50	1.75	2.00	2.25	2.50	2.75
Number of texture elements	–	1089	785	625	484	400	324

cover-plate allowed subjects to touch only one texture at a time and served as the resting position for the hand in between exploration trials. This haptic texture presentation device was placed over the thighs of the participant and was attached to the scanner table. The right hand of the subject was placed on top of the cover-plate and the arm was supported by foam padding to reduce movement of the elbow and shoulder. The presentation of the haptic stimuli was controlled by the experimenter who was standing next to the scanner bore during the functional scans (see Fig. 2). Visual stimuli were displayed centrally on a black background and subtended 5.7 degrees of visual angle. The images were projected onto a rear-projection screen at the end of the scanner bore and subjects viewed the stimuli via a mirror mounted to the head-coil.

Experimental procedure

Stimulus timing and presentation was controlled by Presentation® software (Neurobehavioral Systems, Inc., Albany, CA, USA). Subjects were informed that they would be presented with one visual and one haptic texture at each trial. Participants were instructed to explore the textures by sweeping twice with their right index-, middle- and ring fingers across the surface while simultaneously focusing on the visual image presented on the screen. The importance of the simultaneous start and termination of the visual and haptic exploration was specifically stressed by the experimenter in order to control the temporal synchrony of the sensory input. Trial intervals were intermixed with intervals of rest. Auditory cues delivered via headphones instructed the experimenter to turn the haptic presentation device to the correct stimulus during the inter-stimulus-intervals. Right before scanning started, subjects practiced the exploration movement in the scanner with two dot pattern textures that were not used in the experiment. These textures had an average inter-dot spacing of 7.00 and 7.50 mm respectively. The practice session lasted until the movement was experienced by the subject as effortless, it was synchronized with the duration of the exploration interval and all other motion was reduced to a minimum. This took on average five minutes but never longer than ten minutes. The practice session ensured that the attention of the subject was not focused on the motion sequence but on the tactile and visual sensations.

There was a visual, haptic, and visual–haptic condition in which the availability of texture information for the tactile and visual sense was varied but the input modalities and motor task demands were kept constant. Thus, subjects always explored the stimuli both visually and haptically, but in the haptic condition a smooth control stimulus without any texture information was presented visually (unimodal haptic dot pattern condition) and in the visual condition vice versa (unimodal visual dot pattern condition). In the visual–haptic condition matching dot patterns were presented visually and haptically (bimodal dot pattern condition). Each dot pattern was repeated 19 times in each condition over the course of the experiment. A fast event-related design was utilized, consisting of alternating exploration periods (2 s) and inter-stimulus intervals (4 s) in which a fixation cross was displayed (see Fig. 3). The condition and stimulus presentation was semi-randomized and the 342 events of interest were randomly interspersed with 108 null events. The experiment was split into 3 functional runs. The event-related fMRI design was based on an approach described by Kao et al. (2009).

After the scanning session, subjects assessed the perceived haptic roughness and visual spatial density of each stimulus on a 10-point rating scale ranging from 1 (very smooth/sparse) to 10 (very rough/dense). In order to avoid conscious rating of the stimuli during the fMRI experiment participants were not aware that they would be asked to assess these texture characteristics at a later time point.

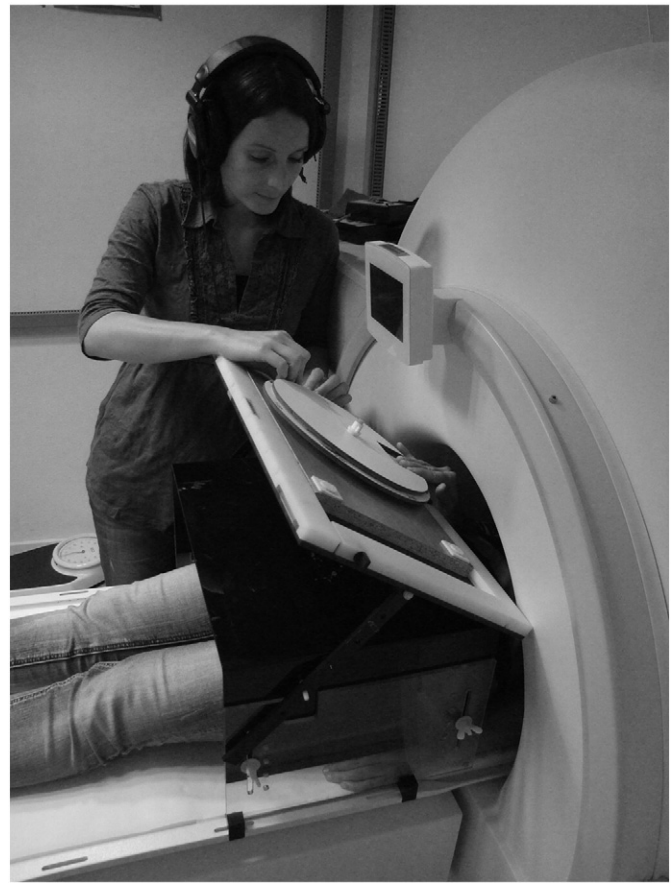

Fig. 2. Presentation of the experimental setup. In the functional runs the experimenter presented the haptic stimuli to the participants. Auditory cues delivered via headphones to the experimenter controlled the stimulus timing of the haptic presentation.

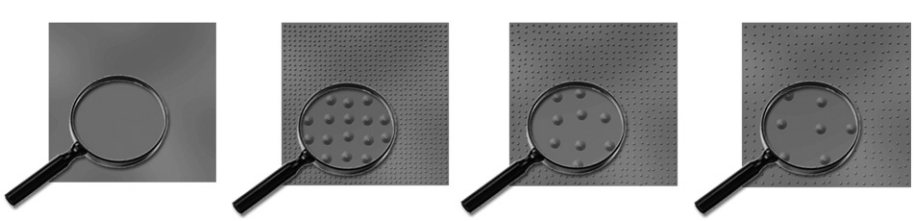

Fig. 1. Examples of textures used in the experiment. The texture on the left shows the control stimulus without any dots. The other three textures are presented in order of increasing mean inter-dot spacing, from left to right: 1.50 mm, 2.00 mm, and 2.50 mm (corresponding to stimuli 1, 3 and 5 in Table 1).

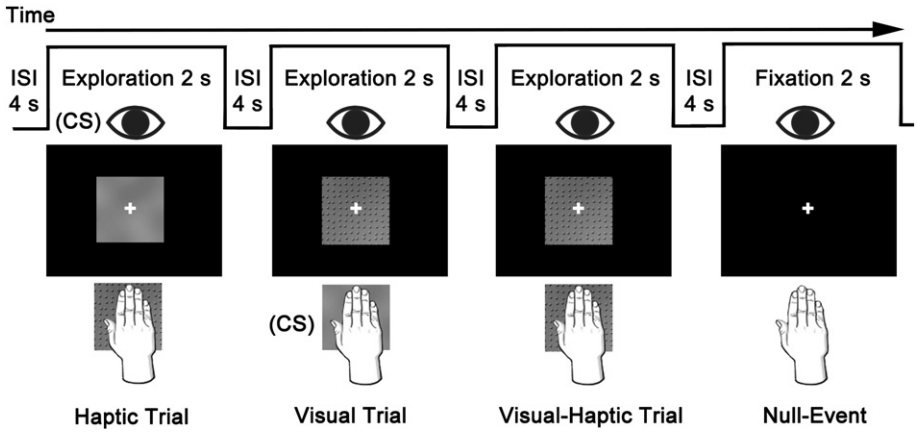

Fig. 3. Schematic description of all experimental trials. During the inter-stimulus interval a fixation cross was presented. CS = control stimulus; ISI = inter-stimulus interval.

Data acquisition

Data were acquired using a 3 Tesla MRI head scanner (Siemens Allegra, Erlangen, Germany) at the Maastricht Brain Imaging Center (Maastricht, The Netherlands). Subjects were placed comfortably in the scanner and foam padding around the head was used to minimize head movement. Functional images were obtained with a T2*-weighted echo-planar imaging (EPI) sequence (scan parameters: TR = 2000 ms, TE = 30 ms, flip angle (FA) = 90°, matrix = 64 × 64, field of view (FOV) = 224 × 224, slice thickness = 3.5 mm, 32 slices, no gap) and comprised 458 volumes for each run. In between the second and third functional runs a standard 3D high-resolution data set (MPRAGE) covering the whole brain was acquired (scan parameters: TR = 2250 ms, TE = 2.6 ms, FA = 9°, matrix: 256 × 256, voxel size: 1 × 1 × 1 mm, 192 slices).

Data analysis

Post-scanning roughness estimates and spatial density scores of all subjects were analyzed with SPSS 18 (SPSS Inc., Chicago, IL, USA).

Functional and anatomical data were analyzed with BrainVoyager QX 2.3.1 (Brain Innovation, Maastricht, The Netherlands). The first 2 scans of each functional run were discarded from analysis to eliminate T1 saturation effects. Preprocessing of the functional data included the following steps: slice scan time correction, intra-session alignment to detect and correct for small head movements by rigid body transformations, temporal filtering removing linear trends and non-linear temporal frequencies of 3 or less cycles per run and spatial smoothing with an isotropic Gaussian kernel of 6 mm FWHM. None of the participants moved more than 2.9 mm/degrees in any direction. Functional images of all runs were co-registered to the anatomical volumes of the respective subject and transformed into Talairach space resulting in an interpolated functional voxel size of 3 × 3 × 3 mm.

For group analysis a two-level general linear model (GLM) approach was used. At single-subject level a whole-brain fixed-effects regression analysis was performed with 4 different models, each addressing a different aspect of the research questions.

Differences in the BOLD response between unimodal and bimodal dot pattern conditions

Model 1 Comparison of modality effects. For each subject a set of three task-related regressors was defined, one for each modality condition (visual dot pattern condition — V, haptic dot pattern condition — H, visual–hapticdot pattern condition — VH), irrespective of the explored dot pattern. Furthermore, seven z-transformed confound regressors including a predictor for the instruction interval in the beginning of each run and the six motion parameters to account for residual motion artifacts in the time courses were added.

For visualization of the estimated hemodynamic response function (HRF) of all modality conditions, we used a deconvolution analysis. This was necessary because BOLD responses to individual stimuli substantially overlap in rapid event-related designs, which renders the raw signal useless for visualization of mean signal changes between conditions. A set of ten consecutive stick predictors of 1 TR was defined for each modality condition in order to cover the temporal extent of the hemodynamic response (20 s). Beta weights of these stick functions were used to plot the shape of the estimated HRF of all modality conditions.

Differences related to parametric dot pattern variation within each modality condition

Model 2 Test for modulation of the BOLD response by objective texture characteristics (mean inter-dot spacing). The regression model consisted of a set of three main predictors for all modality conditions (Vmain, Hmain, VHmain) and three predictors coding for the parametric modulation of the HRF by the mean inter-dot spacing of the stimuli in the three modality conditions (Vpara, Hpara, VHpara). Additionally, we included the same confound predictors as in model 1. All predictors of this model were z-transformed.

Model 3 Test for modulation of the BOLD response by haptically perceived roughness. Model 3 was identical to model 2, but for the parametric predictors the haptically estimated roughness of the stimuli was used.

Model 4 Test for modulation of the BOLD response by visually perceived spatial density. This model was also identical to model 2, but this time visually perceived spatial density was used for the parametric predictors in the three modality conditions.

In order to visualize the mean BOLD response of each dot pattern texture in all three modality conditions, a deconvolution analysis was computed. A set of ten consecutive stick predictors of 1 TR, covering a temporal interval of 20 s, was defined for each texture in all three modality conditions. Beta weights of these stick functions were used to plot the shape of the estimated HRF for all dot pattern textures in different cortical regions.

All predictor time courses in models 1–4 with the exception of the motion parameters were convolved with a 2-gamma HRF.

At group level, whole-brain random-effects analyses were performed for all models defined at the single subject level. A statistical model of the main modulation effect of sensory modality (model 1) was fitted to the data to reveal brain regions that respond differently depending on the texture information accessible to the visual and haptic modality. We were interested in the difference between the visual–haptic (VH) and

both visual (V) and haptic (H) dot pattern conditions ([VH > V], [VH > H]) as well as in the difference between both unimodal information variation conditions (V ≠ H). Furthermore, in order to reveal brain regions that show an enhanced response when texture information varies bimodally compared to either unimodal variation of information, we computed the following conjunction contrast: [V] ∩ [H] ∩ [VH > V] ∩ [VH > H].

Additionally, models related to the parametric texture modulation (models 2–4) were fitted to the data to explore cortical areas that differ in their response with respect to objective texture characteristics (mean inter-dot spacing) or subjectively perceived differences between textures (haptically perceived roughness and visually perceived spatial density). The specificity of the result was provided by the conjunction contrast of the main and parametric predictor for each modality condition ([Vmain] ∩ [Vpara], [Hmain] ∩ [Hpara], [VHmain] ∩ [VHpara]), requiring both a significant main effect of modality and a significant parametric modulation of the HRF in the same cortical location.

The voxel-threshold for statistical significance was first set to $\alpha = 0.005$ uncorrected and all statistical contrast maps were then corrected for multiple comparisons using cluster-size thresholding (Forman et al., 1995; Goebel et al., 2006) with a cluster-level false positive rate of $\alpha = 0.05$.

Results

Behavioral results

In general perceived haptic roughness increased with increasing inter-dot distance while the visually perceived spatial density decreased (see Fig. 4). This was expected from earlier work conducted by our group (Eck et al., 2011) and it was confirmed by a significant linear effect of spacing in two repeated measures ANOVAs of spacing on perceived roughness by touch and visual spatial density ($F(1, 16) = 174.82$, $p < 0.001$, partial $\eta^2 = 0.92$ and $F(1, 16) = 167.8$, $p < 0.001$, partial $\eta^2 = 0.91$, respectively). Bonferroni-corrected post-hoc tests showed significant differences between all levels of spacing for roughness perceived by touch as well as for spatial density perceived by vision.

The average correlation of inter-dot spacing with perceived roughness and spatial density across subjects was 0.90 and −0.97 respectively. The correlation of both subjective texture characteristics was −0.93 across subjects.

fMRI results

Model 1 Differences in the BOLD response between unimodal and bimodal dot pattern conditions

[V] ∩ [H] ∩ [VH]. As presented in Fig. 5, texture exploration activated a cortical network involving early and higher-order visual, motor and somatosensory regions as well as prefrontal and cingulate areas. The consistency of this network across the different modality conditions is considerable as would have been expected by the constant sensory task demands across modality conditions.

Despite the spatial consistency of the network involved in texture perception, there are noticeable differences in response to the presence of dot patterns in the visual or haptic modality only versus congruently in both sensory modalities. These differences are summarized in Fig. 6 and Table 2.

[V > H]. The contrast of the visual and haptic dot pattern condition identified a region in both hemispheres of the early visual cortex that showed increased activation in the visual condition. This region was located in the posterior part of the calcarine sulcus (pCS) extending to the lateral part of the posterior occipital cortex (pOCC) and the right lingual gyrus (LG).

[H > V]. The opposite was true for the left postcentral gyrus (PoCG) which responded stronger in the haptic than in the visual condition.

[VH > H]. In the visual–haptic dot pattern condition increased activation was found bilaterally in pCS, lateral pOCC and LG compared to the haptic condition.

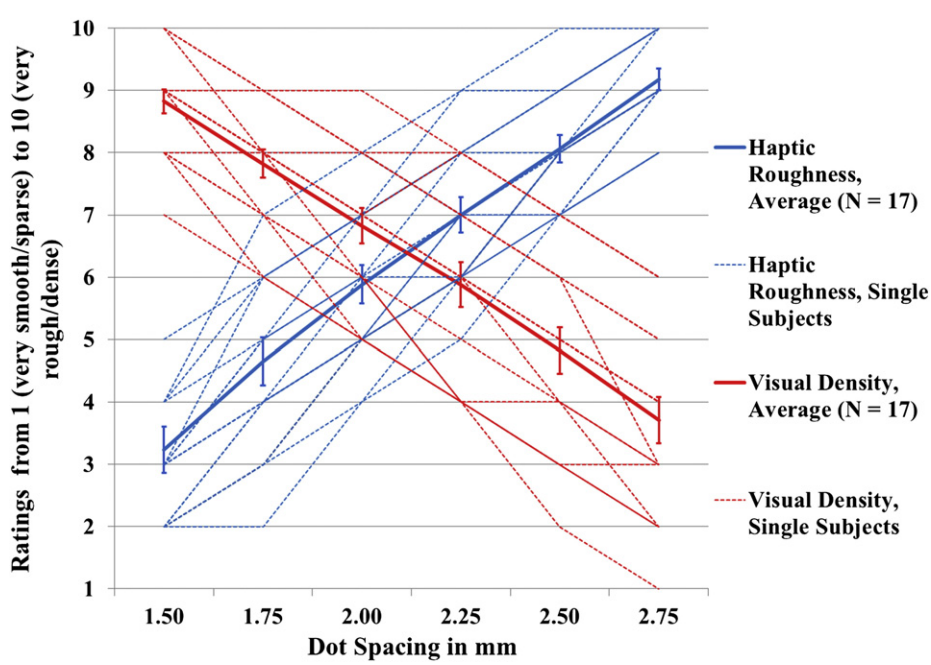

Fig. 4. Visual spatial density and haptic roughness judgments of all dot pattern textures. Roughness and density ratings of each participant and averaged over all subjects. Bars represent the standard error of the mean (SEM).

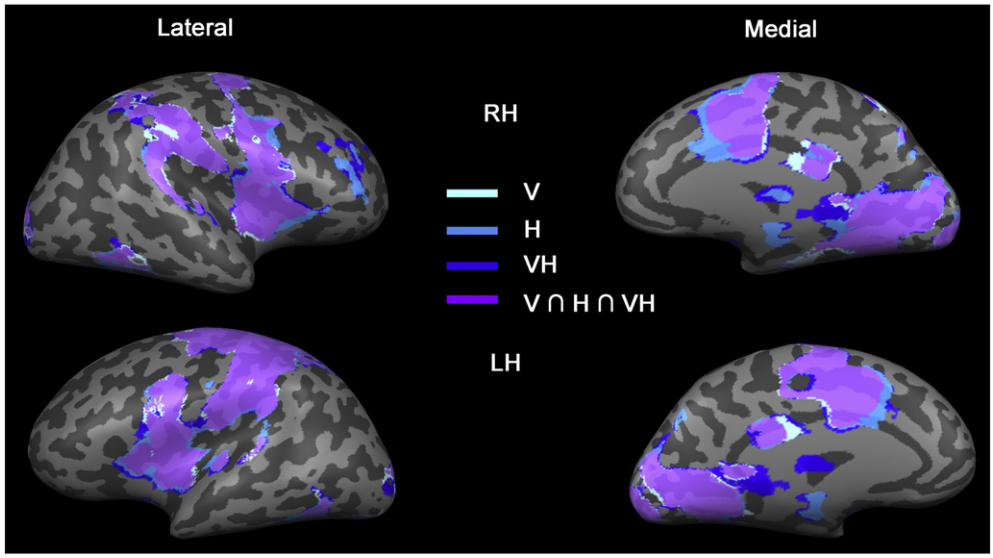

Fig. 5. Overlap of modality maps. Random effect maps of each modality condition versus baseline and the conjunction of these three maps displayed on an inflated surface reconstruction of a single representative subject; V = dot pattern information in visual modality (haptic control stimulus); H = dot pattern information in haptic modality (visual control stimulus); VH = matching dot pattern information in visual and haptic modality; $p < 0.05$ corrected at cluster level; LH = left hemisphere, RH = right hemisphere.

[VH > V]. The bimodal as compared to the visual dot pattern condition showed increased activation in left-hemispheric frontal, somatosensory and visual regions; namely the medial frontal gyrus (MeFG), the pre- and postcentral gyrus, (PrCG, PoCG), the supramarginal gyrus (SMG), pCS, lateral pOCC and the fusiform gyrus (FG) but also bilaterally in the basal ganglia, the thalamus and the cerebellum. The increased activation of early visual regions in the visual–haptic condition as contrasted to the visual condition is especially interesting considering that the visual information accessible to the subjects was the same in both the unimodal visual and the bimodal dot pattern condition.

[V] ∩ [H] ∩ [VH > V] ∩ [VH > H]. A similar left lateralized region in pCS and lateral pOCC was identified in the conjunction contrast asking for brain areas that respond to visual and haptic dot pattern exploration but significantly more so to congruent visual–haptic texture information (see Fig. 7).

Differences related to parametric dot pattern variation within each modality condition

Model 2 Test for modulation of the HRF by objective texture characteristics (mean inter-dot spacing). All parametric effects for this model are summarized in Fig. 8 and Table 3.

[Vmain] ∩ [Vpara]. No parametric effects were found in the visual dot pattern condition.

[Hmain] ∩ [Hpara]. However, a small but significant positive parametric effect of inter-dot spacing was identified in the haptic condition in the right-hemisphere in pOCC as well as in the right cerebellum.

[VHmain] ∩ [VHpara]. For the congruent visual–haptic condition more extended positive parametric effects of inter-dot spacing were identified, namely bilaterally in pCS, the lateral pOCC and LG, right hemispheric in anterior LG (aLG) and in a contralateral cluster comprising PreCG and PoCG and the inferior parietal lobe (IPL). These parametric effects were quite small, as shown in the deconvolution plots of Fig. 8, but the slight linear increase of the BOLD response with increasing inter-dot spacing is nevertheless visible.

Models 3 and 4 Test for modulation of the HRF by individually perceived texture characteristics (haptic roughness and visual spatial density). All parametric effects for these models are summarized in Table 3 and Supplementary Fig. 1.

[Vmain] ∩ [Vpara], [Hmain] ∩ [Hpara]. Interestingly, no modulation by perceived roughness and spatial density was found in either unimodal dot pattern condition.

[VHmain] ∩ [VHpara]. However, there were parametric effects of these subjective measures in the visual–haptic condition. They resemble the effects found for the physical inter-dot spacing in this condition albeit with a more limited spatial extent. Left lateralized positive effects of perceived roughness on the BOLD signal were found in pCS and PoCG. Negative parametric effects of spatial density were shown in the left pCS and LG, the bilateral pOCC, in the right aLG as well as in the left PoCG and IPL.

Discussion

Differences between unimodal and bimodal dot pattern conditions

Texture perception generated a very similar activation pattern irrespective of the modality in which texture information was varied, with activation overlapping primarily in early and higher-order visual, somatosensory and motor regions. These activations coincided with brain regions that were previously suggested to play a role in haptic and visual texture perception, namely the parietal operculum and insula, regions in the early visual cortex as well as the middle occipital gyrus, the collateral sulcus and the posterior fusiform and lingual gyrus (Cant and Goodale, 2011; Cant and Xu, 2012; Cavina-Pratesi et al., 2009; Deshpande et al., 2008; Kitada et al., 2005; Sathian et al., 2011; Stilla and Sathian, 2008). The consistent spatial overlap across conditions is in line with findings from Mouraux et al. (2011) who reported that a wide network of brain regions shows multimodal activations, i.e. responses that can be elicited by stimuli from more than a single sensory modality. Furthermore, since we only varied the sensory information content between the different conditions but not the stimulated modalities, the even greater spatial consistency, including also early sensory regions in the current study, is not surprising. In contrast to other studies we did

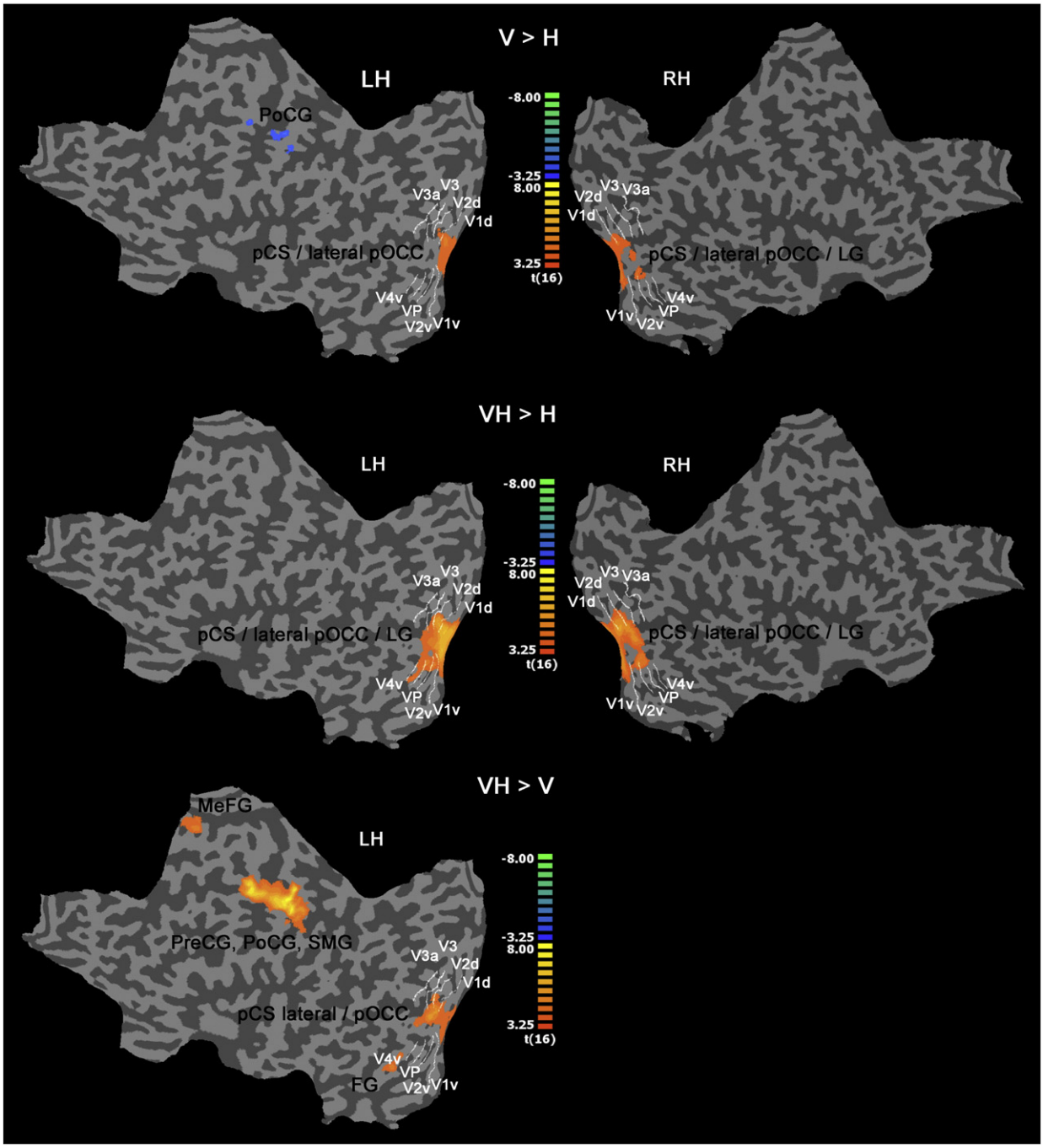

Fig. 6. Differences in the BOLD response between unimodal and bimodal dot pattern conditions. Random effect maps are displayed on a flattened surface reconstruction of a single representative subject for which early visual areas were delineated by retinotopic mapping; V = dot pattern information in visual modality (haptic control stimulus); H = dot pattern information in haptic modality (visual control stimulus); VH = matching dot pattern information in visual and haptic modality; PoCG = postcentral gyrus; pCS = posterior calcarine sulcus; pOCC = posterior occipital cortex; LG = lingual gyrus; PreCG = precentral gyrus; SMG = supramarginal gyrus; FG = fusiform gyrus; $p < 0.05$ corrected at cluster level; LH = left hemisphere, RH = right hemisphere.

not find a strong engagement of prefrontal areas (Kitada et al., 2005; Simões-Franklin et al., 2011). One potential explanation for this difference is the engagement in an active cognitive task in most paradigms versus the mere exploration of the textures in the experiment presented here.

Despite the close resemblance of the activation maps in the different texture variation conditions, we did find a change of the BOLD response in both visual and somatosensory cortex when subjects explored dot patterns only visually, only haptically or bimodally. Irrespective of the visual input, haptic dot pattern exploration induced increased activation in the contralateral PoCG, the putative location of the primary somatosensory cortex. This result indicates independence of the average dot-pattern-elicited activation level in PoCG from other sensory input. It is likely that perception of dot patterns is mediated mainly by slowly adapting type 1 (SA1) mechanoreceptive afferents (Bensmaia et al., 2006; Bergmann Tiest, 2010; Hollins et al., 2006). The different SA1 input during dot pattern versus smooth texture exploration might be represented in a different cortical activation pattern in the postcentral cortex (Chen et al., 2001; Friedman et al., 2004). Presumably, these differences would be at a fine-grained level (Pei et al., 2009) unlikely to be discovered by the data acquisition parameters used in our study, i.e. a voxel size of $3.5 \times 3.5 \times 3.5$ mm^3, and the smoothing applied to the data. Alternatively, the literature demonstrates that attention modulation

Table 2
Differences in the BOLD response between unimodal and bimodal dot pattern conditions (model 1). V = dot pattern information in visual modality (haptic control stimulus); H = dot pattern information in haptic modality (visual control stimulus); VH = matching dot pattern information in visual and haptic modality; pCS = posterior calcarine sulcus; pOCC = posterior occipital cortex; LG = lingual gyrus; PoCG = postcentral gyrus; MeFG = medial frontal gyrus; PreCG = precentral gyrus; SMG = supramarginal gyrus; FG = fusiform gyrus; x, y, z = Talairach coordinates of peak voxel; t = peak t value; R = right hemisphere; L = left hemisphere; $p < 0.05$ corrected at cluster level.

Contrast	Region	Hemisphere	x	y	z	t
[V > H]						
	pCS, lateral pOCC, LG	R	17	−89	−9	4.80
	pCS, lateral pOCC	L	−13	−98	−12	4.29
	PoCG	L	−46	−23	48	−4.30
[VH > H]						
	pCS, lateral pOCC, LG	L	−16	−95	−6	5.77
	pCS, lateral pOCC, LG	R	14	−89	−12	5.37
[VH > V]						
	MeFG	L	−10	13	45	4.79
	PreCG, PoCG, SMG	L	−37	−35	66	8.04
	pCS, lateral pOCC	L	−25	−95	−6	5.47
	Basal ganglia, thalamus	L	−22	−2	6	5.57
	Basal ganglia	R	8	7	9	4.66
	FG and cerebellum	L	−40	−68	−24	4.71
	Cerebellum	R/L	8	−47	−21	5.82
[V] ∩ [H] ∩ [VH > V] ∩ [VH > H]						
	pCS, lateral pOCC	L	−19	−95	−6	4.29

of sensory processing exists already as early as in the primary somatosensory cortex (e.g. Dionne et al., 2010; Karns and Knight, 2009; Sterr et al., 2007; for a review see Johansen-Berg and Lloyd, 2000). It is possible that the more salient dot pattern textures resulted in a shift of attention towards haptic texture exploration as compared to the visual condition in which only a smooth texture was explored by touch. In summary the comparison of all modality conditions indicates that visual information has no effect on haptic texture processing in somatosensory regions.

In early visual cortex the picture is slightly different. Here we also find an increase of the BOLD signal with texture variation in the visual condition but the size of the increase depends on the type of haptic information provided, reaching its maximum when matching haptic texture information is available. The increased activation in the visual dot pattern trials as compared to the presentation of the visual smooth control stimulus is expected, since dot pattern textures have more features and hence a higher contrast than the smooth control stimulus. This dependence of the BOLD signal on contrast changes of visual stimuli in early visual regions was already presented by Boynton et al. (1996) and later confirmed by others (e.g. Buracas et al., 2005).

However, the increased BOLD response in the bimodal dot pattern condition can only be explained by the matching haptic texture information, since the visual input was the same in the visual and in the visual–haptic condition. This indicates a crossmodal interaction of haptic and visual information in early visual cortex, and confirms our hypothesis that haptic information can modulate visual information processing already at a very early processing stage (as suggested by Lunghi et al., 2010). The existence of crossmodal effects in the visual cortex was reported by several studies in the last decade, focusing for example on target detection (Bauer et al., 2009), spatial attention (Macaluso et al., 2000), shape perception (Amedi et al., 2001; Lacey et al., 2009), tactile distance judgments (Merabet et al., 2004, 2007), tactile threshold-tracking (Nordmark et al., 2012) and tactile orientation discrimination (Zangaladze et al., 1999). However, the present study is to our knowledge the first one showing a direct influence of haptic information on visual processing in early visual cortex for a microspatial task, i.e. by dealing with small-scale surface deviations as in comparison to large-scale features like shape and size (macrospatial) (Roland and Mortensen, 1987).

This result is consistent with studies emphasizing that early visual regions play a role in both visual and haptic texture perception, speculatively by housing bisensory neurons or intermingled populations of modality-specific neurons (Kim et al., 2012; Sathian et al., 2011; Stilla and Sathian, 2008). Several studies used measures like superadditivity or inverse effectiveness to address the question of neuronal or areal

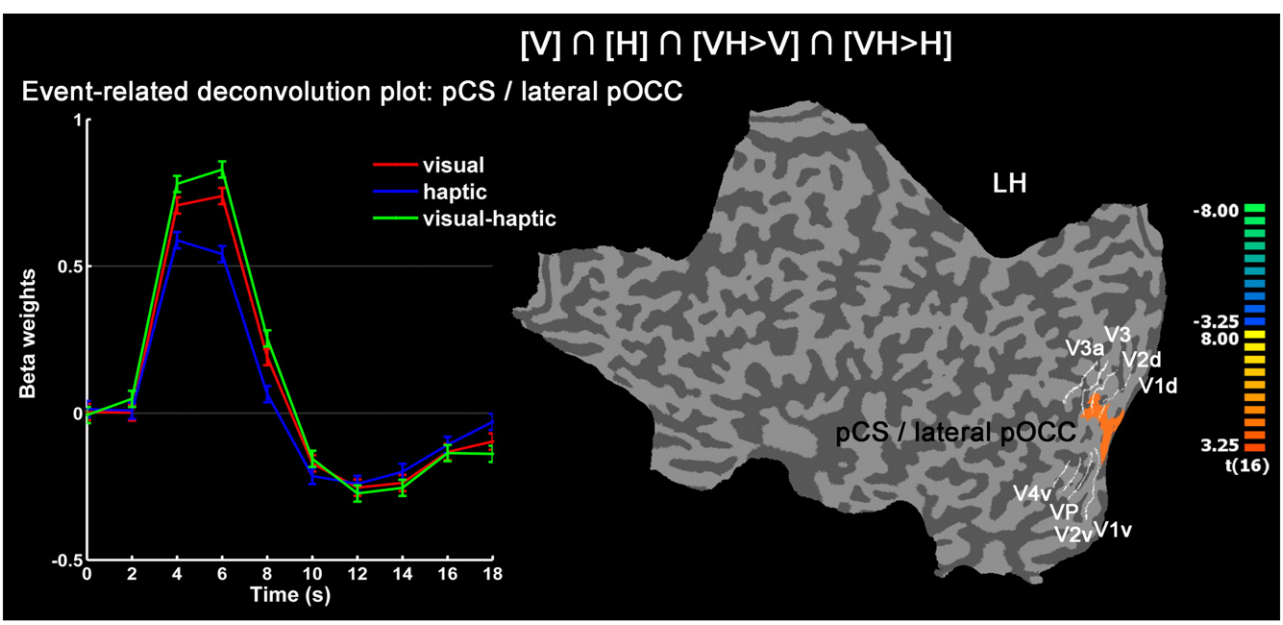

Fig. 7. Increased activation for bimodal as compared to both unimodal dot pattern conditions. Right: Random effect map of the conjunction contrast projected on a flattened surface reconstruction of a single representative subject for which early visual areas were delineated by retinotopic mapping; V = dot pattern information in visual modality (haptic control stimulus); H = dot pattern information in haptic modality (visual control stimulus); VH = matching dot pattern information in visual and haptic modality; pCS = posterior calcarine sulcus; pOCC = posterior occipital cortex; $p < 0.05$ corrected at cluster level; LH = left hemisphere. Left: Event-related deconvolution plot depicting an increased BOLD response for the visual–haptic dot pattern condition compared to both unimodal dot pattern conditions in the occipital cluster identified in the conjunction contrast; bars represent the standard error of the mean (SEM); 0 on the time axis represents stimulus onset.

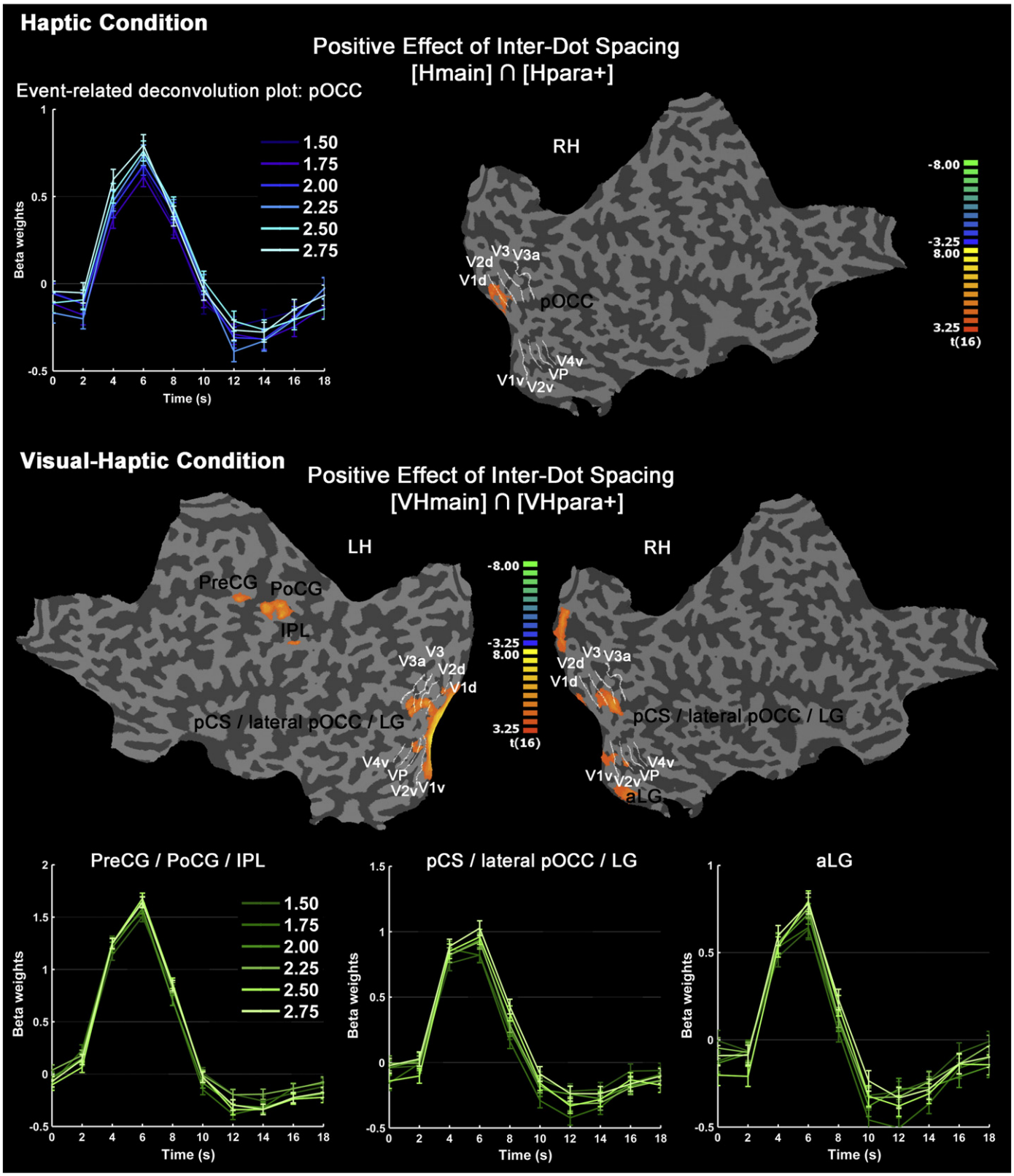

Fig. 8. Brain regions showing graded BOLD responses with varying objective texture characteristics (inter-dot spacing) in different modality conditions. Random effects maps of the conjunction contrast of the main modality predictor and the positive parametric predictor projected on a flattened surface reconstruction of a single representative subject for which early visual areas were delineated by retinotopic mapping; H = dot pattern information in haptic modality (visual control stimulus); VH = matching dot pattern information in visual and haptic modality; pOCC = posterior occipital cortex; PreCG = precentral gyrus; PoCG = postcentral gyrus; IPL = inferior parietal lobe; pCS = posterior calcarine sulcus; aLG = anterior lingual gyrus; $p < 0.05$ corrected at cluster level; LH = left hemisphere, RH = right hemisphere. Event-related deconvolution plots depicting a small linear effect of the inter-dot spacing of the textures on the BOLD response in brain regions identified by the conjunction contrast of the main and the parametric predictor; bars represent the standard error of the mean (SEM).

Table 3
Differences related to parametric dot pattern variation within each modality condition (models 2–4). H = dot pattern information in haptic modality (visual control stimulus); VH = matching dot pattern information in visual and haptic modality; pOCC = posterior occipital gyrus; pCS = posterior calcarine sulcus; aLG = anterior lingual gyrus; PreCG = precentral gyrus; PoCG = postcentral gyrus; IPL = inferior parietal lobe; x, y, z = Talairach coordinates of peak voxel; t = peak t value; R = right hemisphere; L = left hemisphere; $p < 0.05$ corrected at cluster level.

Parametric modulation	Contrast	Region	Hemisphere	x	y	z	t
Inter-dot spacing of textures							
	[Hmain] ∩ [Hpara+]						
		pOCC	R	8	−95	0	4.74
		Cerebellum	R	2	−44	−6	6.09
	[VHmain] ∩ [VHpara+]						
		pCS, lateral pOCC, LG	L/R	−13	−95	−6	6.99
		aLG	R	11	−56	3	5.33
		PreCG, PoCG, IPL	L	−46	−32	60	5.96
Roughness perceived by touch							
	[VHmain] ∩ [VHpara+]						
		pCS	L	−13	−89	−15	4.33
		PoCG	L	−52	−29	54	4.91
Spatial density perceived by vision							
	[VHmain] ∩ [VHpara-]						
		Lateral pOCC	R	17	−83	−12	4.62
		pCS, lateral pOCC, LG	L	−13	−92	−6	7.41
		aLG	R	8	−56	3	4.92
		PoCG, IPL	L	−49	−29	54	5.43

convergence in brain regions activated by stimuli from multiple sensory modalities (e.g. Calvert et al., 2000; Kim et al., 2012). For a recent discussion of different measures used to investigate multisensory phenomena in fMRI studies see James and Stevenson (2012). Our study was not designed to answer this question for visual–haptic texture processing. No purely unimodal stimuli were presented which would be needed to compare the BOLD response of these stimuli to responses elicited by bimodal stimuli. However, it can be concluded from our results that haptic texture information influences the processing of visual information in early occipital regions. Further implications of this finding with respect to neuronal or areal convergence have to be investigated using experimental designs optimized for direct comparisons of unimodal and bimodal texture processing.

Effects of parametric dot pattern variation within each modality condition

The analysis of the behavioral data showed a linear increase of roughness perceived by touch for textures with increasing average dot-spacing and a linear decrease of visual spatial density. The results indicate that on average subjects were able to discriminate the roughness as well as the density of all textures. These results were expected from earlier work of our (Eck et al., 2011) and other groups (Merabet et al., 2004, 2007). However, the individual ratings, displayed in Fig. 4, show that there are nevertheless small inter-individual differences in haptic roughness as well as visual density perception. Therefore we decided to use both subjective texture characteristics and the objective inter-dot spacing of the textures for the parametric modulation of the HRF in all modality conditions. The parametric modulation of the BOLD signal by all three measures resulted in very similar spatial characteristics of the statistical maps, as expected by the high correlation between the ratings and the objective texture characteristics. Nevertheless, the variation of the BOLD response was captured slightly better by inter-dot spacing than by perceived texture characteristics, as indicated by the increased spatial extent of the former mentioned parametric effects. Therefore, we will focus on discussing the effects of inter-dot spacing. In general, the parametric effects of texture variation on the BOLD response in this study were rather small. However, these effects are nevertheless remarkable for the following reasons. First, there were only very small differences between all dot pattern textures and although subjects were able to differentiate the textures after the fMRI experiment, the differences were not large enough to expect tremendous differences in the evoked BOLD response. This is especially true for the fast event-related stimulus presentation that was chosen to prevent subjects from actively judging the texture dimensions and to avoid boredom. Second, subjects were only instructed to focus on the simultaneous visual and haptic texture exploration. While it cannot be excluded that some evaluation processes occurred, active cognitive processing is expected to be absent or highly limited. Very similar instructions resulted in a lack of parametric responses in the cortex in previous unimodal studies (Kitada et al., 2005). Despite the rather subtle texture differences, we saw small activation changes with varying texture characteristics in both early visual and somatosensory cortex. A parametric variation of the BOLD response in the left PoCG was exclusively found for matching visual and haptic texture information (bimodal dot pattern condition). This indicates that visual information has an effect on relative activation differences elicited by varying tactile texture characteristics in early somatosensory cortex. Crossmodal influences on somatosensory cortex were already reported by Meehan and Staines (2009) and Dionne et al. (2010), using vibrotactile stimulation. Both studies found variations of somatosensory elicited BOLD responses in PoCG with visual information.

Interestingly, we failed to find a parametric effect on the BOLD signal of the visual cortex in the visual texture variation condition. Only with varying haptic texture information a parametric effect was observed in the right posterior OCC, independent of the visual information provided. One explanation for the parametric effect in the visual cortex in a haptic texture variation condition would be visual imagery. However, if this interpretation applies we would have expected a similar parametric effect in the visual condition, which was not the case in the present study. An alternative explanation is that the visual cortex responds not only to visual but also to a certain extent to tactile stimulation. This result contradicts the traditional view that early sensory cortices are limited to information processing from a single modality. However, as already indicated above, many studies have demonstrated the same pattern of results, i.e. responsiveness of the visual cortex to non-visual stimuli (for a summary see Sathian and Lacey (2007) and Lacey et al. (2008). These studies focused mainly on shape perception (Amedi et al., 2001; Kassuba et al., 2012; Kim and James, 2009), describing regions in the occipital cortex, i.e. the lateral occipital complex (LOC), that are not only responsive to visual object perception but also to haptic perception of 3D objects. Importantly, these findings were not a mere result of visual imagery as expected at the beginning of this line of research (Deshpande et al., 2010; Lacey et al., 2010). In the last years even more studies were published suggesting a contribution of the visual cortex also to other tactile tasks, as for example grating orientation discrimination (Zhang et al., 2005), dot pattern judgments (Merabet et al., 2004, 2007) and texture matching (Stilla and Sathian, 2008). However, we did not only find a parametric effect of inter-dot spacing in the visual cortex, when only haptic dot patterns were presented; additionally, we observed that the parametric effect on the BOLD signal expanded to the left pOCC as well as to the pCS and the lingual gyrus when haptic and visual texture characteristics were varied congruently. This clearly indicates an interaction of visual and haptic dot pattern information in early visual cortex.

We did not find any parametric effects in the classical brain regions implicated in texture perception, as for example the collateral sulcus and the parietal operculum and the insula; while Kitada et al. (2005) reported parametric effects of tactile roughness estimation in the latter two areas as well as in prefrontal regions. However, in contrast to previous studies we asked subjects to explore the textures without any active cognitive task. We would expect an involvement of these

higher-order brain regions with increasing task demands, e.g. when an evaluation of the presented textures along a specific dimension or a comparison of the textures is necessary, consistent with the report of Kitada. The parametric effects on the BOLD response in early sensory cortices in our study rather indicate a modulation already at an early processing stage without cognitive evaluation demands. This view can be well integrated in the interpretation of Hiramatsu et al. (2011), that early visual regions, i.e. V1/V2, V3 contain image-based representations of material properties rather than higher-region perceptual representations. Retinotopic information was only available for two subjects in our sample and the retinotopic map of one of these subjects was used to present the results. Although we cannot be certain in which early visual regions the significant activations were located, the exemplary retinotopic map suggests an involvement of V1–V3. This is partly in accordance with the findings of Merabet et al. (2007) who showed a clear activation of primary visual cortex (V1) by tactile stimulation and deactivation of extrastriate regions (V2, V3, V3a, hV4). Individuals were blindfolded in Merabet's experiment, while subjects in the current study received non-matching and matching visual stimulation. This additional visual stimulation would be a plausible explanation for the difference in the findings across both studies. The connectivity analyses by Sathian et al. (2011), showing that tactile texture information is first processed in the PoCG before flowing to higher-order cortices, also indicate that the parametric effects of varying texture characteristics in the present study represent a rather early and automatic cortical processing stage. The result that inter-dot spacings rather than perceived texture differences were slightly better qualified to capture parametric BOLD modulation with texture variation also points to that interpretation.

Taken together, the results of the parametric analyses confirm our hypothesis that the additional presentation of matching visual texture information is sufficient to observe parametric effects of varying texture characteristics on the BOLD response, even when subjects are not required to evaluate the presented textures. This extends the findings of Kitada et al. (2005), who did not find a parametric variation of the BOLD signal when subjects explored the textures tactually without a judgment task. Crossmodal interaction effects of visual and haptic texture information in early sensory cortices are the probable cause of the differences between both studies.

Integration of results

To summarize the results above, we found an effect of matching visual–haptic texture information in early visual and somatosensory regions. However, the kind of crossmodal interaction was slightly different in both sensory cortices. In the contralateral somatosensory cortex (PoCG) the activation level did not change between the presentation of unimodal haptic and bimodal visual–haptic dot pattern information. However, in the bimodal dot pattern condition, small changes in the BOLD response were detected with varying texture characteristics, indicating a crossmodal effect on relative differences in the BOLD signal of the contralateral somatosensory cortex in response to different textures.

The average BOLD response in a posterior occipital cluster in the left hemisphere increased when bimodal as compared to unimodal visual or haptic dot pattern information was provided, indicating a crossmodal effect on the overall signal in the left early visual cortex. Parametric effects on the BOLD response in early visual cortex were already found when only haptic texture information was varied, though right-lateralized only. When matching visual dot pattern information was added, the parametric effects were more pronounced in the same hemisphere and extended also to the left visual cortex. This indicates, as with the somatosensory cortex, a crossmodal effect on relative differences in the BOLD signal of the visual cortex in response to different textures.

In contrast to the classical view that different sensory information converges only at higher association areas, our findings lead us to believe that crossmodal interactions occur already at an early automatic stage of texture processing. The reasons for that interpretation are twofold. First, overall and relative effects of matching visual–haptic texture variation were primarily observed in early sensory cortices without a contribution of prefrontal regions and higher sensory cortices. Second, inter-dot spacing was slightly better qualified to capture parametric BOLD modulation with dot pattern variation than perceived texture characteristics.

Our study design does not allow us to identify the source of the crossmodal interactions; however we propose two possible explanations. The first would be hierarchical feedback of top-down influences from higher sensory areas on early sensory cortices. This explanation is consistent with the finding of projections from parietal association areas to V1 and V2 in the macaque (Borra and Rockland, 2011) and with connectivity analyses by Sathian et al. (2011) showing that visual texture information flows from the higher-order fusiform gyrus to early visual cortex. However, no visual texture information flow to early somatosensory regions was reported by the latter study. Hence, the fact that only matching visual–haptic texture information induced a parametric modulation of the BOLD response in the contralateral somatosensory cortex (PoCG) cannot be explained in this way. An alternative, and in our opinion more likely interpretation would be direct or indirect cortico-cortical connections between early sensory cortices (Cappe and Barone, 2005), explaining the crossmodal texture effects in both early somatosensory and visual cortex. This is partly in accordance with the results by Deshpande et al. (2008) and Sathian et al. (2011) who showed a direct flow of haptic texture information from the PoCG to bilateral early visual cortex.

Conclusion

The present study aimed to investigate whether cortical processing in early sensory cortices changes when matching as compared to non-matching visual–haptic texture information is provided. Earlier research has shown that crossmodal interactions for texture perception exist at the behavioral level. However, neuroimaging studies focused primarily on visual and haptic texture processing separately, allowing to investigate only the overlap of both sensory processing streams. The variation of texture information in a bimodal task in the present study permitted the exploration of crossmodal interactions at the cortical level. More specifically, we hypothesized that parametric effects on the BOLD signal can be expected with varying texture characteristics when matching visual–haptic textures are explored, even when a cognitive evaluation of the textures is not required.

Indeed, both early visual and somatosensory cortex showed crossmodal interactions of visual–haptic texture processing. These effects were slightly different in both sensory cortices, with bimodal visual–haptic dot pattern information increasing the average activation level as well as inducing relative differences of the BOLD signal with varying texture characteristics in early visual cortex, and only the latter effect in somatosensory cortex.

The results presented here challenge the notion that the cortical processing of texture information in the visual and haptic modality is independent of each other. Rather than a rigid sensory separation between classical visual and somatosensory brain regions, the results suggest a flexible cooperation of sensory cortices.

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Conflit of interest

I am one author declaring on behalf of all co-authors of the manuscript that there is no conflict of interest with any financial organization or any other people regarding the material discussed in the manuscript.

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