Comparing tactile pattern and vibrotactile frequency discrimination: a human fMRI study

Yiwen Li Hegner (李逸文)¹,²*, Ying Lee (李莹)³, Wolfgang Grodd⁴, Christoph Braun⁵,⁶

¹Institute of Medical Psychology and Behavioral Neurobiology, University of Tübingen, Germany; ²MEG Center, University of Tübingen, Germany; ³Graduate School of Neural & Behavioural Sciences, International Max Planck Research School, University of Tübingen, Germany; ⁴Section of MR Imaging of the CNS, Neuroradiology, University of Tübingen, Germany; ⁵Center for Mind/Brain Sciences, University of Trento, Italy; ⁶Department of Cognitive and Education Sciences, University of Trento, Italy

Spatial and Temporal Tactile Discrimination

Yiwen Li Hegner
MEG-Center
Otfried-Mueller-Str. 47
72076 Tuebingen, Germany
Email: yiwen.li@med.uni-tuebingen.de
Phone: +49 7071 29 87750
Fax: +49 7071 29 5706
Abstract
We investigated to which extent the discrimination of tactile patterns and vibrotactile frequencies share common cortical areas. An adaptation paradigm has been used to identify cortical areas specific for processing particular features of tactile stimuli. Healthy right-handed subjects performed a delayed-match-to-sample (DMTS) task discriminating between pairs of tactile patterns or vibrotactile frequencies in separate functional magnetic resonance imaging sessions. The tactile stimuli were presented to the right middle fingertip sequentially with a 5.5 s delay. Regions-of-interest (ROIs) were defined by cortical areas commonly activated in both tasks and those which showed differential activation between both tasks. Results revealed recruitment of many common brain regions along the sensory motor pathway (such as bilateral somatosensory, premotor areas and anterior insula) in both tasks. Three cortical areas, the right intraparietal sulcus (IPS), supramarginal gyrus (SMG)/parietal operculum (PO) and PO, were significantly more activated during the pattern than in the frequency task. Further blood-oxygen-level-dependent (BOLD) time course analysis was performed in the ROIs. Significant BOLD adaptation was found in bilateral IPS, right anterior insula and SMG/PO in the pattern task, while there was no significant BOLD adaptation found in the frequency task. In addition, the right hemisphere was found to be more dominant in the pattern than in the frequency task, which could be attributed to the differences between spatial (pattern) and temporal (frequency) processing. From the different spatio-temporal characteristics of BOLD activation in the pattern and frequency tasks, we concluded that different neuronal mechanisms are underlying the tactile spatial and temporal processing.
Introduction

Tactile perception relies on both spatial and temporal information from tactile stimuli. There have been strong evidence showing that slowly and rapidly adapting neural afferents mediate mainly spatial (e.g. tactile pattern) and temporal (e.g. vibrotactile flutter: 5 – 50 Hz) aspects of tactile information respectively (Johnson and Hsiao 1992; Romo et al. 1998). A previous psychophysical study suggested that different aspects of tactile information might be stored in different cortical sub-modules in human (Harris et al. 2001a). Their experimental results indicated that vibrotactile information seems to be shortly stored in Brodmann area (BA) 3b of the primary somatosensory cortex (S1, located in postcentral gyrus), whereas tactile punctate pressure and roughness information appears to be maintained in downstream areas beyond S1, such as the secondary somatosensory cortex (S2, located in parietal operculum, PO). It is thus likely that tactile spatial and temporal information are processed either by separate sub-populations of neurons in the same somatosensory areas or by different cortical areas. Furthermore, it has been shown that the left hemisphere has a better temporal resolution while the right hemisphere has a better spatial resolution in processing of visual and auditory stimuli (for review, see Brancucci et al. 2009). Extensive research has focused upon cortical processes involving either vibrotactile frequency or tactile spatial discrimination. However, it is to date unclear as to whether a differential involvement of somatosensory areas exists when these two types of discrimination tasks are carried out under similar experimental settings.

Cortical areas which subserve tactile pattern discrimination have yet to be completely characterized. Various studies have shown the involvement of both S1 and S2 in tactile texture discrimination (Sinclair and Burton 1991; Chapman and Ageranioti-Belanger 1991; Ageranioti-Belanger and Chapman 1992; Sinclair and Burton 1993; Tremblay et al. 1996). Arabzadeh and colleagues have found that rat S1 (barrel cortex) neurons could reliably decode texture in spike count and spike pattern code (Arabzadeh et al. 2006). Moreover, S2 neurons were shown to be involved in tactile roughness encoding and discrimination (Sinclair and Burton 1993; Jiang et al. 1997; Pruett et al. 2000; Pruett et al. 2001). Fitzgerald and colleagues have recently reported orientation-selective S2 neurons in monkeys, which could serve to extract fine local spatial features such as the decoding of Braille dot patterns (Fitzgerald et al. 2006a; Fitzgerald et al. 2006b). In addition, our previous magnetoencephalography (MEG) study revealed an active role of right temporo-parietal cortex in tactile dot pattern discrimination (Li Hegner et al. 2007a).
Frequency discrimination of vibrotactile stimuli has been widely studied using single- and multi-unit recordings in animals (Talbot et al. 1968; Mountcastle et al. 1969; Romo and Salinas 2003; Arabzadeh et al. 2004; Luna et al. 2005), as well as psychophysical experimentation in human (LaMotte and Mountcastle 1975; Mountcastle et al. 1990; Harris et al. 2001b; Harris et al. 2002; Harris et al. 2006). Romo and colleagues have shown in monkeys that S1 drives and interacts closely with higher cortical areas such as S2, premotor as well as prefrontal cortex during vibrotactile frequency discrimination (Zainos et al. 1997; Romo et al. 2002a; Romo et al. 2002b; Romo et al. 2004; Romo et al. 2006). Human psychophysical studies by Harris and colleagues have additionally suggested that S1 stores transient vibrotactile information (Harris et al. 2002) in a somatotopic fashion (Harris et al. 2001b). Furthermore, the authors have proposed that multiple brain regions and distinct cortical mechanisms are related to vibrotactile frequency encoding, such as the adaptive processes of S1 neurons (Harris et al. 2006). Using an event-related functional magnetic resonance imaging (fMRI) adaptation paradigm, we have previously identified a network of cortical areas involved in vibrotactile frequency discrimination (Li Hegner et al. 2007b). Other human brain imaging studies using vibrotactile stimuli have revealed activation of a similar network of cortical areas, including S1, S2, insula and posterior parietal cortex (Francis et al. 2000; Tuunanen et al. 2003; Nelson et al. 2004; Preuschhof et al. 2006; Soros et al. 2007; Kostopoulos et al. 2007; Albanese et al. 2009; Preuschhof et al. 2009). More importantly, accumulating evidence has revealed a key role of anterior insula (Soros et al. 2007; Albanese et al. 2009) and posterior parietal cortex (Preuschhof et al. 2006; Preuschhof et al. 2009) in vibrotactile working memory.

Stimulus-specific fMRI adaptation (also known as repetition suppression) refers to a relative decrease of blood-oxygen-level-dependent (BOLD) signal for repeated versus novel stimulus presentation in regions selective for a stimulus feature. An adaptation paradigm takes the assumption that the responses of a neuronal population selective for certain stimulus feature will be reduced or adapted if the same stimulus feature is repeated and will be released from adaptation when a change within this stimulus feature is presented (for review, see Grill-Spector et al. 2006). A BOLD adaptation analysis will reveal brain regions which are sensitive to stimulus repetition, and thus reveal potential stimulus-specific regions as well as their feature specificities. BOLD response adaptation, which has been observed when two vibrotactile stimuli of the same vibrating frequency were sequentially presented with a 0.6 s delay, was speculated to be a reflection of vibrotactile sensory memory (Li Hegner et al.
Furthermore, Jiang and colleagues suggested that BOLD adaptation seems to manifest an automatic visual working memory tag in the visual cortices (Jiang et al. 2000).

The main objective of the current fMRI study was to investigate whether differences do exist in the cortical processes of discriminating tactile pattern and vibrotactile frequency information within the same experimental setup. Our focus of this comparison was in the underlying storage and discrimination processes of each tactile stimulus feature. We have asked healthy volunteers to perform a delayed-match-to-sample (DMTS) task in which they compared either tactile pattern or vibrotactile frequency of two stimuli serially delivered to their right middle fingertips, during which brain activity was measured using event-related fMRI. BOLD adaptation analysis will thus reveal the necessary information on whether a brain region is sensitive to a change in the subsequent stimulus on tactile patterns or vibrotactile frequencies. As a secondary objective of this study, we were interested in whether BOLD response adaptation would be observed with a longer (5.5 s) delay between the two stimuli and if yes, whether it would be observed in regions similar to those identified previously (Li Hegner et al. 2007b). We hypothesized that working memory would be reflected by BOLD adaptation in the somatosensory areas that maintain the sample stimulus information.

Materials and Methods

Participants

Ten healthy right-handed subjects (mean age: 26 years, standard deviation [SD]: 3.2 years, five females) participated in this study. Handedness was assessed according to the Edinburgh Handedness Inventory (Oldfield 1971). One subject was excluded from the data analysis due to chance-level performance in both discrimination tasks during the fMRI scan. The protocol of the current human investigation was approved by the local ethics committee of the University of Tübingen. Prior to fMRI data acquisition, all subjects gave their written informed consent.

Tactile stimulation

Both tactile pattern and vibrotactile frequency stimuli were presented using the same piezoelectric wafers (piezo: TeleSensory, CA, USA; casing and electrical connectivity board: metec AG, Stuttgart, Germany) driven by 200 V pulses from custom-made amplifiers, which were controlled by a computer running on a real time operation system. The stimulation surface consisted of a panel of nine rods (rod size Ø 1 mm, a 3 x 3 matrix, panel size 8 x 8
mm², see Fig.1), each of which could be controlled individually to ascend, cause a skin indentation of about 1.5 mm and descend. All stimuli were made up from five protruding rods. The right middle fingertip of each subject was kept gently restrained to the piezoelectric wafer case during the task to ensure minimal finger movement. The two types of stimuli differed as follows: rods protrude simultaneously and remain stationary for 0.6 s to create a two-dimensional stationary pattern; rods protrude and vibrate sinusoidally in the flutter range of 16-34 Hz (2 Hz steps) for 0.6 s to create a consistent ‘pattern’ which vibrates (see Fig.1).

**Experimental Design**

An event-related fMRI paradigm was used in this study. All subjects were required to carry out the pattern and frequency tasks in separate, consecutive sessions, the order of which was counterbalanced across subjects. During each trial, two tactile stimuli with duration of 0.6 s each were serially presented with an inter-stimulus interval (ISI) of 5.5 s (see Fig. 1). In order to account for the slow hemodynamic response (BOLD effect), the duration of the ISI was chosen as such to provide a good separation of the BOLD responses to the first (sample) and second (comparison) stimuli while ensuring an intermediate trial length to minimize overall scanning time. In a two-alternative forced-choice manner for every trial, subjects were asked to perform a DMTS task where they were to decide if the sample (stimulus 1) and comparison (stimulus 2) stimuli were the same or different. In each session (36 trials), only one task (either tactile pattern or vibrotactile frequency discrimination) was presented. The inter-trial interval (ITI) was made to vary between 7.5 s and 9.5 s as a temporal jittering of the functional imaging trigger (mean ITI: 8.5 ± 1.4 s). A rest period of 15 s was added to the beginning as well as the end of each session. The number of trials with identical (same) stimuli was equivalent to that with non-identical (diff) stimuli. Subjects responded to indicate same or diff by pushing buttons with their left index or middle finger respectively. All subjects received behavioral training with performance feedback (~ 50 trials per task) one day prior to the fMRI scan. In order to control for attentional load across tasks within-subject, the difficulty level of the frequency task was individually adjusted (to one of the following frequency differences: ± 6 Hz, ± 12 Hz, ± 18 Hz) based on their training accuracy rates. This was to increase the likelihood that the subject would perform as well for the frequency task as the pattern task during the actual fMRI scan. Therefore the attentional load for both tasks would be as similar as possible. Prior to each fMRI scan, subjects were reminded to keep their eyes closed during the entire session and pay attention to the right middle fingertip where the tactile stimuli were presented. The presentation order of the same and diff trials was
pseudorandomized and counterbalanced within and across subjects. The trial sequences were identical within-subject for pattern and frequency sessions to allow for a straightforward comparison between the two tasks.

Image Acquisition
The experiment was conducted with a 3-Tesla MR scanner (Siemens Trio, University Hospital Tübingen, Germany). Each functional scan was acquired with an echo-planar imaging (EPI) sequence (TR = 2.5 s, TE = 35 ms), consisted of 36 axial slices (thickness: 3.2 mm) covering the whole brain in a descending order, with a planar resolution of 3 x 3 mm² and an inter-slice gap of 0.8 mm. A high-resolution (1 mm, isotropic) T1-weighted structural image was then acquired with an MPRAGE sequence directly after the functional imaging for every subject.

Data analysis
Statistical analysis of the behavioral data was carried out with SPSS (SPSS Inc., USA). The fMRI data was analyzed using Brain Voyager QX 2.0 (Brain Innovation B.V., The Netherlands). Prior to analysis, the first two volumes of the functional data were discarded. Preprocessing of the functional data included slice scan time correction, 3D motion correction and temporal high-pass filtering (general linear model with Fourier basis set: 2 sines / cosines, including linear trend removal). Anatomical images were transformed into Talairach space and the cortices were reconstructed for each subject. In order to achieve a better spatial correspondence mapping of cortical areas among subjects, each hemisphere was morphed into a spherical representation allowing a cortex-based inter-subject alignment among subjects (Fischl et al. 1999). Cortices of eight subjects were then aligned to that of one target subject. After functional and anatomical data within each subject were co-registered, correspondence mapping parameters across subjects were then used to align the functional data for the subsequent group analysis.

A multi-subject random-effects General Linear Model (GLM) analysis was performed with four predictors (stimulus 1, delay, stimulus 2 and response) and the six motion correction parameters for both tasks. All predictors were of the same duration (0.6 s). The delay predictor was set at the middle of the whole delay period and the onset of the response predictor was set upon each button press. Each event was then convolved with a two-Gamma hemodynamic response function (with response peak at 5 s) for the GLM computation. For the second level analysis, a conjunction of random effects analysis was first applied to unveil
common cortical areas involved in both tasks across subjects. We then performed \( t \)-contrasts to reveal task-specific cortical areas from direct comparison between the BOLD activations of the two tasks. Multiple comparison correction was done by cluster thresholding via Monte Carlo simulations (Forman et al. 1995) integrated in the BrainVoyager QX 2.0 software package.

All areas identified in the second level analysis were then used as ROIs for the BOLD adaptation analysis. In theory, BOLD adaptation should take place during the presentation of stimulus 2. However, due to the temporal proximity of the delay and stimulus 2 predictors, we cannot totally rule out the possibility that the delay predictor could also have taken some of the BOLD signals generated from the presentation of stimulus 2. Thus for the ROI selection, both the conjunction analysis (pattern and frequency) and the \( t \)-contrast analyses (pattern > frequency or frequency > pattern) were constrained to the predictors of delay and stimulus 2. As the GLM calculation took into account the information of the inter-subject cortex-based alignment, the BOLD activation maps resulting from group analysis had equivalent anatomical locations for each subject. The BOLD time courses averaged from voxels within each ROI for each subject were extracted and spline-interpolated into seconds. Event-related averaging was then performed separately for both tasks for each ROI by subtracting the mean BOLD signal at 0 s (stimulus 1 onset) derived from every correct trial to compute the percent BOLD signal change.

The trials were separated into two categories, namely *same* (stimulus 1 = stimulus 2) and *diff* (stimulus 1 ≠ stimulus 2). A one-tailed paired \( t \)-test was first applied between the peak values (between 3 s and 14 s post stimulus 1 onset) of the *same* and *diff* time courses across subjects for each ROI. We were thus able to examine which brain areas responded significantly stronger in *diff* than in *same* trials. Finally, within the areas identified, one-tailed paired \( t \)-tests were performed at each time point to reveal the time range of the significant BOLD response adaptation along the trial.

## Results

### Behavioral data

The average performance was 81.3 % (SD: 12.3 %) correct responses for pattern and 79.2 % (SD: 10.7 %) for frequency task. The average reaction time (only correct trials) was 0.81 s (SD: 0.27 s) for pattern and 0.94 s (SD: 0.30 s) for frequency task (see Fig. 2). A repeated-measures two-factorial (task [pattern vs. frequency]; pair [same vs. diff]) ANOVA was performed on the accuracy and reaction time data. The accuracy did not differ significantly
between tasks (task: $F[1, 8] = 1.07$, $p = 0.33$) and between pairs (pair: $F[1, 8] = 0.36$, $p = 0.57$). Although it was not statistically significant, subjects seemed to have responded slightly faster in pattern than in frequency task (task: $F[1, 8] = 4.32$, $p = 0.07$). No significant difference in reaction time was found between pairs (pair: $F[1, 8] = 0.604$, $p = 0.46$). However, there was a significant interaction for the reaction time between task and pair (task x pair: $F[1, 8] = 6.12$, $p = 0.04$) with shorter reaction time in diff than in same for the frequency task and longer reaction time in diff than in same for the pattern task.

Functional imaging data

Conjunction analysis revealed the following areas to be commonly activated in both tasks during delay and stimulus 2 presentation: left / contralateral postcentral gyrus (S1), right / ipsilateral central sulcus (primary motor cortex, M1), bilateral postcentral sulci, precentral sulci (premotor cortex), intraparietal sulci (IPS), PO (S2), anterior insula / frontal operculum and superior frontal gyri (supplemental motor area, SMA; see Fig. 3A, cluster threshold: 19 mm$^2$ for the left and 18 mm$^2$ for the right hemisphere, $P_{corrected} < 0.0001$). Further time course analysis of same and diff trials in each of these regions revealed no significant BOLD adaptation for the frequency task. However, left IPS (peak $p = 0.02$), right IPS (peak $p = 0.006$) and anterior insula (peak $p = 0.049$) showed significant BOLD adaptation during the pattern task (see Fig. 3B). While the t-contrast of BOLD activation during the delay and stimulus 2 presentation did not reveal any cortical areas with stronger BOLD activity in frequency than pattern tasks, IPS, supramarginal gyrus (SMG)/PO and PO (cluster threshold: 51 mm$^2$, $P_{corrected} < 0.005$) in the right hemisphere displayed significantly stronger BOLD activity in pattern than frequency tasks (see Fig. 4). The difference seemed to be throughout the entire time course of the trial. Further time course analysis of same and diff trials in each of these regions revealed significant BOLD adaptation in the right SMG/PO (peak $p=0.026$) and a trend of adaptation in the right IPS (peak $p =0.057$) for the pattern task. No significant BOLD adaptation was found for the frequency task.

Discussion

The current fMRI study employed a DMTS task during which subjects were presented with two tactile stimuli serially, and they were to decide if those stimuli were the same or different. The experiment consisted of two separate sessions with the same experimental setup, only differing in the tactile feature of the stimuli in question, namely tactile pattern or vibrotactile
frequency. It was hypothesized that working memory (maintenance of the feature information of stimulus 1 during the delay period) could be reflected in the form of a BOLD response adaptation in the somatosensory areas. The aim of the experiment was to identify common and task-specific neural substrates, in particular, cortical areas involved in the representation and storage of stimulus features, which underlie tactile pattern and vibrotactile processing.

Cortical processes of spatial and temporal tactile information

Subjects performed equally well in both tasks, but their reaction time was slightly slower for vibrotactile frequency discrimination. This was as expected as the entire stimulus presentation period might have been necessary for the encoding of frequency information, a temporal tactile feature, whereas pattern information, a spatial tactile feature, could have been extracted instantaneously upon stimulus onset.

Our findings from the functional imaging data showed left S1 (contralateral to tactile stimulation), right M1 (contralateral to button press), bilateral postcentral sulci, precentral sulci (premotor cortex), IPS, PO (S2), anterior insula/frontal operculum and SMA to be involved in the DMTS tasks of both pattern and frequency discrimination. This is largely consistent with previous studies (e.g., Preuschhof et al. 2006; Soros et al. 2007) as tactile working memory seems to reside in a network of brain regions, such as somatosensory and parietal areas (Zhou et al. 2007). A direct comparison using t-contrasts between BOLD activations during pattern and frequency tasks revealed right IPS, SMG/PO and PO to be more activated during pattern than frequency discrimination. Conversely, no regions were found to be more activated during frequency than pattern discrimination.

Upon a detailed examination of the BOLD time courses in these areas, the differences between pattern and frequency were already significant at 2 s or 3 s post trial onset. We would like to propose two possible explanations behind this phenomenon. Firstly, it could be due to the different physical characteristics between the two types of stimuli per se. Although both stimuli were of the same duration (0.6 s), the pattern stimulus was static whereas the frequency stimulus was a vibration. The neuronal responses of somatosensory areas could thus have been more suppressed during the repetitive stimulation from the vibrotactile stimulus. However, this discrepancy in the BOLD responses (except in the right IPS) was not apparent in the cortical areas which were commonly activated in both tasks. Therefore, this difference in BOLD response between the pattern and frequency task cannot be explained by the differing nature of the stimuli alone. This brings us to our second possible explanation for
this observation is that these brain regions revealed by the t-contrast were indeed more involved in pattern than in frequency discrimination.

A closer examination of the BOLD adaptation within all the ROIs has provided us with evidence that different neuronal mechanisms do underlie tactile spatial (pattern) and temporal (frequency) processing. Our results showed BOLD adaptation in bilateral IPS, right SMG/PO and anterior insula/frontal operculum during the pattern task, but none in the frequency task.

Different neuronal representations for maintenance of pattern and frequency information during a delay period of 5.5 s might explain the absence of BOLD adaptation in the frequency task. Though robust BOLD adaptation in a similar vibrotactile frequency discrimination experiment has been observed (Li Hegner et al. 2007b), the delay period of 0.6 s was very much shorter. Hence it was stipulated that only sensory memory was necessary to maintain the frequency information ‘online’ for a short duration without the need for any higher order processing. In this study, however, given the longer delay period involved, it is unclear to us how exactly the frequency information is represented, such as in the form of tactile, auditory, abstract number count or verbal [high, low] memory. It is also possible that the subjects might have formed an internal representation of the mean frequency derived from the training session and solved frequency tasks by integrating frequency information of stimulus 1 and the mean (Preuschhof et al. 2009). All of this could have made the frequency task more challenging and different subject might have used a different combination of internal frequency representations, which might have resulted in a lack of consistent BOLD adaptation in the same cortical areas across subjects. Conversely, it could have been more homogeneous across subjects in the pattern than in the frequency task as the pattern information was likely represented as a tactile-visual pattern. As such, the inconsistency of neuronal representations of frequency information across subjects could have manifested as a lack of BOLD adaptation observed in the frequency task.

As for the pattern task, BOLD adaptation seems to reflect tactile pattern working memory in bilateral IPS, right SMG/PO and anterior insula/frontal operculum. Bilateral IPS was found to be active in various multi-modal tasks, especially in visuospatial working memory (Todd and Marois 2004). There has been evidence showing the right hemisphere dominance in spatial processing (Jonides et al. 1993; D'Esposito et al. 1998), which is in line with our current observation. Our previous MEG study on a similar tactile pattern working memory task has suggested an important role of right temporo-parietal cortex in maintaining tactile dot pattern information in working memory (Li Hegner et al. 2007a). The fMRI results from this study has affirmed the anatomical location and provided evidence for the potential neuromagnetic
source in our previous MEG finding. We have noted that there were at least three independent
activation clusters located in the right PO area involved in the pattern task. Ledberg and
colleagues (Ledberg et al. 1995) reported that minimally two activation sites were found at the
ipsilateral PO when the right hand was tactually stimulated. Accumulating evidence has
shown that up to four anatomically adjacent but functionally distinct areas exist in PO
(Disbrow et al. 2000; Eickhoff et al. 2006). As it is unclear whether all BOLD activation sites
in PO observed in this study belong to S2, we prefer to describe them anatomically. The
activation cluster in right PO revealed by the conjunction analysis is most likely to correspond
to S2. At the upper bank of the right lateral sulcus, two independent clusters were found to
exhibiting stronger activation during pattern than frequency discrimination. While the
posterior cluster closer to SMG displayed significant BOLD adaptation in the pattern task, the
anterior cluster did not. This could imply distinct functions of the two PO areas. Therefore,
we concluded that the right SMG/PO could be the neuromagnetic source underlying tactile
pattern working memory.

The interpretation of long lag BOLD response adaptation

In this paper, we refer to long lag BOLD response adaptation as the adaptation paradigm used
in this study as opposed to rapid fMRI adaptation paradigm where stimuli were presented in a
rapid succession (< 1 s) as used in our previous study (Li Hegner et al. 2007b). As the
underlying neural mechanism of BOLD adaptation is unclear, its interpretation is intricate
despite being proven useful in various studies (for reviews, see Grill-Spector et al. 2006;
Krekelberg et al. 2006). For example, BOLD adaptation in object-selective areas seems to be
distinct from that observed in the early visual areas (Sayres and Grill-Spector 2006). Early
sensory areas appear to show robust stimulus-specific BOLD adaptation, whereas higher
cortical areas, such as prefrontal cortex, do not necessarily behave as such (Verhoef et al.
2008). Furthermore, BOLD adaptation is very sensitive to the duration of stimulus
presentation (for review, see Krekelberg et al. 2006). Hence, it is important not to rule out the
functional roles of cortical areas in working memory based on the lack of BOLD response
adaptation effect observed.

Different neuronal mechanisms could be involved when comparing short and long lag BOLD
adaptation (Epstein et al. 2008). The rapid adaptation paradigm is generally preferred for
investigating neuronal selectivity as additional processes might take place with longer delay
periods. However, as we were more interested to explore the additional processes, such as the
traces of tactile working memory during a longer delay period of 5.5 s, the long lag BOLD adaptation paradigm was the preferred choice in this study. Previous studies have suggested that BOLD adaptation due to repeated stimulus presentation reflects memory processes (Jiang et al. 2000; Ranganath and Rainer 2003). In this study, we postulate that the following processes might have occurred during the task. As stimulus 1 is encoded, a mental representation of it has to be held online during the delay period before it is engaged during the comparison phase when stimulus 2 is presented. This maintenance of the mental representation is undertaken by a network of tactile working memory areas, which have been identified in other studies as well, such as S2, anterior insula and posterior parietal cortex (Preuschhof et al. 2006; Soros et al. 2007; Albanese et al. 2009). BOLD responses of these cortical areas become adapted when stimulus 2 is identical to stimulus 1 as they were involved in the working memory storage of information during the task.

In conclusion, we have found cortical areas commonly activated for tactile pattern and vibrotactile frequency discrimination tasks, as well as areas which were more activated in tactile pattern than in vibrotactile frequency discrimination tasks. We have shown evidence that cortical processing of spatial and temporal features of similar tactile stimuli are indeed different, and their differences could be attributed to differing physical nature of the stimuli, differing ways of internal representation of the tactile information thus different strategies undertaken in solving the tasks, or simply different neuronal populations involved in the network. We have affirmed the anatomical location of tactile pattern working memory of our previous MEG study, which gives us greater confidence in BOLD response adaptation paradigm for deciphering the underlying cortical networks of tactile working memory. Though we have found BOLD response adaptation during pattern discrimination to be predominantly in the right hemisphere, it is important to take into consideration that other areas which were not included as ROIs as they did not survive the statistical threshold could also be involved in the working memory network and display BOLD response adaptation.

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Figure Legends

**Figure 1. Tactile stimuli and trial structure.** The upper plot illustrates the four dot patterns used in the tactile pattern discrimination task. The lower plot shows the dot pattern used in the vibrotactile frequency discrimination task. While the dot pattern remained the same for vibrotactile stimulation, it vibrated within the flutter frequency range of 16 to 34 Hz. Within a trial, two tactile stimuli lasting 0.6 s each were serially presented with a delay of 5.5 s.

**Figure 2. Behavioral data.** The average accuracy of both tactile discrimination tasks is as shown on the left. There was no significant difference (n.s.) between the accuracy of pattern and frequency tasks. The average reaction times for both tasks are as shown on the right. There was a trend of shorter reaction time in pattern than frequency discrimination (p=0.07). Error bars indicate standard deviations across nine subjects.

**Figure 3. BOLD activation maps resulted from a conjunction analysis between pattern and frequency discrimination.** Conjunction of random-effects analysis was performed for the delay and stimulus 2 presentation (overlaid on the inflated cortices reconstructed from the target subject). A. Right central sulcus, bilateral postcentral gyri and sulci, precentral sulci, intraparietal sulci (IPS), parietal operculum, anterior insula / frontal operculum and superior
frontal gyri (supplemental motor area, SMA) were found to be activated during both pattern and frequency tasks (cluster threshold: 19 mm² for the left and 18 mm² for the right hemisphere, Pcorrected < 0.0001). B. Left IPS (peak p=0.02), right IPS (peak p=0.006) and anterior insula (peak p=0.049) showed significant BOLD adaptation during the pattern task. Black rectangles represent the first (sample) and the second (comparison) tactile stimuli (separated by a 5.5 s delay). Grey shades indicate different levels of p-values resulted from time-point-wise paired t-tests (one-tailed) between the percent BOLD changes of the same and diff time courses. Error bars indicate standard deviations across nine subjects.

**Figure 4.** BOLD t-contrast between tactile pattern and vibrotactile frequency discrimination tasks. The contrast showed stronger BOLD activity for pattern than frequency task during the delay and stimulus 2 presentation (overlaid on the inflated cortex reconstructed from the right hemisphere of the target subject). The contrast did not reveal any cortical areas showing stronger BOLD activation during frequency than pattern task. Three cortical areas in the right (ipsilateral to tactile stimulation) parietal region (cluster threshold: 51 mm², Pcorrected < 0.005) revealed significantly stronger BOLD activation during pattern than frequency task. Further extraction of the BOLD time courses of each cortical area are shown correspondingly. In addition, the right SMG/PO displayed significant BOLD adaptation (peak p=0.026) and the right IPS a trend (peak p =0.057) for same pattern pairs. Grey shades indicate different levels of p-values resulted from time-point-wise paired t-tests (one-tailed) between the percent BOLD changes of the same and diff time courses. Black rectangles represent the first (sample) and the second (comparison) tactile stimuli (separated by a 5.5 s delay). Error bars indicate standard deviations across nine subjects.
tactile pattern

A  B  C  D

vibrotactile frequency

8 mm

16 - 34 Hz

1st stimulus  delay  2nd stimulus  inter-trial interval

0.6 s  8.5 s  0.6 s  7.05 s / 9.35 s