



Brain regions that retain the spatial layout of tactile stimuli during working memory – A ‘tactospacial sketchpad’?



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ABSTRACT

Working memory (WM) studies have been essential for ascertaining how the brain flexibly handles mentally represented information in the absence of sensory stimulation. Most studies on the memory of sensory stimulus features have focused, however, on the visual domain. Here, we report a human WM study in the tactile modality where participants had to memorize the spatial layout of patterned Braille-like stimuli presented to the index finger. We used a whole-brain searchlight approach in combination with multi-voxel pattern analysis (MVPA) to investigate tactile WM representations without *a priori* assumptions about which brain regions code tactospacial information. Our analysis revealed that posterior and parietal cortices, as well as premotor regions, retained information across the twelve-second delay phase. Interestingly, parts of this brain network were previously shown to also contain information of visuospatial WM. Also, by specifically testing somatosensory regions for WM representations, we observed content-specific activation patterns in primary somatosensory cortex (SI). Our findings demonstrate that tactile WM depends on a distributed network of brain regions in analogy to the representation of visuospatial information.

Introduction

Most information that we explicitly represent in working memory (WM) is derived from the visual and auditory modalities. However, our brains have the capacity to maintain contents derived from all sensory modalities and to represent them in various formats. An important goal of WM research is to identify what types of mental contents are represented by what types of neuronal codes. Of particular interest is which contents are stored in sensory-like formats, and which are transformed to more abstract, non-sensory or symbolic codes that are represented independently of the modality that they were derived from (Christophel et al., 2017). Thus, to establish cross-modal perspectives, studies outside the visual or auditory domain are essential.

To test which brain regions contain information on WM contents, multivariate pattern analysis (MVPA) for fMRI has been instrumental (Haynes, 2015; Norman et al., 2006). The possibility to link activation patterns within a brain region to different WM conditions is the crucial feature that makes MVPA sensitive to the content of WM and thus, it has been applied in studies on various WM contents. When study participants memorized visual features such as orientation (Albers et al., 2013), position (Jerde et al., 2012), motion direction (Christophel and Haynes,

2014; Emrich et al., 2013), or the layout of a stimulus (Christophel et al., 2012; Lee et al., 2013) evidence for stimulus information in early visual and parietal regions was reported. The involvement of visual cortices is viewed as support for ‘sensory recruitment’ models of WM that emphasize the importance of sensory regions for coding WM content. The models suggest that sensory regions are re-activated in the absence of sensory stimulation so that the same sensory regions that perform perceptual processing also realize the mental maintenance of WM content (Pasternak and Greenlee, 2005).

The ‘sensory recruitment’ account of WM aligns well with the influential ‘multicomponent model of WM’ introduced by Baddeley & Hitch, which describes the theoretic construct of a ‘visuospatial sketchpad’ as a type of screen on which a mental representation is drawn and stored (Baddeley, 2012). This model suggests that the short-term retention of different types of mental contents is realized by different storage mechanisms, as some types of content interfere with each other while others do not. It suggests a sketchpad- or buffer-like representation of visuospatial stimulus features and it has been speculated that the ‘visuospatial sketchpad’ might be implemented by retinotopically organized regions, such as early visual cortices (Albers et al., 2013). Aside from WM studies, the study of mental imagery has also built heavily on the assumption that

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mental content is realized as ‘*depictive representations*’ for which the neuronal activation should reflect the isomorphic or physical stimulus properties in the real world, as for example spatiotopically organized brain representations (Cichy et al., 2012; Harrison and Tong, 2009; Kosslyn, 2005; Schmidt et al., 2014; Tong, 2013). However, recent fMRI MVPA studies suggest that WM representations are not only found in sensory regions but throughout the cortical hierarchy (Christophel et al., 2017; Schmidt et al., 2017). As it is unlikely that a single brain region solitarily implements a particular cognitive function, it is unlikely that only visual cortices process the ‘*visuospatial sketchpad*’ or function in isolation buffer-like to store WM content. Nevertheless, it remains a critical question, under which conditions some aspects of mental content representations are realized by sensory cortices, and in how far this implies that additional modality-specific buffers can be constituted, such as a ‘*tactospatial sketchpad*’.

Early sensory cortices in the visual and the tactile system directly reflect spatial stimulus properties via a retinotopic or somatotopic organization. For example, in line with the well-established orientation coding in the primary visual cortex, orientation tuned neurons can also be found in SI area 3b (Bensmaia et al., 2008). Additionally, feature specific response properties increase in complexity along the somatosensory pathway from the first to the second somatosensory cortex (SII) (DiCarlo and Johnson, 2002; Sripati, 2006) emphasizing the role of SI and SII in the processing of simple shape features (Hsiao et al., 2002), in analogy to the organization of the visual system (Yau et al., 2009). While the functional role of regions processing higher-level features and their relation to attentional supramodal processes are less well-understood (Burton et al., 2008), it has been established that multiple re-mappings, such as between retinotopic or ego- and allocentric coordinate systems were related to posterior parietal regions (Grefkes and Fink, 2005). However, it is unclear, in which format or on what level of hierarchical processing, the information regarding the spatial layout of a tactile stimulus in WM is maintained.

Tactile WM has previously been studied with a variety of methods: ranging from recordings of spike activity and local field potentials in monkeys (Romo et al., 1999; Zhou and Fuster, 1996) to human EEG (Katus et al., 2015; Katus and Eimer, 2015; Spitzer et al., 2013, 2010; Spitzer and Blankenburg, 2012) and fMRI studies (Kaas et al., 2013; Preuschhof et al., 2006; Ricciardi et al., 2006; Schmidt et al., 2017; Spitzer et al., 2014). Influential research by Romo and colleagues in non-human primates has revealed that mnemonic representations of vibratory frequency are found predominantly in non-sensory frontal and prefrontal regions (Romo et al., 2012; Romo and de Lafuente, 2012; Romo and Salinas, 2003). However, the quantity-like stimulus feature of vibratory frequency, may be retained in a different manner than spatial, somatotopic stimulus properties. The mental representations of spatial tactile stimulus features have, as of yet, not been investigated with fMRI and MVPA. To close this gap, and to allow a comparison with visual WM studies, we designed Braille-like tactile stimuli with spatial properties similar to recently applied visual stimuli (Christophel et al., 2012) that were presented to the fingertips. We used an assumption-free searchlight approach to map brain regions containing multivariate activation patterns that code corresponding stimulus information during a 12 s WM delay.

‘*Sensory-recruitment*’ models would predict that somatotopically organized sensory cortices, i.e., SI and SII, contain content-specific WM codes. Previous work from visual WM suggests that also higher-order brain regions contain content-specific representations as part of a distributed network of WM representations, where WM content is stored in different formats, and correspondingly different brain regions, to flexibly adapt to task requirements (Christophel et al., 2017; Serences, 2016).

Material and methods

Participants

All participants (N = 24, age: 25.5 ± 2.95 years, 15 female) were

neurologically intact and right-handed, as assessed by the Edinburgh Handedness Inventory (EHI: 0.81 ± 0.20 ; Oldfield, 1971). The sample size was motivated by previous WM studies using MVPA (Christophel et al., 2012; Lee et al., 2013). All participants provided written informed consent for the procedure in accordance with protocols approved by the local ethics committee of the Freie Universität, Berlin. Two participants were excluded from the analysis due to low mean performance (57.3% and 62.5% correct responses) and chance-level performance (50%) in at least one run, leaving N = 22 participants for the fMRI data analysis.

Tasks and stimuli

We used a retro-cue WM paradigm wherein the presentation of two spatial tactile sample stimuli was followed by a visual cue, indicating which of the two samples had to be memorized (Fig. 1B). Participants performed a two-alternative forced choice task after 12 s delay to indicate which of two test stimuli was identical to the memorized sample. Button-press responses were performed with the middle and index finger of the right hand. The left/right-response mapping was randomized across participants.

Vibrotactile stimuli were delivered to the left index finger using a 16-dot piezoelectric Braille display (4×4 matrix with 2.5 mm spacing) controlled by a programmable stimulator (Piezostimulator, QuaeroSys, St. Johann, Germany). The spatial layout of the vibrotactile stimuli was a composition of pins with different vibration amplitudes (Fig. 1A). To enable the classification of stimulus identity in the fMRI analysis, the set of sample stimuli was limited to four. Pins were driven by a 30 Hz sinusoidal amplitude modulation with smoothed stimulus on- and offsets of 700 ms duration. To prevent any stimulus-specific confounds, a unique set of stimuli was created for each participant. This is particularly important as the physiological finger constitution, receptor density as well as skin properties (Sripati, 2006) vary between participants and might alter the perception of spatially distributed vibration intensity. For each participant, four samples were generated that were equidistant in similarity space, defined as correlation coefficient between stimulation amplitude matrices to be between 0 and 0.05. Every stimulus delivered the same amount of physical stimulation by applying vibrotactile stimulation with the same amount of overall pin-amplitudes across the display. After the presentation of two sample stimuli, a 30 Hz mask stimulus consisting of all 16 pins vibrating with maximum amplitude was applied together with the WM retro-cue for 500 ms to overwrite potential peripheral perceptual residues. The WM delay was followed by a two-alternative forced choice task, in which the memorized sample stimulus was presented together with a foil stimulus (random, balanced order). To ensure the same difficulty in each trial, a set of 50 foil stimuli per sample stimulus with fixed similarity to the sample (correlation coefficient with sample between 0.5 and 0.75) was composed. In each trial, a random foil for the sample was presented with the sample. The (dis)similarity between sample and foil was chosen based on pilot data with the goal of an overall performance of approximately 75% in the final study. Participants had 1.5 s to respond via button press and indicate which of the two stimuli was the memorized sample (See Fig. 1). None of the participants was able to determine how many different stimuli were used in the experiment.

Each experimental run constituted 48 trials with a 12 s WM delay, supplemented by 12 catch trials with a shorter delay of 4 or 8 s. Catch trials were included to motivate the participants to continuously retain a precise stimulus representation throughout the delay phase and discourage any potential alternative memory strategies. Each run started with an 8 s rest phase before the first trial and trials were randomly interleaved with an inter-trial-interval of 2.800 or 4.800 ms, which assured that each trial started with the beginning of data collection of a volume (time locked to the image acquisition). Trials lasted 17.200 ms, where sample stimuli were presented in the first 2 s, followed by a 12 s delay period and a two-alternative forced choice task (See Fig. 1). Each of 6 stimulus pairs was presented equally often in balanced order, where

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