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Working memory of somatosensory stimuli: An fMRI study

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ABSTRACT

In a previous study, we have shown that passive recognition of tactile geometrical shapes (i.e. no exploratory movement) engages prefrontal and premotor areas in addition to somatosensory regions (Savini et al., 2010). In the present study we tested the hypothesis that these regions are involved not only in the perception but also during working memory of such somatic information.

We performed functional magnetic resonance imaging (fMRI) during the execution of N-BACK tasks, with 2D geometrical shapes blindly pressed on the subjects' right hand palm. Three conditions with increasing memory load (0-BACK, 1-BACK, 2-BACK) were used. Results showed that primary somatosensory area (SI), secondary somatosensory area (SII) and bilateral Insula were active in all conditions, confirming their importance in coding somatosensory stimuli. Activation of fronto-parietal circuit in supplementary motor area (SMA), right superior parietal lobe (rSPL), bilateral middle frontal gyrus, left inferior frontal gyrus, and right superior frontal sulcus was significantly larger during 1-BACK and 2-BACK than 0-BACK. Left superior parietal lobe and right frontal eye field showed a higher activation during the 2-BACK than 0-BACK. Finally, SMA and rSPL were characterized by a statistically significant higher activation during 2-BACK than 1-BACK, revealing their sensitivity to the memory load. These results suggest that working memory of tactile geometrical shapes (no exploratory movement) involves a complex circuit of modal and supramodal fronto-parietal areas.

1. Introduction

Working memory (WM) is defined as the ability to transiently store and manipulate information held "on-line" to be used for cognition or for behavioral guidance (Baddeley, 1996, 2003). WM is typically modeled as a "central executive" attentive system supported by a second, more peripherally-based storage system, interacting together for information encoding and manipulation, in order to subserve planning, reasoning and problem solving (Baddeley, 1996, 2003; Goldman-Rakic, 1996).

Neuropsychological studies have used several paradigms to disentangle different aspects of working memory in humans, such as continuous updating of information (i.e. on-line manipulation), maintenance of information, and information storage. One of the most used paradigms is the N-BACK task, which combines maintenance and encoding, as well as monitoring of a continuous sequence of stimuli (Fletcher and Henson, 2001). The majority of neuroimaging studies of human working memory mainly employed visuo-spatial and verbal N-BACK tasks. A meta-analysis of 24 neuroimaging (positron emission tomography and functional magnetic resonance imaging, fMRI) studies using N-BACK tasks of verbal and visuospatial information has emphasized the role of a fronto-parietal network including lateral premotor cortex, dorsal cingulate and medial premotor cortex, dorsolateral and ventrolateral prefrontal cortex, frontal poles, medial and lateral posterior parietal cortex (Owen et al., 2005).

Nevertheless, the cortical circuits underlying the working memory load elicited by N-BACK tasks using tactile inputs are still poorly understood. Several studies have used 1-BACK condition (i.e. subject has to maintain in WM the stimulus before the target) to investigate a sequential discrimination of haptically explored objects (Kaas et al., 2006) and visual and/or tactile stimuli (Stoeckel et al., 2003; Ricciardi et al., 2006). The results showed that during visual and tactile spatial WM a supramodal frontal or fronto-parietal network was recruited in all sensory modalities.

Noteworthy, the lack of studies performing a tactile 2-BACK task limits a detailed analysis of memory load effects on tactile input processing. In particular, it is not clear if the premotor and parietal networks sensitive to the verbal and visual memory load (Ragland et al., 2002; Carlson et al., 1998; Owen et al., 2005) are involved even in the manipulation and maintenance in memory of somatosensory information.

In a previous study, we have shown that passive recognition of tactile geometrical shapes (i.e. no exploratory movement) engages prefrontal and premotor areas in addition to somatosensory regions (Savini et al., 2010). In the present study we tested the hypothesis that these regions are involved not only in the perception but also

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during working memory of such somatic information. We performed fMRI during the execution of N-BACK tasks, with 2D geometrical shapes blindly pressed on the subjects' right hand palm. Two conditions with increasing memory load (1-BACK, 2-BACK) were used in addition to a recognition condition with no memory load (0-BACK). In order to identify regions underlying WM of somatosensory stimuli we compared the different memory loads to the recognition condition. For the exploratory nature of the present study, we focused on the well known general features of the N-BACK task. This is a well known reference task that combines "maintenance of task instructions and previous target sensory information in a short term buffer" and "inhibition of impulse responses related to the sensory information of the distracters". This is why the N-BACK is considered a WM task but not merely a short term memory task. For this reason, we designed a variant of this task for the specific and original evaluation of the cortical correlates of somatic WM for 2D tactile shapes in the present study.

2. Methods

2.1. Subjects and stimulation procedures

We used the same stimuli and experimental procedures validated in a previous reference study (Savini et al., 2010). Briefly, stimuli were delivered to the subjects right hand palm by means of four wooden pieces, each having one face with a geometrical shape: a circle (area = 3.14 cm^2), a square (area = 2.89 cm^2), a triangle (area = 2.71 cm^2) and an ellipse (area = 3.07 cm^2) (Fig. 1a). In order to standardize the force applied on the hand, the pieces were mounted on flexible bars with a graduate scale (Fig. 1b). This device allowed the investigator to manually present the shapes with the same force (4 N) across subjects and trials. A group of 12 healthy male volunteers, ranging in age from 19 to 32 years (mean age of 23.9 ± 3.5 SD), was enrolled for the fMRI experiment with these stimuli. All subjects were right handed according to the Edinburgh Inventory (Oldfield, 1971), gave their written informed consent according to the Declaration of Helsinki (World Medical Association Declaration of Helsinki, 1997), and could request an interruption of the investigation at any time; the general procedures were approved by the Ethics Committee for Biomedical Research of University "G. d'Annunzio", Chieti (IT). We enrolled only male subjects to maintain a more homogeneous sample, avoiding intersubject variability effects due to e.g. different phases of the menstrual cycle in females.

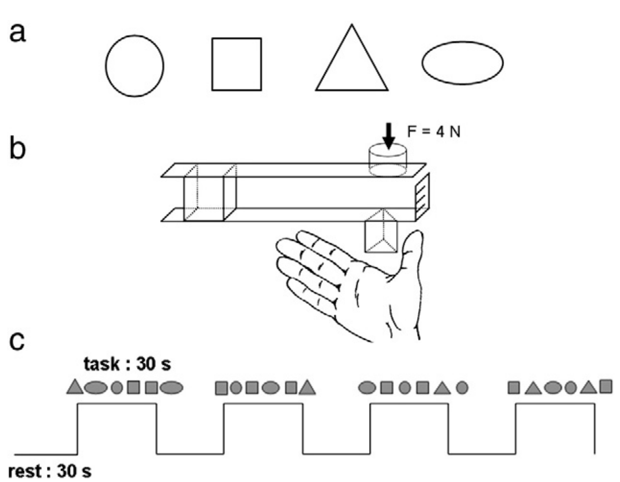

Fig. 1. a) Bi-dimensional shapes of wooden pieces pressed on the right hand palm; b) device with wooden flexible bars, with a reference scale indicating the applied force. In the picture, the device bearing the triangular shape is shown; c) schematic of the block paradigm: 30 s of rest, 30 s of stimulation, 6 shapes presented per block, and 4 stimulation blocks, for a total of 24 shapes.

A training session was performed following the same procedure of our previous study (Savini et al., 2010) in order to allow the subjects to recognize the geometrical shapes using the tactile presentation. Then all the subjects were trained to memorize the shape and they were able to do the N-BACK task.

2.2. Experimental design

Three tasks were performed: i) 0-BACK in which the subjects were asked to press (with the left hand) the button corresponding to the shape of the wooden surface pressed on their right hand palm; ii) 1-BACK in which the subjects were asked to press the button corresponding to the shape presented one time before (maintaining in memory the preceding shape); 2-BACK in which the subjects were asked to press the button corresponding to the shape presented two times before (maintaining in memory the preceding two shapes). Subjects were instructed to keep their gaze on a fixation cross while doing the task.

The fMRI session was performed in three different runs (corresponding to the three memory load tasks: 0-BACK, 1-BACK, 2-BACK) according to a block paradigm alternating 30 s of stimulation with 30 s of a control state. For each run, 4 stimulation blocks and 4 control blocks were used starting with a control state. In the control blocks subjects were required to rest and keep their gaze on the fixation cross. During each stimulation block, 6 trials were presented. Each trial consisted of 2 s, during which a shape was pressed – in a blind condition – on the subject right hand palm, and 3 s of release. The presentation order of the geometrical shapes was pseudorandom and a total of 24 shapes were presented per run (Fig. 1c).

The tactile stimuli were delivered by an experimenter following instructions transmitted via fMRI compatible headphones. To allow a standardized administration of stimuli, the pressure level was controlled by a reference on the flexible bars (Fig. 1b), whereas the pressure duration and the pseudo-random order of presentation of the different shapes were controlled by means of a Matlab® (Mathworks, Natick, MA, USA) code. The program transmitted to the experimenter a registered voice, indicating the shape to press, followed by a 2 s of beep indicating the pressure duration. The button press (MRI-compatible response pad Lumina LSC-400 controller, Cedrus, California, USA) was recorded by the same Matlab code, allowing to record reaction times and behavioral responses (correct/incorrect shape recognition).

The three fMRI tasks (0-BACK, 1-BACK, 2-BACK) were completely randomized across subjects to avoid any habituation or order effect.

2.3. fMRI recordings

BOLD contrast functional imaging was performed with a Siemens Magnetom Vision scanner at 1.5 T by means of T2*-weighted echo planar imaging (EPI) free induction decay (FID) sequences with the following parameters: TR 3 s, TE 60 ms, matrix size 64 × 64, FOV 256 mm, inplane voxel size 4 mm × 4 mm, flip angle 90°, slice thickness 4 mm and no gap. A standard head coil was used and the subject head was fixed with foam pads to reduce involuntary movement. Subject right hand was blocked on a soft pad by means of tape to avoid any exploratory movement (the experimenter giving the stimulation continuously checked it). 83 functional volumes consisting of 28 transaxial slices parallel to the AC–PC line were acquired per run.

A high-resolution structural volume was acquired at the end of the session via a 3D MPRAGE sequence with the following features: sagittal, matrix 256 × 256, FOV 256 mm, slice thickness 1 mm, no gap, in-plane voxel size 1 mm × 1 mm, flip angle 12°, TR = 9.7 ms, TE = 4 ms.

2.4. Data analysis

Raw data were analyzed by means of the Brain Voyager QX software (Brain Innovation, The Netherlands). Due to T1 saturation effects, the