NeuroImage 47 (2009) 367–375

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

The neural representation of extensively trained ordered sequences

Filip Van Opstal [a,*], Wim Fias [a,b], Philippe Peigneux [c], Tom Verguts [a]

[a] Department of Experimental Psychology, Ghent University, H. Dunantlaan 2, B-9000 Ghent, Belgium
[b] Ghent Institute for Functional and Metabolic Imaging, B-9000 Ghent, Belgium
[c] UR2NF - Neuropsychology and Functional Neuroimaging Research Unit, Université Libre de Bruxelles, B-1050 Bruxelles, Belgium

ARTICLE INFO

Article history:
Received 20 October 2008
Revised 2 April 2009
Accepted 8 April 2009
Available online 17 April 2009

Keywords:
Ordinal sequences
Transitive inference
Intraparietal sulcus
Inferior frontal gyrus

ABSTRACT

The role of the intraparietal sulcus (IPS) in number processing is largely agreed on. A current debate however concerns the specificity of the involvement of the IPS in representing numbers or ordinal sequences more generally. To test this specificity, we investigated whether the IPS would be activated by extensive training on an arbitrary ordered sequence. We found that the hippocampal-angular gyrus activation initially involved in learning the ordered sequences extends with extensive training to the left inferior frontal gyrus (left IFG), but not to the IPS. These results suggest that left IFG can be involved in processing ordinal information, and that there is no need for an IPS area specifically dedicated to the representation of all ordinal sequences. Instead, we propose that the locus of the representation might be determined by the nature of the stimuli rather than its ordinal nature *per se*.

The neural basis of numerical cognition has been the subject of much research. Besides a large agreement on the involvement of the intraparietal sulcus (IPS) in number processing (Dehaene et al., 2003; Cohen Kadosh et al., 2008), the specificity of the IPS to numbers is debated. Close links between space, time, and quantity in behavioral (Church and Meck, 1984) and neurological studies (Zorzi et al., 2002) have raised the suggestion that there exists a generalized magnitude system rather than a specific number system in the IPS (Walsh, 2003). Although there is some evidence for a common encoding of physical dimensions and numbers (Fias et al., 2003; Cohen Kadosh et al., 2005), a recent review proposed that both shared and distinct representations could exist (Cohen Kadosh et al., 2008). Likewise, the relationship between brain areas that process numerical and non-numerical ordinal information is unclear. Some studies found a stronger IPS response to number processing compared to non-numerical order processing (Le Clec'H et al., 2000). For example, in an experiment by Thioux et al. (2005), participants had to compare and categorize numbers and animal names. When animals were compared, only left temporal lobe activation was observed, although this comparison task relied on ordinal information. Parameter estimates in left and right IPS showed strong activation in the number tasks, but no activation in the animal tasks. Others, however, have suggested shared representations of ordinal knowledge in the IPS (Fias et al., 2007; Ischebeck et al., 2008). Marshuetz et al. found parietal activation when participants had to recall the order of two probe letters after storing five letters for a brief period (Marshuetz et al., 2000, 2006). They observed parietal activation that was modulated by the distance between the two probe letters (Marshuetz et al., 2006). It was suggested that order information is represented via magnitude codes, and that these magnitude codes are processed in parietal cortex.

A different approach to settle the debate on the specific role of the IPS in ordinal processing is to use a transitive inference (TI) task in which participants gradually acquire the ordinal relations between a set of novel elements (Van Opstal et al., 2008b). In a typical TI task participants learn the ordinal structure of a sequence of stimulus elements (e.g., ABCDE) on the basis of premises consisting of adjacent elements in the sequence (e.g., AB, BC, CD, DE). After an initial learning phase participants are then tested on non-adjacent elements in a test phase to investigate if they acquired the ordinal relations between the different elements in the sequence. In fact, in such a design, a test phase is identical to a simple comparison task that has been frequently used to study ordinal stimuli like numbers (Fias et al., 2003, 2007; Pinel et al., 2004), or letters (Fias et al., 2007). Neuroimaging data revealed activation in a hippocampal-angular gyrus network when participants learned a new sequence, and identified the left angular gyrus (ANG) as the parietal area for storing the ordinal sequence knowledge, rather than the IPS (Van Opstal et al., 2008b). However, it might be argued that more extensive training would eventually lead to IPS activation.

To clarify this issue, the present experiment was designed to investigate whether extensive training would change the neural network involved in learning a novel sequence of arbitrary elements. As in Van Opstal et al. (2008b), participants learned a sequence of arbitrary figures using a TI task, but were now trained for seven sessions on seven consecutive days instead of one single session. Participants were scanned in sessions 1, 2, 4, and 7, so that the neural

* Corresponding author. Fax: +32 9 264 64 96.
E-mail address: Filip.VanOpstal@UGent.be (F. Van Opstal).

1053-8119/$ – see front matter © 2009 Elsevier Inc. All rights reserved.
doi:10.1016/j.neuroimage.2009.04.035

network initially involved in acquiring the ordinal knowledge (changes within session 1), and how this network evolves with training (changes between sessions 2, 4, and 7), could be studied. Our working hypothesis was that if extensive training could alter the initial representation into a more abstract representation, it would thereby shift the loci of activation involved in the TI task from ANG to IPS. Alternatively, if ordinal representations are not necessarily processed in IPS, the loci of activation might shift to cortical regions other than IPS or remain in the cortical areas initially involved in the acquisition of the ordinal knowledge.

Materials and methods

Participants

Fourteen participants (all male, right-handed, aged between 19 and 26 years) from Ghent University were studied after they gave written informed consent in a manner approved by the ethical committee and the trial bureau of the Medical Department of Ghent University. None of the participants reported any neurological, psychiatric or medical history, or had any bodily ferromagnetic materials. Brain morphology, as assessed with T1-weighted MR images did not reveal any abnormalities. Participants were rewarded 130 Euros after full completion of the study.

fMRI task design

Prior to scanning, participants received instructions on the details of the experimental procedure. They were explicitly informed that the goal of the study was to investigate the effect of training on the neural correlates of TI. Before acquiring the fMRI time series, a high resolution structural image (see Data acquisition for details) was obtained.

The experiment consisted of seven sessions. Each session took place at the same time of the day on seven consecutive days. The task was the same throughout the seven sessions, except for the first session. The design of the first session was nearly identical as the one used in our previous study (Van Opstal et al., 2008b), and is illustrated in Fig. 1A. This session was divided into six blocks, each block

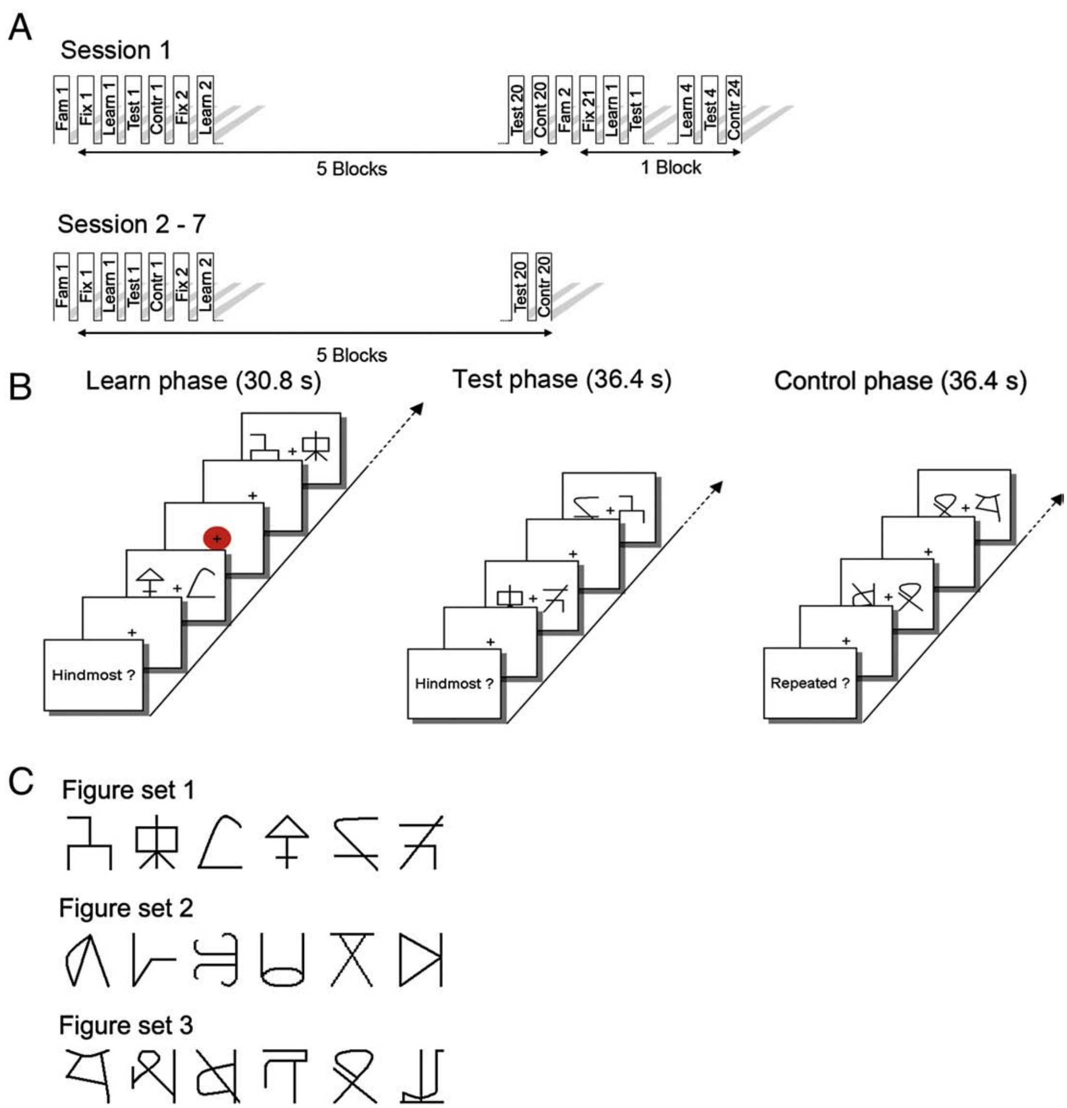

Fig. 1. Experimental design. (A) An outline of the scanning sessions (Fam = familiarization, Fix = fixation, Learn = learn phase, Test = test phase, Contr = control phase; e.g., Fam1 = first familiarization phase, Learn18 = 18th learn phase). Participants were trained to learn a sequence of six arbitrary figures using a TI task. An experimental session consisted of a continuous repetition of a fixation, learn, test, and control phase. An illustration of the learn, test, and control phase is shown in (B). In a learn phase, participants were presented with adjacent stimuli only. Feedback was provided after each trial in the learn phase by a colored circle. In the test phase, participants were presented with non-adjacent stimuli only, and no feedback was presented. In order to accurately perform in the test phase, participants need to infer the non-adjacent relations between the stimuli from the adjacent relations presented in the learn phase. The control phase was a one-back task with a similar sensory input and motor response as the test phase. The different sets of figures used are presented in (C).