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The effect of gender on planning: An fMRI study using the Tower of London task

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Since the introduction of brain mapping, evidences of functional gender differences have been corroborating previous behavioral and neuropsychological results showing a sex-specific brain organization. We investigated gender differences in brain activation during the performance of the Tower of London (TOL) task which is a standardized test to assess executive functions. Eighteen healthy subjects (9 females and 9 males) underwent fMRI scanning while solving a series of TOL problems with different levels of difficulty. Data were analyzed by modeling both genders and difficulty task load. Task-elicited brain activations comprised a bilateral fronto-parietal network, common to both genders; within this network, females activated more than males in dorsolateral prefrontal cortex (DLPFC) and right parietal cortex, whereas males showed higher activity in precuneus. A prominent parietal activity was found at low level of difficulty while, with heavier task demand, several frontal regions and subcortical structures were recruited. Our results suggest peculiar gender strategies, with males relying more on visuospatial abilities and females on executive processing.

Introduction

Behavioral differences between men and women have been documented across several cognitive domains. The brain can be considered an important sex organ because it controls functions and behaviors that are advantageous in one gender but not in the other and it contains structures that are adaptive mostly in one gender.

In terms of behavioral and cognitive differences in the general population, sex differences in intellectual functions do not seem to lie in overall levels of intelligence, but more in specific patterns of ability. A consistent finding is that women perform better on verbal and memory tasks (Fenson et al., 1994; Kramer et al., 1997), whereas men outperform women on some spatial tasks such as construction tasks, the Embedded Figure Task, map reading, and in all activities involving spatial cognition and spatial learning (Gaulin and Hoffman, 1988; Galea and Kimura, 1993; Voyer et al., 1995; Geary, 1996; Astur et al., 1998; Waller et al., 1998; Kimura, 1999; Geary et al., 2000; Saucier et al., 2002). Females are also consistently found to be superior to males in social skills from an early age, with more empathy, sensitivity of facial expressions and a more highly developed theory of mind (Dunn et al., 1991; Baron-Cohen, 2002). All these data in humans confirm those obtained in animal studies (Jonasson, 2005); nevertheless, it is important to remember that this distinction is not so simple and absolute (Silverman and Eals, 1992). In fact, the validity of these studies continues to be criticized because the tasks used are poorly characterized and task performance can be confounded with socialization and gender-bias expectation (Caplan et al., 1985; Persaud, 1991; Voyer et al., 1995; Esposito et al., 1996).

Nonetheless, this debate on neuropsychological task performances suggests that relevant differences between genders may appear in the underlying neuroanatomical substrates. In fact, the brain is highly dimorphic between genders both in size and structure, with differences in volumes of specific regions (Witelson, 1991), some of them affecting cognitive function. Support for neuroanatomical differences between genders comes from studies in both normal and pathologic adult brain (McGlone, 1978; Kimura, 1987; Kulynych et al., 1993) and from neurodevelopment data (Goldman et al., 1974; Hagger et al., 1987; Bachevalier and Hagger, 1991; Yurgelun-Todd et al., 2002). For instance, anatomical brain differences between genders were found in the temporo-parietal region, in Wernicke's and Broca's language-associated areas (Wada et al., 1975; McGlone, 1977, 1978; Kimura and Harshman, 1984; Witelson and Kigar, 1992; Kulynych et al., 1994; Schlaepfer et al., 1995; Paus et al., 1996;

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Harasty et al., 1997), in the hypothalamic suprachiasmatic nucleus, corpus callosum (Lacoste-Utamsing and Holloway, 1982; Witelson, 1989) and some areas of neocortex (Witelson, 1991; George et al., 1996). Further, a very recent voxel-based morphometric study found that men and women achieve similar IQ results using different brain regions; stronger correlation between full IQ and grey matter volumes was found in bilateral frontal lobes (BA 8, 9) and in left parietal lobe (BA 39, 40) in men and in bilateral frontal lobes (BA 10, 44, 45) in women (Haier et al., 2005).

Consistent with these differences in structure and behavioral data, functional neuroimaging studies identified gender differences in neural processing underlying emotion (Bremner et al., 2001; Killgore and Yurgelun-Todd, 2001; Killgore et al., 2001; Cahill, 2003; Wager et al., 2003; Zald, 2003; Hamann and Canli, 2004) and cognition (Jaeger et al., 1998; Salmelin et al., 1999; Lambe, 1999; Gur et al., 2000; Thomsen et al., 2000; Speck et al., 2000; Kansaku and Kitazawa, 2001; Phillips et al., 2001; Goldstein et al., 2005; Azim et al., 2005).

The Tower of London task (TOL) is a widely recognized test to assess executive functions such as planning (Shallice, 1982) and working memory. It consists of determining the minimum number of moves required to match a starting configuration to a given target one; these configurations are represented by a set of colored balls arranged in a set of pegs (see Materials and methods and Fig. 1). The ability of planning involves different processes, such as strategy information, coordination and sequencing of mental functions and holding information on-line. An important part of the cortical network of planning ability seems to be the prefrontal cortex, as suggested by several studies in which the TOL task was administered to patients affected by frontal brain lesions (Shallice, 1982; Owen et al., 1990; Pantelis et al., 1997), frontal lobe dementia (Carlin et al., 2000) and schizophrenia (Morris et al., 1995; Pantelis et al., 1997; Schall et al., 1998). Furthermore, the TOL task was used in a number of previous brain activation studies, using single photon emission computed tomography (SPECT), positron emission tomography (PET) and functional magnetic resonance (fMRI) (Andreasen et al., 1992; Morris et al., 1993; Baker et al., 1996; Dagher et al., 1999; Lazeron et al., 2000; Rowe et al., 2001; Fincham et al., 2002; Newman et al., 2003; Van den Heuvel et al., 2003; Schall et al., 2003; Rasser et al., 2005), which demonstrated activation of a fronto-parietal-occipital network. Some of these studies focused on frontal activity in both normal (Fincham et al., 2002; Newman et al., 2003; Van den Heuvel et al., 2003) and schizophrenic subjects (Andreasen et al., 1992; Rasser et al., 2005), highlighting the crucial role of those brain areas, and thus corroborating the abovementioned clinical results. Although the functional brain correlates of the TOL task are well established, an explicit investigation of gender differences at neural level is still lacking.

In this paper, we focused specifically on examining neuroimaging evidence pertaining to gender effects in the brain, using the TOL task as a specific index of planning. The major objective was to determine how the manipulation of task demand can modulate the amount of neural activation in a network of brain regions in both genders. We hypothesized that in the two genders a different pattern of activation is present during increased memory load and planning processing. Indeed, since previous studies showed higher spatial skills in males, the increase of task load might be associated with higher activation in occipito-parietal areas in males, while females might solve problems with stronger activation of the dorsolateral prefrontal cortex (DLPFC).

Materials and methods

Participants

Eighteen healthy right-handed participants (9 males and 9 premenopausal females; mean±SD age: males 35±4.4 years, females 36.7±7.1 years; age range: males 27–41 years; females 28–43 years) were submitted to a fMRI protocol to explore executive functions in both genders at the University of Turin, Department of Neuroscience, Neurological, Neuroradiological and Psychiatric Sections. These subjects were enrolled to constitute the control group for a larger research project exploring executive

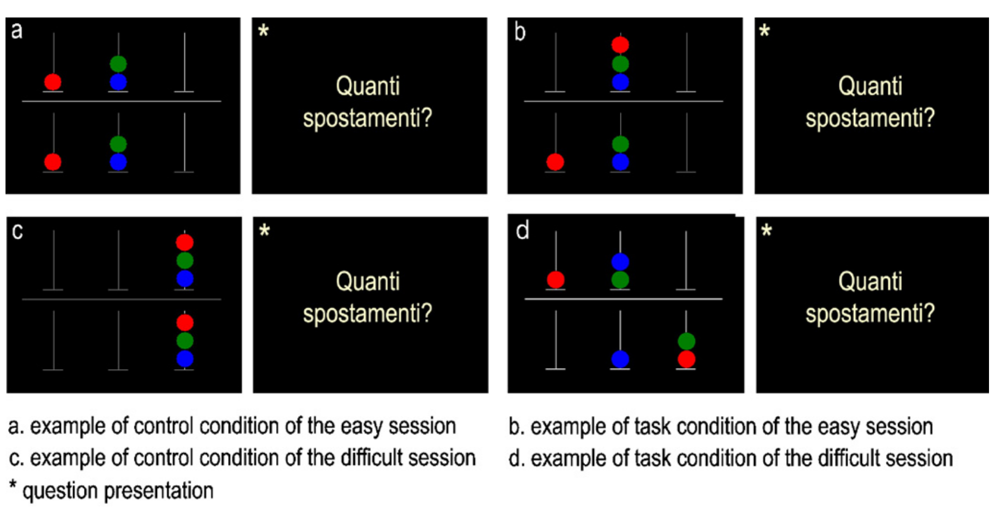

Fig. 1. The TOL task layout used in the fMRI sessions. Example of the Tower of London problems presented during the fMRI experiment (control condition on the left, activation condition on the right): easy problem (top row, 1 to 3 moves) and difficult problem (bottom row, 4 to 6 moves). The target configuration was presented in the upper half of the display and the starting configuration was in the lower half. Each subject was asked to mentally determine the minimum number of moves to reach the target configuration, given the starting one. One second before the end of each epoch, subjects were visually asked to whisper the solution. Problems were presented for 15 s (easy) or 30 s (difficult). "Quanti spostamenti?" in Italian means "How many moves?".