

Gender differences revealed in the right posterior temporal areas during Navon letter identification tasks

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Published online: 29 February 2012
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Abstract Gender differences in temporo-spectral EEG patterns during verbal cognitive performance are poorly understood. The aim of the present study was to examine whether the event-related dynamics of EEG differ between genders during the performance of Navon letter identification tasks (NLITs). To this end, the EEG patterns of 40 subjects were recorded during the NLIT performance. We compared behavioral outcomes, event-related temporo-spectral dynamics, and source distribution of neural oscillations within cortical regions of male and female subjects. We found that male subjects exhibited greater induced neural activities than female subjects in right temporo-parietal areas at theta and alpha frequency bands. Source imaging for the time ranges at which maximal gender differences were observed revealed gender-dependent estimated current densities in the right posterior temporal regions. These gender differences can be explained by the existence of distinct, gender-specific hemispheric specialization. Thus, gender differences should be considered during behavioral tasks and electrophysiological measurements.

Keywords Gender differences · Navon letter · EEG · sLORETA · Hemispheric specialization

Introduction

Gender differences in language functions have been revealed by various studies (Jaeger et al. 1998; Kansaku and Kitazawa 2001). A growing body of evidence indicates that functional differences in neural activities may be rooted in gender-specific differences in brain activities during cognitive performances (Cahill et al. 2001; Canli et al. 2002; Rhodes and Rubin 1999). It is a long-held hypothesis that language functions are more likely to be highly lateralized in males and to be represented in both cerebral hemispheres in females (Hampson and Kimura 1992; Levy 1972), but attempts to obtain proof have often been inconclusive (Harshman et al. 1983; Kulynych et al. 1994). Such gender differences might arise from dissimilar, gender-dependent hemispheric processing contributions to early visual sensory processing. However, gender differences in visual and verbal processing are still not well understood.

Several previous studies have used EEG recordings to observe functional gender differences that correspond to cognitive task performances and that support the aforementioned hypothesis regarding lateralization. Orozco and Ehlers (1998) found that female subjects generated significantly longer latency and higher amplitude P450 components in response to emotional stimuli than male subjects (Orozco and Ehlers 1998). Golgeli et al. (1999) showed that N2-P3 amplitudes were higher at channel Fz than Oz for female subjects only, whereas N2 latencies detected during auditory oddball tasks were longer at channel Fz than Oz for male subjects only (Golgeli et al. 1999). Vaquero et al. (2004) reported that men presented higher P3 amplitudes

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and a right frontal functional asymmetry that was not present in women during visuo-spatial attention tasks (Vaquero et al. 2004). Wirth et al. (2007) examined sex differences during passive reading tasks and reported the same early context effects in the P1-N1 transition period in women and men but earlier and longer-lasting context effects in the N400 components for the female group. Using the mental rotation task, Gootjes et al. (2008) observed that men showed increased involvement of the right hemisphere and an approximately 100 msec shorter response latency in the male vs. female subject groups. However, published findings remain inconsistent and sometimes controversial, and they vary depending on the cognitive tasks and recording methods employed (Frost et al. 1999; Gur et al. 2000; Sabatinelli et al. 2004; IEC Sommer et al. 2004).

The present study investigates whether males and females differ with regard to event-related temporo-spectral EEG dynamics in visual sensory processing of verbal stimuli. We used the Navon letter identification task (NLIT), a cognitive task that is often used to investigate the precedence of global versus local features involved in visual perception (Navon 1969), to examine both the language and visuospatial processing performances and the lateralization differences between groups. We examined event-related spectral perturbation (ERSP), which measures the average dynamic changes in amplitudes of the broad EEG frequency spectrum as a function of time relative to an event (Makeig 1993), inter-trial coherence (ITC), which measures the consistency across trials of EEG spectral phases at each frequency and latency (Makeig et al. 2002), and estimated current source distribution in a 3-dimensional brain model. Recently, event-related synchronization or desynchronization measurements have been used to investigate gender differences during various tasks (mismatch response to sounds: Bishop et al. 2010; emotional face: Knyazev et al. 2009, 2010; creativity: Razumnikova 2004). Based on these studies, we hypothesized that males and females would differ with regard to brain activities at various frequency bands also during verbal sensory processes, particularly with regard to their degrees of lateralization. We expected to observe these gender-related differences via ERSP and ITC, both of which provide information about the temporal cascade of cognitive processing with high time and frequency resolutions.

In our experiment, 40 college students (male/female=21/19) participated in the NLIT, and their performances were recorded (i.e., the percentage of correct answers and response times (RTs)). We utilized ERSP, ITC, and sLORETA (standardized low resolution brain electromagnetic tomography), which uses spatiotemporal EEG patterns to estimate current density distribution in a 3-dimensional brain model (Lamm et al. 2005; Pascual-Marqui et al. 2002). Our results demonstrate how this neuroimaging method can be used to interpret the origin of gender differences in visual processing.

Materials and methods

Ethics statement

Prior to participating, all recruited subjects were informed about all procedures to be used in this study. The study was approved by the Institutional Review Board (IRB) at KAIST (Daejeon, South Korea), and every participant gave written informed consent prior to all experimental procedures.

Subjects

We recruited 41 healthy volunteers (21 males and 20 females) aged 20 to 26 years (male: 22.52 ± 1.78 years, female: 22.40 ± 1.60 years) in Daejeon, South Korea, by means of an advertisement on the website of Chungnam National University. All participants' disorders were assessed by self-report. We assessed handedness using the laterality quotients from the Edinburgh handedness inventory (Oldfield 1971), which ranges from -100 for strong left-handedness to $+100$ for strong right-handedness. Because one female subject exhibited low attention and movement artifacts during the experiment, data obtained from her was excluded from analyses, so behavioral and electrophysiological data from 40 (male/female=21/19) of the original 41 volunteers were evaluated. The demographic details of this study are provided in Table 1.

Cognitive tasks (Navon letter identification task)

Figure 1 contains a schematic diagram of the Navon letter identification task (NLIT). Each stimulus letter had a hierarchical system allowing it to be identified on one of two levels (Navon 1977). Local features of the task were alphabetical letters (A, S, E, and H) written in Arial font. Each global feature consists of multiple local features that form alphabetical letters (A, S, E, and H). All global features were generated in identical size, 5 local features for width and 7 local features for length. The sizes of the local and global features were fit to $1.3 \times 1.3^\circ$ and $10 \times 15^\circ$, respectively.

Table 1 Demographic data, handedness, and behavioral performances of the subjects for the Navon letter identification task (NLIT)

	Male	Female
Number of Participants	21	19
Age (year)	22.5 ± 1.8	22.4 ± 1.6
Education (year)	14.7 ± 1.3	14.4 ± 1.1
Handedness (Laterality Quotients)	86.9 ± 17.8	88.5 ± 18.4
The Percentage of Correct Answer (%)	98.1 ± 2.8	97.1 ± 4.9
Response Time (msec)	$668.9 \pm 113.9^*$	$756.1 \pm 92.6^*$

Mean \pm standard deviation. *, significant differences (t -value = -2.63 , p -value = 0.013)

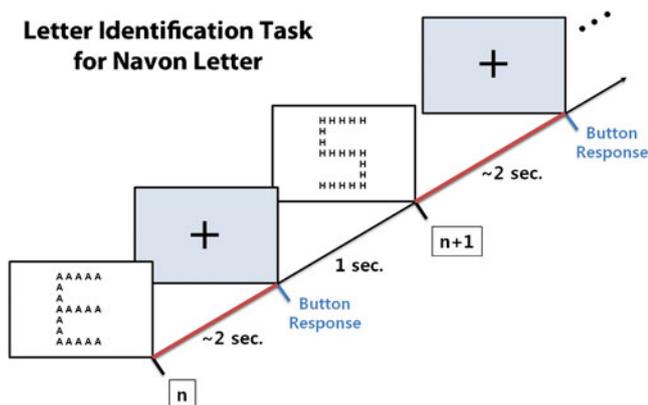


Fig. 1 Schematic diagram of the Navon letter identification task (NLIT) used in this study. A hierarchical stimulus composed of local letters was presented using the upper time limit of the response (2 s). After the button press response, a blank screen was shown for 1 s before the next stimulus was presented

The NLITs consisted of 10 practice trials and 70 main trials. Subjects were seated 60 cm from a 19-inch LCD monitor. Subjects were informed that a stimulus would appear in the middle of the screen and that they should respond to each stimulus by clicking the computer mouse. If either feature of a given stimulus picture matched the informed target (for instance, the alphabetical letter ‘E’ could be the target of the task), the subjects were instructed to click the left mouse button. If neither local nor global feature matches the target, the subjects were told to click the right mouse button. The Navon letter stimuli (one of 16 possible combinations; 4 local features and 4 global features) were presented in pseudo-random order. Instructions that included the target(s) and the start/end of the sessions were provided in the center area of the screen to prevent distraction resulting from experimenters’ actions. Subjects performed practice trials before the main trials. The stimulus presentation was controlled by a computer program (C++) developed by the authors. The maximum response time limit was 2 s per stimulus. Each stimulus picture disappeared when a subject responded or the maximum time limit had passed, and a blank screen was shown for 1 s before the next stimulus appeared (Fig. 1). The entire procedure took approximately 10–20 min, including the practice trials, instruction messages, and main trials.

Data acquisition

EEGs were recorded using a Neuroscan SynAmps² EEG recording system (Compumedics Neuroscan, Australia), with a cap of 32 electrodes (Ag/AgCl Quik-Cap, Compumedics Neuroscan, USA). The standard electrode sites used in the study followed the international 10–20 system (Jasper 1958). We used linked mastoid references, and an extra electrode (FPz) between FP1 and FP2 was employed as a ground. In

addition, we recorded eye movement and eye blinking using horizontal and vertical electro-oculograms (HEOG and VEOG). The impedances of all electrodes were kept below 5 k Ω . EEG data were digitized using a sampling frequency of 1,000 Hz and were amplified with a SynAmps² amplifier (Compumedics Neuroscan, USA).

For behavioral data acquisition, we obtained the response time (RT) from the onset of the stimulus to the subject’s mouse click. Corresponding information regarding the correct answer was recorded automatically by our software for cognitive tasks.

Data analysis

Behavioral data

The performance outcome files from the software for cognitive tasks were analyzed to estimate the percentages of correct answers and the mean RTs. The percentage of correct answers of each subject was calculated by analyzing the outcomes of the subject’s mouse-click responses. Wrong answers and no answers were treated as incorrect answers. We also excluded the RTs for incorrect answers.

We used the SPSS software (version 11.0.1, SPSS Inc., Chicago, IL, USA) for all statistical comparisons of the behavioral data obtained during the experiment. Student’s t-tests were used to compare gender-related differences in RTs and the percentages of correct answers.

Preprocessing of EEG data

We used the EEGLAB software toolbox (v6.03, <http://www.sccn.ucsd.edu/eeglab>) on Matlab v7.0 (Mathworks, USA) for EEG analysis (Delorme and Makeig 2004) to preprocess the EEG data. First, we removed the channel baseline means from the continuous EEG dataset of each subject and re-referenced them to an average reference. Employing the ‘pop_eegfilt’ function of the EEGLAB toolbox, EEG data were band-pass filtered using the basic FIR filter in a range of 1–55 Hz. Then, eye movement artifacts and 60 Hz electrical noise were removed using the independent component analysis provided by EEGLAB and canceling components by visual inspection. For each trial, EEG epochs of 1,500 msec (beginning 500 msec before the onset of visual stimuli) were selected from the continuous EEG records. The epochs of the practice sessions and those for which incorrect or no answers were obtained were excluded from EEG analyses. Furthermore, every epoch containing significant artifacts was removed for analysis via visual inspection. Four frequency bands were defined for further analyses: theta (4–8 Hz), alpha (8–12 Hz), beta (12–30 Hz), and gamma (30–50 Hz). (The delta frequency band was not analyzed because length of the EEG data used for

further analyses (500 msec) was too short to conclude the spectral activities within 1–2 Hz).

Time/frequency spectral analyses: Event-related spectral perturbation (ERSP) and inter-trial coherence (ITC)

For event-related time/frequency analyses, we used ERSP and ITC, both of which provide conceptual frameworks for observing and modeling event-related brain dynamics that occur consistently across a set of trials (Delorme and Makeig 2004; Makeig et al. 2004). In general, the event-related EEG phenomena have both ‘evoked’ and ‘induced’ aspects, which are measured by ITC and ERSP, respectively (for a review, please see Makeig et al. 2004). We used the ‘newtimef’ and ‘newcross’ functions of the EEGLAB software package to compute the ERSP and ITC before and after the Navon letter onset. We used a pre-stimulus baseline correction from –500 msec to 0 msec and expressed all results as increases or decreases relative to this baseline (in logarithmic decibel scale for ERSP and in coherence units ranging from 0 to 1 for ITC). To avoid windowing artifacts, we reported results from –200 msec to 1,000 msec. We used EEGLAB’s default algorithm. Each epoch was subjected to short-time Fourier analysis using fast Fourier transforms (FFTs). In addition, a Hanning window tapering was applied to each epoch. A frequency range of 1–50 Hz and zero padding was employed. The significances of gender differences in ERSP and ITC measurements were tested for each electrode using Student’s *t*-tests. Nineteen electrodes included in the standard international 10–20 systems were analyzed out of the 32 channel locations (extended 10–20 system in the Quick-Cap, Compumedics, USA).

Source localization analysis: sLORETA

To investigate cortical source distributions during visual sensory processing, we selected time intervals of interest, based on the ERSP/ITC analysis for which significant gender differences exist (described in the results section). Each trimmed epoch was converted to a text format for use with the sLORETA software package, the newest version of LORETA. sLORETA has been reported to produce minimal localization errors (R. D. Pascual-Marqui et al. 2002; Wagner et al. 2004) and estimates of current EEG sources in 6,239 cortical gray matter pixels, according to the probability atlases of the Brain Imaging Center, Montreal Neurological Institute (MNI 305) (Sekihara et al. 2005; Talairach and Tournoux 1988). These maps were derived by performing a location-wise inverse weighting of the results of a minimum-norm least-squares (MNLS) analysis along with their estimated variances. The MNLS approach is based on lead field theory and provides an inverse solution for an EEG or MEG that is the best estimate in the least-square sense.

Each trimmed epoch was transformed to a cross-spectrum using the sLORETA software package. Standard 32-channel electrode coordinates of the international 10–20 system were transformed to the transformation matrix using sLORETA tomography and no regularization. In each frequency band and for each of the 40 subjects, we computed the corresponding cortical sources of electrical neuronal oscillators.

Each frequency band of the cortical source was compared between genders using the statistical nonparametric mapping (SnPM) provided in the sLORETA software package. In the current study, gender differences were examined by assessing log of ratio of averages (similar to log of F-ratio; see R. Pascual-Marqui 2002 for details). Electrode/voxel-wise normalization and 5,000 randomization with no smoothing for SnPM were also used. Voxels with significant differences were mapped in the MNI template provided by the sLORETA software package.

Results

Behavioral data

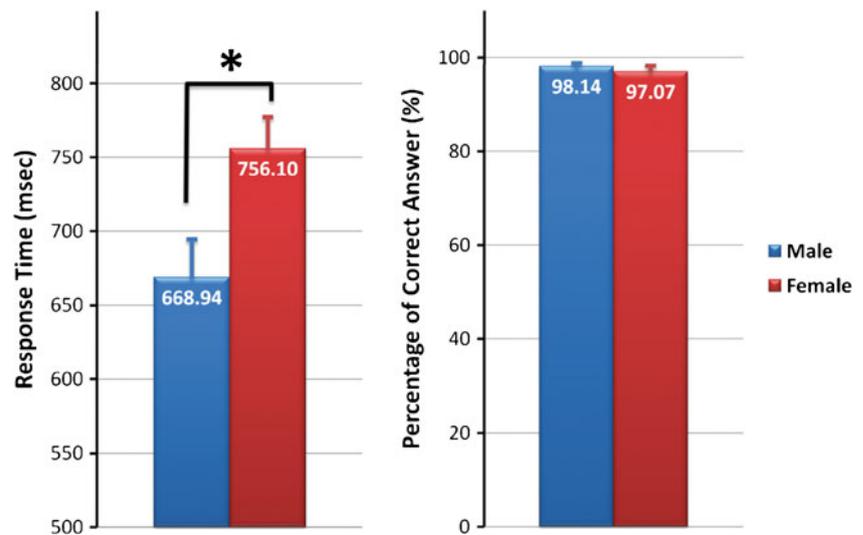
Table 1 shows the demographic data for the participants in this study. The mean age and the degree of education were matched, and no statistical differences were found between male and female subject groups. The age range was confined to 20 to 26 years to minimize possible biases based on age variation. All subjects were right-handed, and there were no statistical differences in the laterality quotients obtained via the Edinburgh handedness inventory (Oldfield 1971).

Table 1 also provides the behavioral performance (i.e., the percentages of correct answers and RTs) of each gender for the NLITs. There were no significant differences in the percentages of correct answers. Both genders showed high percentages of correct answers, but the RTs of male subjects were significantly faster (shorter) than those of female subjects (Table 1 and Fig. 2). This result indicates that both genders are equally able to perform the NLITs and that male subjects are fast responders to the NLITs.

Time-frequency spectral analyses: event-related spectral perturbation (ERSP) and inter-trial coherence (ITC)

Figures 3 and 4 show the grand mean ERSP and ITC planes for each gender. Statistical differences between groups obtained via independent sample *t*-test ($p < 0.05$ uncorrected; significant differences with $p < 0.003$ were marked with green arrows) are indicated by marking the significant areas. The ERSPs at the Fz, C3, Cz, C4, and Pz electrodes at frequency ranges of 4–20 Hz (theta, alpha, and beta)

Fig. 2 Percentages of correct answers and response times (RTs) obtained during the NLIT study. The number within each bar indicate the average value, and the *error bar* indicates the standard error. The male subjects gave significantly faster responses than the female subjects (*: $t=-2.63$, p -value=0.013). There are no statistical differences between genders in the percentages of correct answers



increased from the baseline at the stimulus onset and lasted over 1,000 msec in both genders. In the frontotemporal electrodes (e.g., Fp1, Fp2, F7, F8, T7, and T8), the ERSP increments were higher 500 msec from the stimulus onset. Decreased ERSPs were found at almost all electrodes for the frequency range of 12–15 Hz (beta range) in both genders. In the case of ITC, evoked responses were found for almost all electrodes at a frequency range of 4–25 Hz (theta, alpha, and beta) and a time range of 0–300 msec after the stimulus onset. Females showed significantly higher ITCs than males in all electrodes except FP2 (4–10 Hz) and F8 (4–10 Hz) that males showed higher ITCs than females (Fig. 3). Furthermore, gender differences were found in the ERSPs at the high frequency range (~20 Hz; beta and gamma) at Pz, F4, T7, and T8 electrodes (Fig. 4). Female subjects showed significantly higher ERSPs at the Pz, F4, T7 and T8 electrodes than male subjects, while male subjects showed higher ERSPs at the F4 and T8 electrodes (Fig. 4; blue box).

Statistical nonparametric mapping (SnPM) by sLORETA

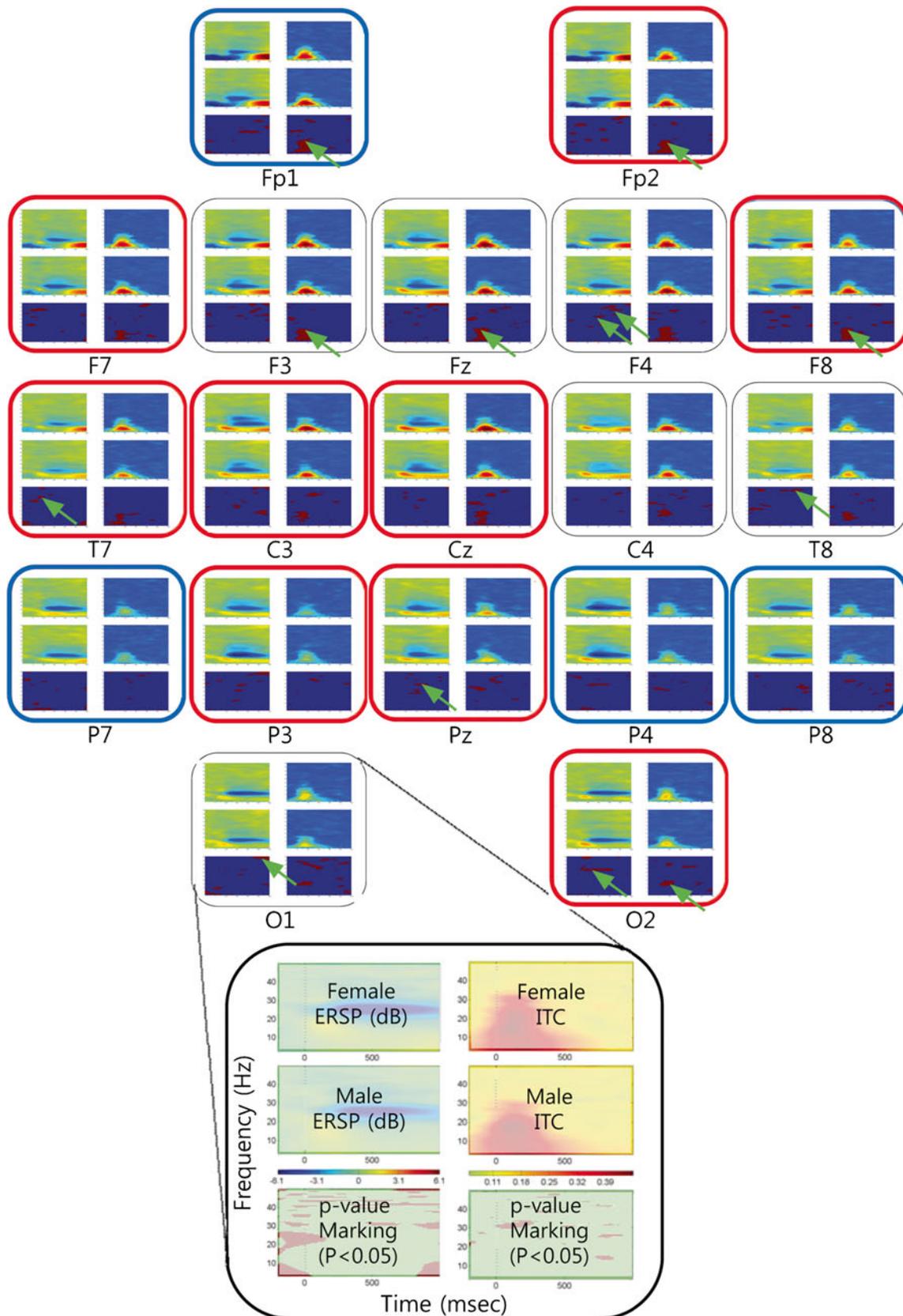
We prepared a topographical map of the statistical differences obtained for male and female subjects during the 0 to 500 msec time interval, at which most of the significant gender differences in ERSP and ITC were observed. Figure 5 shows 3-dimensional cortical mapping of the results from SnPM and compares estimated current sources between genders. Table 2 summarizes the specific areas in which maximal statistical differences in current source densities were observed for each frequency band. Maximal differences were found in the right posterior temporal areas,

with male subjects showing higher theta-band current density magnitudes than female subjects. An unequal contribution of the right temporal lobe during the visual verbal processing was found in males and in females. This result suggests that male subjects may be more dependent on the right temporal lobe than female subjects during visual verbal processing.

Discussion

The present study assesses gender differences in the visual sensory processing of NLITs using ERSP and ITC behavioral measures and estimates the current source distribution in a 3-dimensional brain model assessed by sLORETA. Both males and females showed good accuracy in their NLIT responses, but the response time for male subjects was significantly faster than for female subjects. In event-related temporo-spectral dynamics, the female subjects showed higher induced (ERSP) in beta band and evoked (ITC) activities in theta and alpha bands (at central electrodes such as C3 and Cz) than male subjects. Male subjects showed significantly higher activities at right hemispheric frontal and temporoparietal electrodes, such as F8, P4, and P8, than female subjects. The source analysis (using sLORETA) of time ranges in which ERSP and ITC between genders were statistically different revealed that the right posterior temporal regions are the most significantly different areas (between genders) in theta band oscillation.

This study was designed to investigate gender differences in visual sensory processing of verbal stimuli. The task of



◀ **Fig. 3** Gender comparisons of the ERSPs and ITCs from 19-channel 10/20 system electrodes and their statistical planes. The ERSPs reveal various induced activities depending on the location of the electrodes in a range that varies from 0 to 1,000 msec. Prominently evoked activities in the ITC planes are limited to the range of 0–300 msec in the alpha and beta frequency bands. The electrodes that females showed higher ERSP than males were marked with *red boxes*, and *blue boxes* in other cases. Significant differences with $p < 0.003$ were marked with *green arrows* (no significant activities were found when family-wise-error correction was applied)

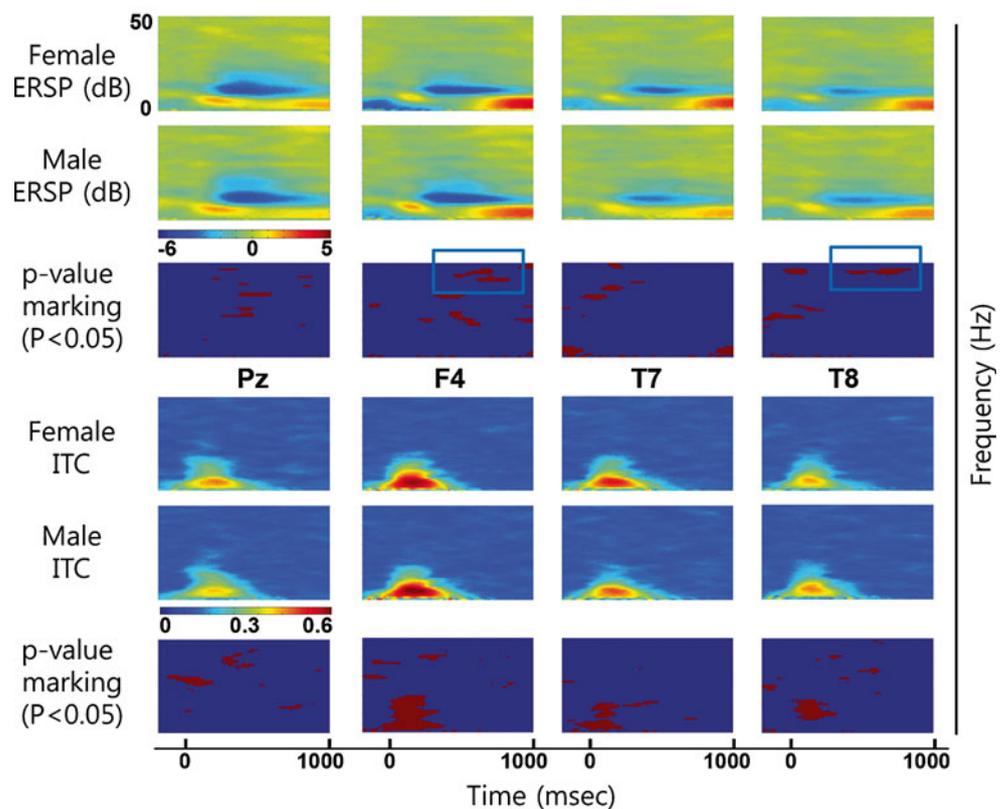
identifying complex Navon letters revealed gender differences that males had higher induced brain activities in the right posterior temporal areas than females. Previous studies have concluded that males have superior visuospatial abilities compared to females (Voyer et al. 1995), which should account for the faster male response time. In general, studies involving the decoding of visually presented language symbols have included the following four levels of complexity: reading letter-like fonts, reading letter strings, reading words, and reading stories (Petersen et al. 1990; Snyder et al. 1989). Without lexical processing (i.e., the Navon letter is meaningless), the NLITs assesses only a low level of language processing that involves ‘reading letter-like fonts’. It is possible that the Navon letter task requires visuospatial recognition of patterns rather than language processing, analogous to Japanese writing.

Japanese writing is most commonly expressed via two symbol systems, Kanji and Kana. Kanji is composed of com-

plex characters representing both phonetic and semantic values. By contrast, Kana is based on phonemes, like most Western languages (Roland 1993). Law et al. (1992) reported that the visual association areas and the posterior inferior temporal region are activated more during Kanji reading than during Kana reading. Conversely, the supramarginal gyrus is activated more during Kana reading than Kanji reading (Koyama et al. 1998; Law et al. 1992). Interestingly, even though NLITs differ from other word-recognition tasks, previous studies have shown that temporal regions of the brain (the superior temporal gyrus and fusiform gyrus) engage in evaluating the random strings or pseudo words (Jessen et al. 1999; Mechelli et al. 2005). Wise et al. (1991) found that the left posterior superior temporal gyrus was more intensely activated when subjects read meaningful words than when they read false fonts. The right hemispheric activation we observed supports the hypothesis that NLITs require visuospatial processing rather than language processing.

Three alternative theories could explain our findings. First, the neural activations we identified might reflect language processing differences between genders because NLITs may also require language processing. Some previous reports indicate that the right hemisphere is involved in critical language functions (Day 1977; Ross 1981; Ross and Mesulam 1979). However, it has long been hypothesized that language functions are more strongly lateralized to the left hemisphere in males than in females (Hampson and

Fig. 4 ERSPs, ITCs, and statistical planes for four exemplar electrodes with significant group differences (Pz, F4, T7, and T8) electrodes. Significant differences marked with *blue square* represent the region that males showed larger ERSP than females (others: female > male)



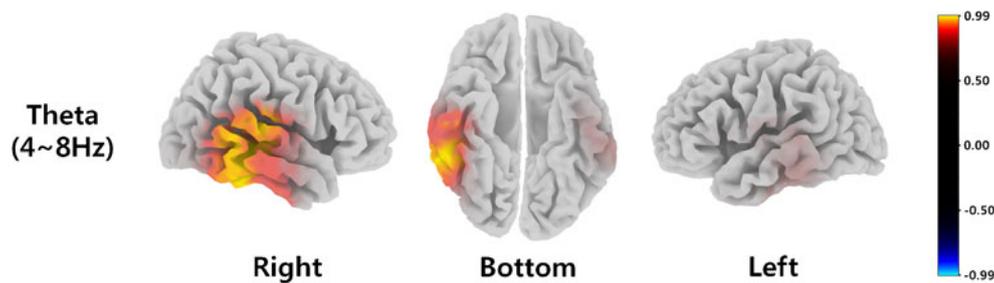


Fig. 5 The statistical cortical mappings of theta bands obtained from the SnPM (male–female). The male subjects show greater advantages regarding theta-band current densities in the *right* posterior temporal

regions. T-values are color-coded from $t=-0.99$ to 0.99 . The critical t-value for $p<0.05$ is 0.89

Kimura 1992; Kimura 1999; Levy 1972), and many studies investigating functional and anatomical sex differences support this hypothesis (Kulynych et al. 1994; Luders et al. 2006; Ortigue et al. 2005; Shaywitz et al. 1995; Steinmetz et al. 1992; Witelson 1989). Several recent studies have emphasized inconsistencies among findings on such gender differences in language processing (Harrington and Farias 2008; Ihnen et al. 2009; IE Sommer et al. 2008; Wallentin 2009). These studies

have suggested that publication bias or task analysis method variability may account for inconsistently observed gender differences. Chen et al. (2007) and Dong et al. (2008) showed that males and females have different neural predictors of visual word learning, suggesting that individual differences might blur gender differences. As described in the Materials and Methods section, the differences obtained in this study were examined with strict statistical constraints. Nonetheless, the gender differences we observed may be limited to the specific task and analysis methods used in the current study.

Table 2 Summary of the sLORETA statistics between genders (Male–female).

	X	Y	Z	Critical val. ^a	Hemisphere/Area
Theta	55	-35	-20	0.991*	Right Inferior Temporal Gyrus, BA20
	55	-40	-20	0.988*	Right Inferior Temporal Gyrus, BA37
	50	-30	-5	0.986*	Right Middle Temporal Gyrus, BA21
Alpha	60	-35	0	0.803	Right Middle Temporal Gyrus, BA22
	65	-40	0	0.802	Right Middle Temporal Gyrus, BA21
	65	-30	5	0.799	Right Superior Temporal Gyrus, BA42
Beta	60	-35	25	-0.348	Right Inferior Parietal Lobule, BA40
	55	-35	20	-0.340	Right Insula, BA13
	60	-35	20	-0.339	Right Superior Temporal Gyrus, BA 42
Gamma	65	-40	35	-0.591	Right Inferior Parietal Lobule, BA40
	50	-25	30	-0.548	Right Postcentral Gyrus, BA2
	45	-70	40	-0.544	Right Inferior Parietal Lobule, BA39

Three highest regions for each band are given. MNI152 coordinates are presented as the values denoting x, y, and z-axis in mm scale. The critical values from SnPM are presented and plus signs indicate males' dominance. ^a Critical value (log of ratio of averages) of one-tailed statistics for $p<0.05$ is 0.892 . * The threshold (log of ratio of averages) above critical point; BA, Brodmann area

Second, we cannot exclude the effects of visual working memory performance, which may also be required for the task used in this study. In the NLITs, the subjects are required to respond to a target provided at the beginning of the session during the series of pseudo-random Navon letters. Thus, it is possible to regard the NLITs as a modified version of a continuous performance task that measures a person's sustained and selective attention (Conners 1994). There is convincing evidence that EEG oscillations in the theta band are related to working memory tasks and, therefore, measure executive attention (for a review, please see Klimesch 1999). Sauseng et al. (2004) observed theta coupling between prefrontal and right posterior temporal electrode sites during visual working memory tasks (Sauseng et al. 2004).

Third, the results may reflect the intensive effects of anatomical differences between genders. It has been suggested that anatomical differences in brain structure and organization may inform the functional differences in cognitive processes between genders (Amunts et al. 2007; Wood et al. 2008). In one large sample study, Sowell et al. (2007) reported that cortical thickness mapping showed thicker cortices in the right inferior parietal and posterior temporal regions in females than in males, even when no corrections were made for total brain volume (Sowell et al. 2007). In their discussion, the authors asserted that the thicker female cortex may not necessarily be better than a thinner one. In normally developing children, cortical thinning of frontal and parietal cortices has been associated with improvements in the performance of language tasks (Sowell et al. 2001, 2004). Reports have suggested that the thinner cortices in the temporoparietal regions of males, if

they result from greater pruning and myelination during development and more efficient computational processing, may contribute to the superior visuospatial skills of males. Of course, these alternative explanations may not be exclusive. In addition, we cannot ignore an opposing view that suggests a causal effect of behavioral gender differences (e.g., social context) on biological and anatomical differences (Kaiser et al. 2009). Consequently, a variety of task designs with Navon letters and more detailed cognitive assessments are required to address these issues. Another limitation of this study is that we did not examine the effects of potentially impacting factors such as the handedness (LQ) and IQ of each subject.

Using ERS, ITC, and sLORETA, we assessed gender differences in events related to temporo-spectral dynamics and cortical oscillators during NLITs. The results revealed that men and women perform differentially across physiological measures of the cognitive processing of Navon letters. This is likely due to gender-specific perceptual processing, particularly regarding the right posterior temporal area. Collectively, our results identify biological correlates for gender-specific hemispheric specialization regarding visuospatial cognition. We suggest that further research should utilize electrophysiological measurements to investigate the gender differences in brain function and processing that we associate with the behavioral differences reported in this study.

Acknowledgements This work was supported by a Korea Science and Engineering Foundation (KOSEF) grant funded by the Korean government (MOST) (No. M10644000005-06N4400-00510, No. R01-2007-000-21094-0, and No. M10644000013-06N4400-01310).

References

- Amunts, K., Armstrong, E., Malikovic, A., Homke, L., Mohlberg, H., Schleicher, A., et al. (2007). Gender-specific left-right asymmetries in human visual cortex. *Journal of Neuroscience*, *27*(6), 1356.
- Bishop, D., Hardiman, M., & Barry, J. (2010). Lower-frequency event-related desynchronization: A signature of late mismatch responses to sounds, which is reduced or absent in children with specific language impairment. *The Journal of Neuroscience*, *30*(46), 15578.
- Cahill, L., Haier, R., White, N., Fallon, J., Kilpatrick, L., Lawrence, C., et al. (2001). Sex-related difference in amygdala activity during emotionally influenced memory storage. *Neurobiology of Learning and Memory*, *75*(1), 1–9.
- Canli, T., Desmond, J., Zhao, Z., & Gabrieli, J. (2002). Sex differences in the neural basis of emotional memories. *Proceedings of the National Academy of Sciences*, *99*(16), 10789.
- Chen, C., Xue, G., Dong, Q., Jin, Z., Li, T., Xue, F., et al. (2007). Sex determines the neurofunctional predictors of visual word learning. *Neuropsychologia*, *45*(4), 741–747.
- Conners, C. (1994). *The Continuous Performance Test (CPT): Use as a diagnostic tool and measure of treatment outcome*.
- Day, J. (1977). Right hemisphere language processing in normal right handers. *Journal of Experimental Psychology*, *3*(3), 518–528.
- Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*(1), 9–21.
- Dong, Q., Mei, L., Xue, G., Chen, C., Li, T., Xue, F., et al. (2008). Sex-dependent neurofunctional predictors of long-term maintenance of visual word learning. *Neuroscience Letters*, *430*(2), 87–91.
- Frost, J., Binder, J., Springer, J., Hammeke, T., Bellgowan, P., Rao, S., et al. (1999). Language processing is strongly left lateralized in both sexes: Evidence from functional MRI. *Brain*, *122*(2), 199.
- Golgel, A., Suer, C., Ozesmi, C., Aciogolu, N., & Sahin, O. (1999). The effect of sex differences on event-related potentials in young adults. *International Journal of Neuroscience*, *99*(1–4), 69–77.
- Gootjes, L., Bruggeling, E. C., Magnee, T., & Van Strien, J. W. (2008). Sex differences in the latency of the late event-related potential mental rotation effect. *Neuroreport*, *19*(3), 349.
- Gur, R., Alsop, D., Glahn, D., Petty, R., Swanson, C., Maldjian, J., et al. (2000). An fMRI study of sex differences in regional activation to a verbal and a spatial task. *Brain and Language*, *74*(2), 157–170.
- Hampson, E., & Kimura, D. (1992). Sex differences and hormonal influences on cognitive function in humans. *Behavioral endocrinology*, 357–398.
- Harrington, G. S., & Farias, S. T. (2008). Sex differences in language processing: functional MRI methodological considerations. *Journal of Magnetic Resonance Imaging*, *27*(6), 1221–1228.
- Harshman, R., Remington, R., & Krashen, S. (1983). *Sex. Language and the Brain: III, Evidence from Dichotic Listening for Adult Sex Differences in Verbal Lateralization*. University of Western Ontario, Canada.
- Ihnen, S., Church, J. A., Petersen, S. E., & Schlaggar, B. L. (2009). Lack of generalizability of sex differences in the fMRI BOLD activity associated with language processing in adults. *Neuroimage*, *45*(3), 1020–1032.
- Jaeger, J., Lockwood, A., Van Valin Jr, R., Kemmerer, D., Murphy, B., & Wack, D. (1998). Sex differences in brain regions activated by grammatical and reading tasks. *Neuroreport*, *9*(12), 2803.
- Jasper, H. H. (1958). The ten-twenty electrode system of the International Federation. *Electroencephalography and Clinical Neurophysiology*, *10*(1), 371–375.
- Jessen, F., Erb, M., Klose, U., Lotze, M., Grodd, W., & Heun, R. (1999). Activation of human language processing brain regions after the presentation of random letter strings demonstrated with event-related functional magnetic resonance imaging. *Neuroscience Letters*, *270*(1), 13–16.
- Kaiser, A., Haller, S., Schmitz, S., & Nitsch, C. (2009). On sex/gender related similarities and differences in fMRI language research. *Brain Research Reviews*, *61*(2), 49–59.
- Kansaku, K., & Kitazawa, S. (2001). Imaging studies on sex differences in the lateralization of language. *Neuroscience research*, *41*(4), 333–337.
- Kimura, D. (1999). *Sex and cognition*. London: Bradford Books.
- Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain Research Reviews*, *29*(2–3), 169–195.
- Knyazev, G., Slobodskoj-Plusnin, J., & Bocharov, A. (2009). Event-related delta and theta synchronization during explicit and implicit emotion processing. *Neuroscience*, *164*(4), 1588–1600.
- Knyazev, G., Slobodskoj-Plusnin, J., & Bocharov, A. (2010). Gender differences in implicit and explicit processing of emotional facial expressions as revealed by event-related theta synchronization. *Emotion*, *10*(5), 678.
- Koyama, S., Kakigi, R., Hoshiyama, M., & Kitamura, Y. (1998). Reading of Japanese Kanji (morphograms) and Kana (syllabograms): A magnetoencephalographic study. *Neuropsychologia*, *36*(1), 83–98.
- Kulynych, J., Vldar, K., Jones, D., & Weinberger, D. (1994). Gender differences in the normal lateralization of the supratemporal cortex: MRI surface-rendering morphometry of Heschl's gyrus and the planum temporale. *Cerebral Cortex*, *4*(2), 107.

- Lamm, C., Fischmeister, F. P. S., & Bauer, H. (2005). Individual differences in brain activity during visuo-spatial processing assessed by slow cortical potentials and LORETA. *Cognitive Brain Research*, 25, 900–912.
- Law, I., Kanno, I., & Fujita, H. (1992). Functional anatomical correlates during reading of morphograms and syllabograms in the Japanese language. *Biomedical Research Tokyo*, 13, 51–52.
- Levy, J. (1972). Lateral specialization of the human brain: Behavioral manifestations and possible evolutionary basis. In J. Kiger (Ed.), *The biology of behavior* (pp. 159–180). Corvallis, OR: Oregon State University.
- Luders, E., Narr, K., Thompson, P., Rex, D., Jancke, L., & Toga, A. (2006). Hemispheric asymmetries in cortical thickness. *Cerebral Cortex*, 16(8), 1232.
- Makeig, S. (1993). Auditory event-related dynamics of the EEG spectrum and effects of exposure to tones. *Electroencephalography and Clinical Neurophysiology*, 86(4), 283–293.
- Makeig, S., Westerfield, M., Jung, T., Enghoff, S., Townsend, J., Courchesne, E., et al. (2002). Dynamic brain sources of visual evoked responses. *Science*, 295(5555), 690.
- Makeig, S., Debener, S., Onton, J., & Delorme, A. (2004). Mining event-related brain dynamics. *Trends in Cognitive Sciences*, 8(5), 204–210.
- Mechelli, A., Crinion, J. T., Long, S., Friston, K. J., Ralph, M. A. L., Patterson, K., et al. (2005). Dissociating reading processes on the basis of neuronal interactions. *Journal of Cognitive Neuroscience*, 17(11), 1753–1765.
- Navon, D. (1969). Forest before trees: The precedence of global features in visual perception. *Perception and Psychophysics*, 5, 197–200.
- Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive Psychology*, 9(3), 353–383.
- Oldfield, R. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, 9(1), 97–113.
- Orozco, S., & Ehlers, C. (1998). Gender differences in electrophysiological responses to facial stimuli. *Biological Psychiatry*, 44(4), 281–289.
- Ortigue, S., Thut, G., Landis, T., & Michel, C. (2005). Time-resolved sex differences in language lateralization. *Brain*, 128(5), E28.
- Pascual-Marqui, R. (2002). Standardized low-resolution brain electromagnetic tomography (sLORETA): technical details. *Methods & Findings in Experimental & Clinical Pharmacology*, 24(Suppl D), 5–12.
- Pascual-Marqui, R. D., Esslen, M., Kochi, K., & Lehmann, D. (2002). Functional imaging with low-resolution brain electromagnetic tomography (LORETA): a review. *Methods & Findings in Experimental & Clinical Pharmacology*, 24(suppl C), 91–95.
- Petersen, S., Fox, P., Snyder, A., & Raichle, M. (1990). Activation of extrastriate and frontal cortical areas by visual words and word-like stimuli. *Science*, 249(4972), 1041–1044.
- Razumnikova, O. M. (2004). Gender differences in hemispheric organization during divergent thinking: an EEG investigation in human subjects. *Neuroscience Letters*, 362(3), 193–195.
- Rhodes, M., & Rubin, R. (1999). Functional sex differences (sexual diergism) of central nervous system cholinergic systems, vasopressin, and hypothalamic-pituitary-adrenal axis activity in mammals: a selective review. *Brain Research Reviews*, 30(2), 135–152.
- Roland, P. (1993). *Brain activation*. New York: Wiley-Liss.
- Ross, E. (1981). The aprosodias: Functional-anatomic organization of the affective components of language in the right hemisphere. *Archives of Neurology*, 38(9), 561.
- Ross, E., & Mesulam, M. (1979). Dominant language functions of the right hemisphere? Prosody and emotional gesturing. *Archives of Neurology*, 36(3), 144.
- Sabatinelli, D., Flaisch, T., Bradley, M., Fitzsimmons, J., & Lang, P. (2004). Affective picture perception: gender differences in visual cortex? *Neuroreport*, 15(7), 1109.
- Sauseng, P., Klimesch, W., Doppelmayr, M., Hanslmayr, S., Schabus, M., & Gruber, W. (2004). Theta coupling in the human electroencephalogram during a working memory task. *Neuroscience Letters*, 354(2), 123–126.
- Sekihara, K., Sahani, M., & Nagarajan, S. S. (2005). Localization bias and spatial resolution of adaptive and non-adaptive spatial filters for MEG source reconstruction. *Neuroimage*, 25(4), 1056–1067.
- Shaywitz, B. A., Shaywitz, S. E., Pugh, K. R., Constable, R. T., Skudlarski, P., Fulbright, R. K., et al. (1995). Sex differences in the functional organization of the brain for language. *Nature*, 373(6515), 607–609.
- Snyder, A., Petersen, S., Fox, P., & Raichle, M. (1989). PET studies of visual word recognition. *Journal of cerebral blood flow and metabolism*, 9, 576.
- Sommer, I., Aleman, A., Bouma, A., & Kahn, R. (2004). Do women really have more bilateral language representation than men? A meta-analysis of functional imaging studies. *Brain*, 127(8), 1845.
- Sommer, I., Aleman, A., Somers, M., Boks, M., & Kahn, R. (2008). Sex differences in handedness, asymmetry of the planum temporale and functional language lateralization. *Brain Research*, 1206, 76–88.
- Sowell, E., Delis, D., Stiles, J., & Jernigan, T. (2001). Improved memory functioning and frontal lobe maturation between childhood and adolescence: a structural MRI study. *Journal of the International Neuropsychological Society*, 7(03), 312–322.
- Sowell, E., Thompson, P., Leonard, C., Welcome, S., Kan, E., & Toga, A. (2004). Longitudinal mapping of cortical thickness and brain growth in normal children. *Journal of Neuroscience*, 24(38), 8223.
- Sowell, E. R., Peterson, B. S., Kan, E., Woods, R. P., Yoshii, J., Bansal, R., et al. (2007). Sex differences in cortical thickness mapped in 176 healthy individuals between 7 and 87 years of age. *Cerebral Cortex*, 17(7), 1550.
- Steinmetz, H., Jancke, L., Kleinschmidt, A., Schlaug, G., Volkman, J., & Huang, Y. (1992). Sex but no hand difference in the isthmus of the corpus callosum. *Neurology*, 42(4), 749–752.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the brain* (pp. 17–23). New York: Thieme.
- Vaquero, E., Cardoso, M., Vazque, M., & Gomez, C. (2004). Gender differences in event-related potentials during visual-spatial attention. *International Journal of Neuroscience*, 114(4), 541–557.
- Voyer, D., Voyer, S., & Bryden, M. (1995). Magnitude of sex differences in spatial abilities: A meta-analysis and consideration of critical variables. *Psychological Bulletin*, 117, 250–250.
- Wagner, M., Fuchs, M., & Kastner, J. (2004). Evaluation of sLORETA in the presence of noise and multiple sources. *Brain Topography*, 16(4), 277–280.
- Wallentin, M. (2009). Putative sex differences in verbal abilities and language cortex: A critical review. *Brain and Language*, 108(3), 175–183.
- Wirth, M., Horn, H., Koenig, T., Stein, M., Federspiel, A., Meier, B., et al. (2007). Sex differences in semantic processing: event-related brain potentials distinguish between lower and higher order semantic analysis during word reading. *Cerebral Cortex*, 17(9), 1987.
- Wise, R., Chollet, F., Hadar, U., Friston, K., Hoffner, E., & Frackowiak, R. (1991). Distribution of cortical neural networks involved in word comprehension and word retrieval. *Brain*, 114(4), 1803.
- Witelson, S. (1989). Hand and sex differences in the isthmus and genu of the human corpus callosum: a postmortem morphological study. *Brain*, 112(3), 799.
- Wood, J., Murko, V., & Nopoulos, P. (2008). Ventral frontal cortex in children: morphology, social cognition and femininity/masculinity. *Social cognitive and affective neuroscience*, 3(2), 168.