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Dysfunctional hemispheric asymmetry of theta and beta EEG activity during linguistic tasks in developmental dyslexia

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Abstract

The phonological deficit hypothesis of dyslexia was studied by analyzing language-related lateralization of theta (4–8 Hz) and beta rhythms (13–30 Hz) during various phases of word processing in a sample of 14 dyslexics and 28 controls. Using a word-pair paradigm, the same words were contrasted in three different tasks: Phonological, Semantic and Orthographic. Compared with controls, dyslexic children showed a delay in behavioral responses which was paralleled by sustained theta EEG peak activity. In addition, controls showed greater theta and beta activation at left frontal sites specifically during the Phonological task, whereas dyslexics showed a dysfunctional pattern, as they were right-lateralized at these sites in all tasks. At posterior locations, and reversed with respect to controls' EEG responses, dyslexics showed greater left lateralization during both Phonological and Orthographic tasks—a result which, in these children, indicates an altered and difficult phonological transcoding process during verbal working memory phases of word processing. Results point to a deficit, in phonological dyslexia, in recruitment of left hemisphere structures for encoding and integrating the phonological components of words, and suggest that the fundamental hierarchy within the linguistic network is disrupted.

Keywords: Theta; Beta; EEG band; Dyslexia; Reading; Lateralization; Working memory; Phonology; Semantics

1. Introduction

Developmental dyslexia is a specific learning disability characterized by clear-cut difficulty in reading, despite the fact that intelligence, motivation, instruction and sensory abilities are relatively spared. Past neurobiological investigations have consistently found anomalies in the left temporo-parieto-occipital regions of dyslexics' brains (Filipek, 1996; Galaburda et al., 1985; Klingberg et al., 2000). Evidence from functional neuroimaging in children and adults with this disorder has also shown a failure of left posterior brain systems (Brunswick et al., 1999; Démonet et al., 2004; Helenius et al., 1999; Paulesu et al., 2001; Salmelin et al., 1996; Shaywitz, 1998; Shaywitz et al., 2002, 2003; Simos et al., 2000; Temple et al., 2001, 2003). As a consequence, depending on the study, the neural activity of dyslexics has been demonstrated to be shifted toward right temporal regions, more anterior left regions or right perisylvian areas (Brunswick et al., 1999; Démonet et al., 2004; Georgiewa et al., 2002; Shaywitz et al., 1998, 2002; Simos et al., 2000). Despite this inconsistency in the main brain regions activated in dyslexia, there is a quite large consensus about the underlying cognitive mechanism which is damaged. Although a number of authors pointed to a main involvement of visual or auditory perception impairment in dyslexia (Ramus, 2004; Ramus et al., 2003), most previous studies have provided clear-cut evidence for a deficit in the phonological component of language (Ramus, 2004; Ramus et al., 2003; Shaywitz, 1998; Shaywitz et al., 2002, 2003; Shaywitz and Shaywitz, 2005; Temple et al., 2001). In fact, whereas a phonological deficit is the core trait of developmental dyslexia, attentional, perceptual and motor deficits are often observed only in a subsample of individuals (for a review, see Ramus, 2004). According to this hypothesis, people with dyslexia are unable to process the phonological structure underlying word reading, and this is associated with a disruption of left hemisphere linguistic networks. Several studies have related dyslexics' phonological disorder to a verbal working memory deficit, consisting of difficulty in manipulating the basic components of language, i.e., graphemes and

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phonemes (Georgiewa et al., 2002; Ramus, 2003, 2004; Shaywitz, 1998). In a number of recent studies, the EEG theta band (frequency range about 4–7 Hz) has been shown to be a reliable electrophysiological index of working memory involvement during cognitive processing (for a review, see Klimesch, 1999). Klimesch et al. (2001a) and Spironelli et al. (2006) have also proposed the theta band as a new tool for studying brain dysfunctions in developmental dyslexia. The analysis of activity in the theta band applied to a validated contingent negative variation (CNV) linguistic paradigm (Angrilli et al., 2000) has been particularly useful in studying the lateralization of linguistic cortical networks and the temporal dynamics of word processing in working memory (Spironelli et al., 2006). With this paradigm, the specificity of dyslexics' deficit has been highlighted, both by a failure to modulate theta activity in the left hemisphere during the Phonological task, and by dysfunctional activation of the right hemisphere. In addition, dyslexics' delayed pattern of theta activity shows that the temporal dynamics of word processing are also pathologically affected (Spironelli et al., 2006).

With the aim of investigating the neurobiological mechanisms underlying different EEG bands involved in linguistic processes, Weiss and Rappelsberger (1998) contrasted beta (13–18 Hz) coherence for concrete and abstract nouns presented in both auditory and visual modalities. They found significantly increased coherence between Fp1/F7 and F3/Fz sites for the processing of concrete nouns, indicating greater beta synchronization of neural systems within the left frontal cortex in comparison to the processing of abstract nouns, independently of the mode of stimulus presentation. The authors explained this pattern as indicative of different encoding and storage strategies for concrete and abstract nouns. In another study on dyslexic children and normal readers, Klimesch et al. (2001b) compared alpha (8–12.5 Hz) and beta (12.5–16 Hz) band activities during different tasks, i.e., reading numbers, words and pseudo-words. With particular regard to the beta band, the authors found a selective deficit in dyslexics' word processing. Controls showed greater beta activity in the left hemisphere during word reading, i.e., in a few electrodes (FC5, CP5/P3) of left frontal and parietal regions, and increased right/midline beta amplitude during number processing. Instead, dyslexic children showed a complete lack of task selectivity. Beta activity was interpreted as a cortical index able to measure and locate the capacity to process and select words and numbers, an ability that is affected in dyslexics. Thus, Klimesch et al. suggest that beta band activity in specific linguistic paradigms reflects grapheme–phoneme word encoding only for controls. Further evidence of dysfunctional beta band alteration in dyslexic children has recently been provided by Milne et al. (2003). These authors compared two subsamples of compensated dyslexic children, six dysphonetics and six dyseidetics,[1] with a control group, during a lexical decision task in which words and pseudo-words were visually presented. The groups showed no overall differences in mean beta power. However, a significant interaction between group and anterior–posterior axis was found: dysphonetics revealed increased beta activity over anterior sites, whereas dyseidetics exhibited increased beta over posterior locations. No antero-posterior differences were found in controls. Milne et al. interpreted these findings as a demonstration of the specific segregation of word processing between anterior and posterior regions of linguistic areas. In agreement with this interpretation, neuroimaging studies have provided converging evidence that, in the left hemisphere, the posterior areas are involved in grapheme–phoneme conversion and storage and retrieval of phonological information, whereas the anterior areas are involved in segmentation, phonological assembling and word production (Burton, 2001; Burton et al., 2000; Zatorre et al., 1992).

The present research aimed at investigating the phonological deficit hypothesis of developmental dyslexia, by using theta and beta band amplitudes as electrophysiological indices of cortical linguistic activity. In detail, in linguistic paradigms, theta activity has been demonstrated to be associated with specific usage of verbal working memory (Klimesch et al., 2001a; Spironelli et al., 2006). In agreement with our previous study (Spironelli et al., 2006), we expected a lack of left hemisphere lateralization for this rhythm, especially during phonological processing. A novel contribution with respect to the current literature on EEG bands and dyslexia is the introduction of the beta band in a paradigm that manipulates only task demands and keeps the word stimuli used constant. At the functional neurophysiological level, theta band activity is measured from the cortex but is controlled by the deep subcortical structures of the temporal lobe involved in working memory (Leung, 1998; Tesche and Karhu, 2000; Vertes, 2005), whereas the beta band is associated with activity of many independent cortical generators (mirrored by high frequency and large neuron desynchronization), typically recruited by high-level cognitive processing (Pantev et al., 1991; Tallon-Baudry and Bertrand, 1999). Since this rhythm is essentially produced by highly confined superficial cortical activity, we introduced the EEG beta band with the aim of collecting more detailed topographical information (not only across hemispheres, but also along the antero-posterior brain axis) of complex cognitive processing during linguistic tasks. For this, the linguistic-CNV paradigm (Angrilli et al., 2000) applied to EEG band analysis (Spironelli et al., 2006) was adopted, to measure various aspects of word processing. In addition, with respect to the latter study, a new, more basic, control task, i.e., the visuo-perceptual Orthographic task, was included. This relatively non-linguistic task was expected to induce the same obligatory (and automatic) verbal processing of words observed for the other tasks, but with particular emphasis to visuo-perceptual features of the stimuli. For this reason, the Orthographic task has been added in order to better understand and clarify the specific linguistic activity induced by both Phonological and Semantic tasks (Spironelli and Angrilli, 2006).

[1] According to Boder (1968), children with dyseidetic dyslexia show difficulty with memory and perception of whole-word configurations, whereas children suffering from dysphonetic dyslexia have difficulty sounding out words.

2. Methods

2.1. Participants

Fourteen dyslexic children (four females; mean age: 10.12 ± 2.23) were recruited from the Children's Neuropsychiatric Medical Facility of San Donà di Piave (Venice, Italy). Twenty-eight normal readers similar to the dyslexic sample in age (mean age: 10.01 ± 0.18, $t(40) = 0.27$, $p = 0.78$) and the distribution of sexes (14 females, $t(40) = 1.32$, $p = 0.19$; $\chi^2(1) = 1.75$, $p = 0.18$) served as the control group. Participants were on average 98% right-handed, according to the Edinburgh Handedness Inventory (Oldfield, 1971), and had normal or corrected-to-normal vision. Dyslexic participants were selected on the basis of a documented history of dyslexia, with inadequate performance on Italian standard tests for the assessment of reading skills: during the contextual reading test (Cornoldi and Colpo, 1998), their mean reading speed (1.50 ± 0.63 syllables/s) was significantly slower than that of controls (3.93 ± 0.88 syllables/s, $t(40) = 8.90$, $p < .001$) and normative data corrected for age (3.30 ± 0.60 syllables/s; Cornoldi and Colpo, 1998). The expert psychologist who treated all children administered the whole "*Battery for the evaluation of Dyslexia and Dysorthographya in Italian*" (Sartori et al., 1995). This battery consisted of seven subtests aimed at assessing children's reading skills, e.g., reading simple single letters, words/pseudo-words, irregular and low-frequency words. After the complete assessment of reading skills, all children were diagnosed as phonological dyslexics. All children showed a normal intelligence quotient (IQ range 93–112 in dyslexics, 95–134 in controls) measured by the Wechsler Intelligence Scale for Children-Revised (WISC-R; Wechsler, 1986). Dyslexic children suffering from Attention Deficit Disorder with hyperactivity (ADHD) were excluded from the experiment to avoid interference and confounding effects.

All participants also performed a digit span test in order to verify the extent of verbal short-term memory.

2.2. Stimuli, tasks, and procedure

Stimuli consisted of bisyllabic Italian content words selected from a frequency dictionary of 5000 written Italian words (Bortolini et al., 1972). Words were presented in pairs on a 17″ screen one at a time, with an interstimulus interval of 2 s: the first word (W1) remained on the screen for 1.5 s and the second word (W2 or target) was presented until the participant responded by pressing a keyboard button, but no longer than 5 s. Word pairs were administered in three separate blocks, which corresponded to three linguistic tasks: thus, the same words were presented as W1 in all tasks, but in different randomized order. In the Phonological task, participants had to decide whether the word pairs rhymed, and in the Semantic task, they had to judge whether target word W2 was semantically related to W1 (see Spironelli et al., 2006, for a complete description of stimuli and procedure). In addition, participants performed a control Orthographic task, in which they had to decide whether word pairs were written in the same case (e.g., LANA-FORNO, or sasso–riso [WOOL-OVEN, or stone-rice]) or not (e.g., coda-ERBA [tail-GRASS]). Participants pressed the button with their left index or middle finger to indicate responses. Each task included 80 trials/word-pairs. In all tasks, 50% matches were randomly interspersed with 50% mismatch trials. The task order was randomly varied across participants.

2.3. Data acquisition and analysis

EEG cortical activity was recoded from 38 tin electrodes, 31 placed on an elastic cap (Electrocap) according to the International 10–20 system (Oostenveld and Praamstra, 2001); the other 7 electrodes were applied below each eye (Io1, Io2), on the two external canthii (F9, F10), nasion (Nz) and mastoids (M1, M2). All cortical sites were on-line referred to Cz. Data were stored using the acquire software NeuroScan 4.1 version. Amplitude resolution was 0.1 μV; bandwidth ranged from DC to 100 Hz (6 dB/octave). Sampling rate was set at 500 Hz. Impedance was kept below 5 KΩ.

The error rates and mean response times of each participant served as behavioral measures, and mean performances were compared between groups and tasks. EEG was continuously recorded in DC mode and stored for off-line analysis. After completion of data collection, EEG raw data were corrected for blinks and eye movement artifacts, according to Ille et al. (2002) by BESA software (Brain Electrical Source Analysis, 5.1 version). Each EEG trial-epoch was divided into four 1024-ms time intervals, and thus included 512 samples with 0.98 Hz FFT resolution. Each interval corresponded to a different processing phase required by the task: 1024 ms before W1 onset (Baseline); 1024 ms after W1 onset (W1); from 1500 to 2524 ms after W1 onset (*Initial* Inter Stimulus Interval, *i*ISI); from 2476 to 3500 ms after W1 onset (*Terminal* ISI, *t*ISI). These time windows were selected based on the previous experiment (Spironelli et al., 2006). Given the constraint of the Fast Fourier Transform (FFT) to use a power of two number of samples, the width of each interval was necessarily forced to 512 samples, corresponding to a 1024-ms interval; therefore, the ISI contained a very small overlap (48 ms, <5%) between *i*ISI and *t*ISI. Artifact rejection was performed on each epoch, with both amplitude and derivative (with respect to time) thresholds (150 μV and 100 μV/ms, respectively). Remaining epochs were then visually inspected for any residual artifacts. Overall, 15% of trials were rejected from controls and 16.6% from dyslexic children, evenly distributed across tasks. For each participant, the FFT was performed on those epochs which, after windowing with a tapered cosine, were averaged for each interval. The last step consisted of the normalization of theta (band 4–8 Hz, effective range: 3.9–7.8 Hz) and beta (band 13–30 Hz, effective range: 12.7–28.5 Hz) amplitudes for all recorded locations: normalization was computed as percentages of theta and beta amplitudes in the 0.98–100 Hz spectral range. As in our previous study, electrodes were clustered into four groups/regions of interest to perform statistics with two spatial factors of two levels each: antero-posterior asymmetry and laterality (Spironelli et al., 2006). Each quadrant, therefore, comprised five electrodes: anterior left (AL: Io1, Fp1, F3, F7, F9), anterior right (AR: Io2, Fp2, F4, F8, F10), posterior left (PL: P7, P3, M1, T7, O1), and posterior right (PR: P8, P4, M2, T8, O2). Although orbitofrontal electrodes (Fp1, Fp2, F9, F10, Nz, Io1, Io2) are typically used to detect and correct eye movements, after applying the ocular artifact correction method of Ille et al. (2002), these electrodes may be considered as active cortical sites and were, therefore, included in the following analyses.

With regard to behavioral measures (mean error rates and RTs), analysis of variance (ANOVA) included the between-participants factor group (two levels: controls vs. dyslexics) and the within-participants factor task (three levels: Orthographic vs. Phonological vs. Semantic). The one-tailed *t*-test has been used in order to verify children's digit span: in line with our previous study (Spironelli et al., 2006) we predicted that dyslexic children have lower verbal working memory skills, i.e., reduced mean digit span levels in comparison with age-matched controls.

On EEG data, ANOVA included the following factors: Group (two levels: Controls vs. Dyslexics), Task (three levels: Orthographic vs. Phonological vs. Semantic), Interval (four levels: Baseline vs. W1 vs. *i*ISI vs. *t*ISI), AP asymmetry (Anterior Posterior asymmetry, two areas: Anterior vs. Posterior) and Laterality (two levels: Left vs. Right hemisphere). In addition, since preliminary statistics had indicated a main Group effect for both theta and beta bands, to rule out the influence of this effect on the main interactions, we ran an analysis of covariance (ANCOVA) by covarying the absolute theta/beta level, collapsed across intervals, tasks and brain regions, for each participant. Post hoc comparisons were computed using the Tukey HSD test ($p < .05$) and the Huynh–Feldt correction was applied when necessary (Huynh and Feldt, 1970).

3. Results

3.1. Behavioral results

Dyslexics showed a significant ($t(40) = 2.13$, $p < .05$, one-tailed) lower digit span (4.46 ± 1.01) compared with controls (5.16 ± 0.99). With regard to error rates, significant main effects of both Group ($F(1,40) = 31.79$, $p < .001$) and Task ($F(2,80) = 25.08$, $p < .001$, HF $\varepsilon = 1.00$) were found. Overall, dyslexics made more errors than controls (14.4% vs. 6.9%, respectively). In addition, regardless of group, the Phonological task turned out to be relatively easier, as it was characterized by

lower error rates (7.9%) than either Orthographic (9.9%, $p < .05$) or Semantic judgments (14.2%, $p < .001$). Response times showed the same pattern of results, with significant main effects of Group ($F(1,40) = 14.34$, $p < .001$) and Task ($F(2,80) = 63.07$, $p < .001$, HF $\varepsilon = 1.00$). The main Group effect on RTs indicated that dyslexics were slower than controls (2208 ms vs. 1690 ms, respectively) and the main Task effect showed, in both groups, slower RTs during Semantic (2343 ms) than either Orthographic (1704 ms, $p < .001$) or Phonological tasks (1801 ms, $p < .001$).

3.2. FFT spectral analysis results

3.2.1. Theta band analysis

ANOVA showed main effects of both Group ($F(1,40) = 27.68$, $p < .001$) and Anterior Posterior (AP) asymmetry ($F(1,40) = 89.02$, $p < .001$), revealing an overall significantly greater theta amplitude in controls rather than in dyslexic children (4.95% vs. 3.55%, respectively), and a greater involvement of posterior regions rather than anterior ones (4.97% vs. 3.54%, respectively). The two-way Group by Interval interaction ($F(3,120) = 3.84$, $p < .01$, HF $\varepsilon = .73$) in controls showed increased theta percentages in W1 compared with Baseline and *i*ISI intervals ($p < .001$ and $p < .01$, respectively; Fig. 1). Instead, dyslexics exhibited a more stable peak of theta activity, which lasted during both W1 and *i*ISI intervals, in which amplitude was significantly higher than during Baseline and *t*ISI ($p < .001$ and $p < .01$, respectively).

Very interestingly, the five-way Group by Interval by Task by AP asymmetry by Laterality interaction was also significant ($F(6,240) = 2.32$, $p < .05$, HF $\varepsilon = .74$). Fig. 2 shows the theta amplitudes of all tasks only during W1 and *i*ISI intervals (we show only these two intervals in the figure to avoid confusion due to excess of data and because both of them correspond to the most important phases of word processing and showed the most important differences between groups).

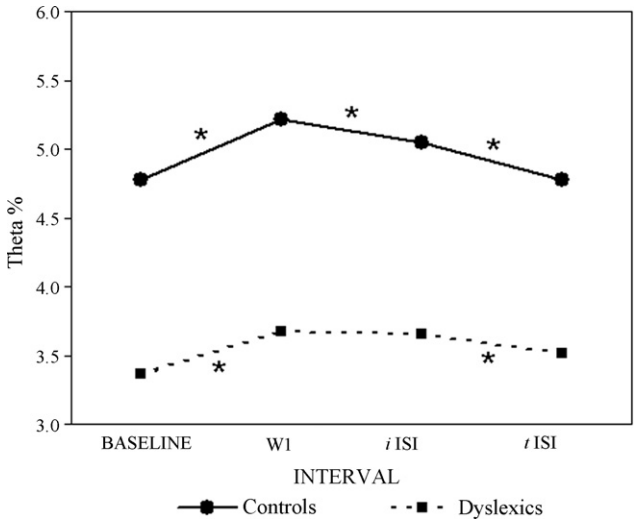

Fig. 1. Theta activity normalized across 0.98–100 Hz spectral range during four time intervals in the word processing tasks. Asterisks: significant post hoc test results.

During the Phonological task, controls always exhibited greater theta amplitude over left than over right anterior areas ($p < .001$; Fig. 2b, upper row) and bilateral theta distribution over posterior locations (Fig. 2b, lower row). Instead, dyslexics showed a reversed pattern in anterior sites: significantly greater theta amplitude over the right hemisphere during all intervals of phonological processing ($p < .001$), with the exception of the W1 interval, in which they showed a bilateral theta distribution (Fig. 2b, upper row). Also in posterior sites, dyslexic children exhibited a quite different pattern of theta amplitude in comparison with controls: greater left than right theta percentages for all intervals ($p < .001$; Fig. 2b, lower row). During the Semantic task, controls showed greater right vs. left theta percentage in all intervals ($p < .001$), whereas dyslexic children were also systematically right-lateralized ($p < .001$), with the exception of the W1 interval, during which they showed bilateral theta distribution (Fig. 2c, upper row). Unlike the Phonological task, in the Semantic task very similar patterns of theta activity were found in posterior regions for both groups: in these locations, theta amplitude was bilaterally distributed in all intervals (Fig. 2c, lower row). Lastly, during the Orthographic visuo-perceptual task, normal readers showed systematic bilateral distribution of theta activity, independently of interval or brain region (Fig. 2a). Instead, dyslexic children revealed a pattern close to that observed during phonological processing, always exhibiting significant right lateralization over anterior sites ($p < .01$) and left lateralization over posterior ones ($p < .001$; Fig. 2a, upper and lower rows, respectively).

Summarizing the main differences found over posterior regions, controls were bilaterally activated in all tasks whereas dyslexics showed bilateral theta activation during the Semantic task and greater left than right theta amplitude during both Phonological and Orthographic tasks. Over anterior regions, controls showed differentiated theta lateralization across tasks—that is, bilateral theta activation during the Orthographic, greater left theta amplitude during the Phonological, and greater right theta amplitude during the Semantic task. Conversely, during all tasks, dyslexics exhibited greater right theta percentages in all intervals, except during the W1 of both Phonological and Semantic tasks, which were associated with bilateral theta distribution.

ANCOVA analysis, which included participants' mean theta level as covariate, affected only the AP asymmetry main effect, which became non-significant ($F(1,39) = 0.01$, $p = 0.91$). All remaining significant differences were unaffected by correcting for absolute theta levels, and thus, relatively independent of groups' mean level of theta amplitude: two-way Group by Interval interaction: $F(3,117) = 5.63$, $p < .001$, HF $\varepsilon = .76$; five-way Group by Interval by Task by AP asymmetry by Laterality interaction: $F(6,234) = 2.78$, $p < .01$, HF $\varepsilon = .75$.

3.2.2. Beta band analysis

Beta band activity closely replicated the hemispherical distribution of theta band activity. Statistical analysis revealed main differences between Groups ($F(1,40) = 56.36$, $p < .001$; and AP asymmetry factors ($F(1,40) = 22.78$, $p < .001$) showing

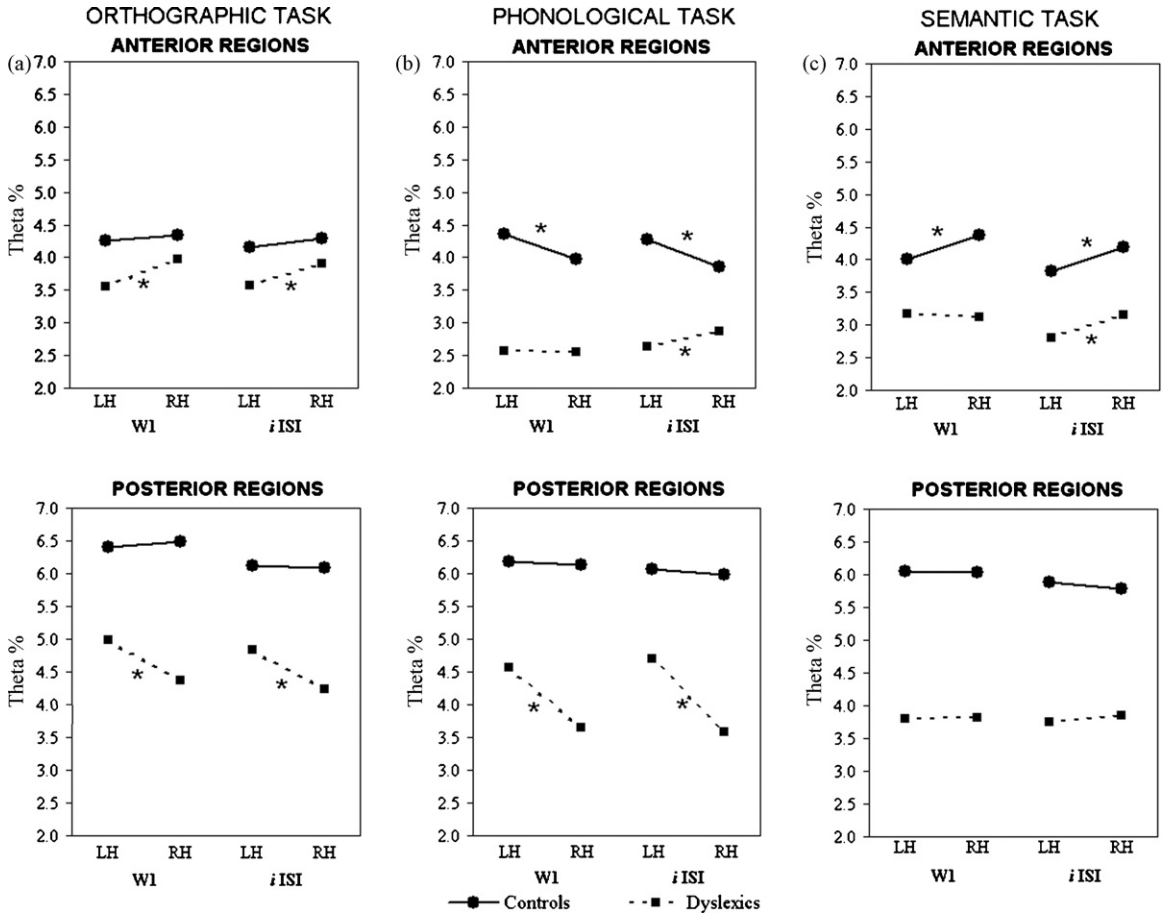

Fig. 2. Theta band (3.9–7.8 Hz) activity of controls (full line) and dyslexics (dashed line) during W1 and *i*ISI intervals in anterior (upper row) and posterior (lower row) regions for (a) Orthographic, (b) Phonological and (c) Semantic task. Asterisks: significant post hoc test results.

significantly greater beta amplitude in controls than in dyslexic children (8.71% vs. 5.62%, respectively) in posterior regions (7.67%) with respect to anterior ones (6.65%). The five-way Group by Interval by Task by AP asymmetry by Laterality interaction was also significant ($F(6,240) = 2.17$, $p < .05$, HF $\varepsilon = .65$). Fig. 3 shows beta amplitude across tasks only during W1 and *i*ISI intervals.

During the Phonological task, normal readers systematically showed a left-lateralized pattern of beta amplitude on anterior electrodes ($p < .001$; Fig. 3b, upper row) and a bilateral distribution over posterior regions (Fig. 3b, lower row). Compared with controls, dyslexic children had an inverted right-lateralized pattern on anterior areas, which was modulated in the time domain, revealing a bilateral beta amplitude during the W1 interval, followed by greater beta activity over right vs. left anterior sites during both ISI intervals ($p < .001$; Fig. 3b, upper row). At posterior regions dyslexics exhibited greater beta amplitude in the left than in the right hemisphere ($p < .001$; Fig. 3b, lower row). During the Semantic task, controls had anterior right lateralization of beta activity in all intervals ($p < .001$; Fig. 3c, upper row). Similarly, dyslexic children were right-lateralized ($p < .01$; Fig. 3c, upper row) in all intervals, with the exception of W1, in which they showed bilateral beta activity distribution. At posterior regions, in contrast with the Phonological task, semantic processing elicited bilateral patterns of beta activity in both groups (Fig. 3c, lower row). In the Orthographic visuo-perceptual task, controls showed a bilateral distribution of beta activity in all intervals (Fig. 3a), whereas dyslexic children had greater beta amplitudes on right than left anterior sites ($p < .001$; Fig. 3a, upper row) and on left vs. right posterior ones ($p < .001$; Fig. 3a, lower row). In sum, the main significant differences found between groups, across all intervals and tasks, were exactly the same as those described for the theta band.

ANCOVA analysis, with Group mean beta level as a covariate, led the previously observed effects to be non-significant: AP asymmetry main effect $F(1,39) = 0.65$, $p = 0.42$; five-way Group by Interval by Task by AP asymmetry by Laterality interaction: $F(6,234) = 1.65$, $p = 0.13$. Although the EEG patterns found after ANCOVA remained similar, the shift of the five-way interaction to non-significance indicates that all the above effects were not entirely independent of differences in absolute beta levels.

4. Discussion

Compared with our past study of phonological and semantic processing by means of the theta band, the present investigation increased our knowledge of dyslexia by adding a relatively non-linguistic control task (Orthographic task) and analysis of beta

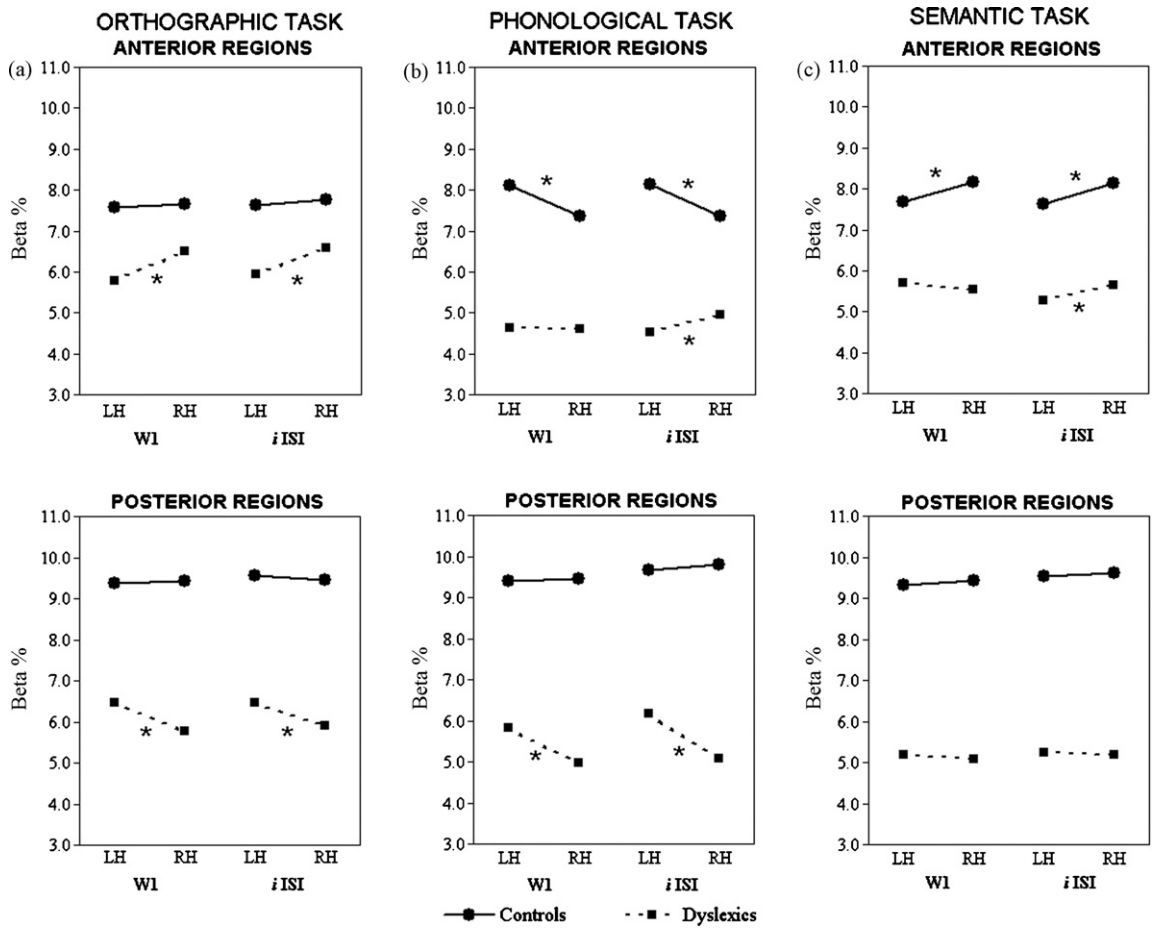

Fig. 3. Beta band (12.7–28.5 Hz) activity of controls (full line) and dyslexics (dashed line) compared during W1 and *i*ISI intervals in anterior (upper row) and posterior (lower row) regions for (a) Orthographic, (b) Phonological and (c) Semantic task. Beta activity normalized across 0.98–100 Hz spectral range. Asterisks: significant post hoc test results.

rhythm, a more clear-cut functional and classical index of cortical activation.

As a main finding, both EEG bands showed very similar patterns of activation, and were, therefore, to some extent functionally correlated. Focusing on theta rhythm, groups revealed different time courses of word processing across tasks: a sustained delayed response for impaired readers was clearly visible starting with the processing of the first word. In controls, the W1 interval was characterized by a significant increase in theta amplitude compared with both Baseline and later phases (Fig. 1)—a result in agreement with those of Spironelli et al. (2006). This increase has been explained to reflect the moment of maximum engagement of verbal working memory. In the present study, dyslexics reached the theta peak in the same W1 interval, but their peak of activation extended to the next *i*ISI interval—a result supporting the interpretation that, for this group, the normal phonological transcoding process is slowed and delayed. With respect to previous results (Spironelli et al., 2006), the present study adds further important information about the distribution of theta activity over the antero-posterior gradient: in fact, the five-way interaction revealed specific patterns of theta percentages for each task and group. During the Phonological task, controls showed clear-cut left-lateralized theta activation over anterior regions, but bilateral distribution of theta percentages on posterior sites. Instead, dyslexic children had the reversed pattern over anterior areas, i.e., right-lateralized theta activation and strong left posterior lateralization (Fig. 2b). In controls, the left frontal cortex, which includes Broca's area, probably represents the neurophysiological correlate of phonological information assembling (Burton, 2001; Burton et al., 2000). Dyslexics' inverted lateralization on anterior regions, therefore, suggests functional impairment of this main linguistic center. They also had greater left lateralization over posterior areas, whereas controls showed a bilateral posterior distribution of activity. At first glance, this result seems to indicate greater activation of regions important for grapheme–phoneme conversion, possibly for efficient compensatory activity. Instead, three lines of evidence point to this effect as a marker of impaired reading in dyslexics. First, behavioral measures support our interpretation of electrophysiological data: both verbal working memory measured by means of the digit span and reading speed measured through the MT reading test (Cornoldi and Colpo, 1998) were impaired compared with controls. Behavioral data (RTs and Error rates), collected during the experiment, also revealed worse performance in the clinical sample. Second, controls had different patterns of activity as a function of tasks, whereas dyslexic children had very similar patterns in the Orthographic and

Phonological tasks. In particular, their left lateralization over posterior regions, compared with bilateral activation in controls, may suggest that in impaired readers difficulties in the visual processing of graphemes which is reflected in the Orthographic task may also become apparent in the Phonological task. Third, the impaired activity of dyslexics' left frontal areas was specifically related to the Phonological task. In the present study, as in research on non-fluent aphasics (Angrilli et al., 2003; Bookheimer, 2002; Hagoort, 2005), Broca's area may play a central role in the organization of the whole linguistic network of the left hemisphere. The involvement of only a portion of this network (as in left posterior activation) in dyslexics, associated with disruption of the original integrated hierarchy within the network (in which Broca's area may induce phonological processes, and therefore, be more activated than posterior areas), provides a coherent picture of dyslexia. Our interpretation of dyslexics' left posterior lateralization as reflecting a dysfunctional cortical mechanism is in agreement with the neuroimaging literature on children and adults suffering from this disorder, which highlights failure of left posterior brain systems (Brunswick et al., 1999; Démonet et al., 2004; Helenius et al., 1999; Paulesu et al., 2001; Salmelin et al., 1996; Shaywitz, 1998; Shaywitz et al., 2002, 2003; Simos et al., 2000; Temple et al., 2001, 2003).

Additional information arose from the analysis of the relatively non-linguistic Orthographic task, in which simple visuo-perceptual matching was required. Indeed, although the cortical distribution of Orthographic and Semantic tasks may appear similar, behavioral data on children's performance revealed that the Semantic was significantly more difficult than the Orthographic task, suggesting a rather different process required to solve the two tasks. From an electrophysiological point of view, controls always had bilateral activation in the Orthographic task, showing that non-phonological (and relatively non-linguistic) processing was occurring, whereas dyslexics revealed a pattern similar to that revealed in the Phonological task. In fact, they showed significantly greater right anterior lateralization and strong posterior left lateralization (Fig. 2a). As already stressed, these findings suggest that dyslexics' left posterior peak of activation, elicited by Phonological and Orthographic (but not Semantic) tasks, reflects a processing block at the visuo-grapheme level of analysis, which cannot spread toward left anterior linguistic centers specializing in phonological integration.

As already mentioned, the beta band reveals a pattern of activity similar to that seen in the theta band: therefore, the same interpretation of lateralized patterns which has been offered for the theta band should be considered. This similarity between the activities in the two bands is in line with past studies which have found strong functional links between the generators of theta and beta rhythms, suggesting a direct connection between these two low- and high-frequency activities, particularly during working memory processes (Leung, 1992; Sarnthein et al., 1998, 2003; Slotnick et al., 2002). The theta rhythm has been related, particularly during linguistic learning processes, to the cortical activity controlled by subcortical structures located deep in the temporal lobe, at the level of the hippocampus (see, e.g., Leung, 1998; Tesche and Karhu, 2000; Vertes, 2005). Beta activity is more confined to the level of the superficial cortical layers, resulting in a typical index of desynchronization. For this reason, the beta EEG signal recorded from the scalp marks the activity essentially produced by highly confined superficial cortical activity, reflecting a direct measure of those regions effectively involved in these cognitive processes (Pantev et al., 1991; Tallon-Baudry and Bertrand, 1999). Thus, beta activity helps us to interpret the theta band as an effective index of complex cognitive processes implemented on the cortical surface. However, although functionally correlated, the two bands are not equivalent, as ANCOVA analyses highlighted the correlation between cortical beta topography and participants' average beta amplitude. Whereas the patterns of theta activity percentages were unaffected by correcting for absolute theta levels, the absolute level of beta activity turned out to affect the differences in the beta activity percentages that were reflected in the significant five-way interaction. This difference may be related to the different importance that these two EEG bands play in children relative to adults. In children, the theta band is well developed and has greater spectral density than the beta band (in our experiment beta activity was the sum of all activity within a 17-Hz range, vs. the theta band, which was the sum within only 4 Hz). The beta band activity, however, is not well developed in children, whereas in adults the relative contribution of beta spectral activity is reversed. Beta activity represents a much greater percentage and spectral density of EEG than the theta band (Anokhin et al., 1996). Thus, in the successful use of lateralized linguistic networks, children may activate relatively more cortical sites (covariation with groups' average beta amplitude) in an effort to fulfill the tasks.

In conclusion, in line with the literature on the phonological deficit theory (Ramus, 2004; Ramus et al., 2003; Shaywitz, 1998; Shaywitz et al., 2002, 2003; Shaywitz and Shaywitz, 2005; Temple et al., 2001), the present experiment confirms our hypothesis of a deficit in dyslexics of phonological activity which, relative to controls, is topographically inverted at anterior sites during the rhyming task. Our study allows further considerations: theta and beta EEG bands provide converging evidence that their amplitude reflects activation of cortical functional areas involved in language (task-dependent left lateralization) and differentiated across tasks in the control group, although using the same linguistic sample of words tends to elicit overlapping activity across tasks. The modulation of these bands along intervals points to their capability to separate different phases of word encoding in working memory, and the similar cortical distribution found in dyslexics for beta and theta activities is in line with literature on working memory and on the involvement of deep structures within the temporal lobe (theta band) controlling activity of linguistic cortical activity (theta and beta bands). However, the different statistical effects obtained from average participants' beta and theta amplitudes as covariates also points to the different neurophysiological properties of the two bands in the developing brain of children.

Given the difficulty of measuring language lateralization in children through Evoked Potentials (see Grossi et al., 2001) because lateralization processes are probably not yet completed, EEG theta and beta bands promise to be a very useful instrument for assessing task-related language lateralization and its impairment in developing participants.

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