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Foreign speech sound discrimination and associative word learning lead to a fast reconfiguration of resting-state networks



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ABSTRACT

Learning new words in an unfamiliar language is a complex endeavor that requires the orchestration of multiple perceptual and cognitive functions. Although the neural mechanisms governing word learning are becoming better understood, little is known about the predictive value of resting-state (RS) metrics for foreign word discrimination and word learning attainment. In addition, it is still unknown which of the multistep processes involved in word learning have the potential to rapidly reconfigure RS networks. To address these research questions, we used electroencephalography (EEG), measured forty participants, and examined scalp-based power spectra, source-based spectral density maps and functional connectivity metrics before (RS1), in between (RS2) and after (RS3) a series of tasks which are known to facilitate the acquisition of new words in a foreign language, namely word discrimination, word-referent mapping and semantic generalization. Power spectra at the scalp level consistently revealed a reconfiguration of RS networks as a function of foreign word discrimination (RS1 vs. RS2) and word learning (RS1 vs. RS3) tasks in the delta, lower and upper alpha, and upper beta frequency ranges. Otherwise, functional reconfigurations at the source level were restricted to the theta (spectral density maps) and to the lower and upper alpha frequency bands (spectral density maps and functional connectivity). Notably, scalp RS changes related to the word discrimination tasks (difference between RS2 and RS1) correlated with word discrimination abilities (upper alpha band) and semantic generalization performance (theta and upper alpha bands), whereas functional changes related to the word learning tasks (difference between RS3 and RS1) correlated with word discrimination scores (lower alpha band). Taken together, these results highlight that foreign speech sound discrimination and word learning have the potential to rapidly reconfigure RS networks at multiple functional scales.

1. Introduction

Word learning is not only an important aspect of children's cognitive development (Johnson and Munakata, 2005; Kuhl, 2004) but also manifested in everyday life situations in adults (Shtyrov, 2012). In fact, during conversations in either the mother tongue or a familiar foreign language, it is not uncommon to encounter unknown words or items with ambiguous meanings or referents. Learning the meaning of novel words is a multistep process that relies on different perceptual and cognitive functions, and involves word discrimination, word-referent mapping (i.e., the association of word forms with a meaning) and semantic generalization abilities. The discrimination and recognition of novel words relies on acoustic and phonetic analyses, auditory attention as well as on short-term and working memory functions (Dittinger et al., 2021; Elmer et al., 2021a; Kuhl, 2004). In fact, children characterized by language impairments often have deficits in processing sound signals, and this perceptual weakness has been proposed to be a possible factor contributing to non-word repetition dysfunctions which in turn are predictive of language processing difficulties (Bishop, 1997; Gathercole and Baddeley, 1990; Metsala, 1999). Such a relationship between speech sound discrimination skills and word or language learning abilities has, for example, also been documented in healthy adults (Basso et al., 2001; Elmer et al., 2021a; Lotto and de Groot, 1998; vanHell and Mahn, 1997)

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as well as in individuals suffering from aphasia (Breitenstein et al., 2004; Grossman and Carey, 1987; Kelly and Armstrong, 2009). Moreover, sensory-to-motor coupling mechanisms have been shown to be crucial for discriminating phonemes because associations between sensory inputs and motor representations enable to increase phonological sensitivity and benefit short-term phonological memory and working memory functions (Hickok and Poeppel, 2000; Reuterskiold-Wagner et al., 2005; Torgesen et al., 1999). This perspective is also compatible with previous studies showing that the phonological loop of working memory contributes to novel word learning (Gathercole and Baddeley, 1990). Nevertheless, the recruitment of sensory-to-motor coupling mechanisms varies as a function of task demands with greater engagement, for example, during same-different phonetic judgements compared to phoneme repetition detection tasks (Hickok and Poeppel, 2000; Meister et al., 2007). In a further crucial step, novel words have to be associated with a meaning by accessing semantic representations stored in the mental lexicon. Such word-referent mapping mechanisms rely on short-term and working memory resources (Smith et al., 1998) as well as on episodic memory functions which are needed for the initial storage and the consolidation of novel word forms in long-term memory (Nadel and Moscovitch, 1997). Moreover, once novel words have been acquired, semantic generalization abilities enable to associate the meaning of the novel words with semantically related items (Rodriguez-Fornells et al., 2009). Although these various processes are assumed to operate in combination, it is still unclear whether they are executed sequentially or in parallel (Dittinger et al., 2016).

In recent years, a growing number of electroencephalography (EEG) studies have attempted to non-invasively trace word learning processes in the human brain with a specific focus on the dynamics of brain activity (Bakker et al., 2015; Borovsky et al., 2010; Dittinger et al., 2019; Dobel et al., 2009a; Elmer et al., 2021a; Francois et al., 2017; Ramos-Escobar et al., 2021). These studies typically used associative word learning tasks relying on word-referent mapping, and consisting of acquiring the meaning of new speech sounds through pictorial representations (word-to-picture mapping) or already known lexical items (word-to-word mapping) in both children (Dittinger et al., 2017; Francois et al., 2017; Friedrich and Friederici, 2008; Junge et al., 2012) and adults (Bakker et al., 2015; Borovsky et al., 2010; Dittinger et al., 2016; Dobel et al., 2009b; Francois et al., 2017; Ramos-Escobar et al., 2021). Results originating from the evaluation of Event-Related Potentials (ERPs) during associative word learning tasks converged on two key findings, namely that novel word learning based on word-referent mapping mechanisms is a fast process (Borovsky et al., 2010; Carey, 1978), and that it is generally manifested in a shift of the N200 and N400 components from anterior to central-posterior scalp sites (Dittinger et al., 2016; Elmer et al., 2021a; Ramos-Escobar et al., 2021). Since different topographies imply the involvement of distinct neural populations, it has been proposed that the anterior N200 component that develops at the beginning of the learning phase potentially reflects phonetic discrimination, whereas the N400 component has been associated with the maintenance of novel information in short-term and working memory (Dittinger et al., 2016; Elmer et al., 2021a; Ramos-Escobar et al., 2021). In contrast, the learning-dependent displacement of ERP components along the anterior-posterior topographical axis might mirror the incorporation of new word forms into episodic and semantic memory (Dittinger et al., 2016; Elmer et al., 2021a; Ramos-Escobar et al., 2021).

While several studies have examined functional ERP changes using EEG during phonetic discrimination (Callan et al., 2003; Elmer et al., 2017; Raizada et al., 2010; Wong et al., 2007) and word learning tasks (Dittinger et al., 2019; Ramos-Escobar et al., 2021; Takashima et al., 2014, 2017), only a few focused on the relationships between RS brain activity and novel word or language learning (Emberson et al., 2015; Kliesch et al., 2022; Kliesch et al., 2021; Küssner et al., 2016; Prat et al., 2016; Prat et al., 2019). In this context, some EEG studies have tested the suitability of different RS metrics at baseline as predictors of foreign language learning attainment, and provided evidence for an explained vari-

ance in the range of 26-60 % (Emberson et al., 2015; Kliesch et al., 2022; Kliesch et al., 2021; Küssner et al., 2016; Prat et al., 2016; Prat et al., 2019). For example, Prat and colleagues (Prat et al., 2016) looked at associations between scalp RS power spectra at baseline and foreign language learning achievement in a sample of monolingual English speakers who were exposed for two month to French through an immersive virtual scenario. As a main result, results revealed that beta and lowgamma power at temporoparietal electrodes correlated with learning attainment, and the explained variance was about 60%. Also Kliesch and colleagues (Kliesch et al., 2021) made use of RS EEG measures to predict foreign language learning in a sample of older German adults who intensively practiced English for three weeks. Results showed that lower beta power across all pools of electrodes was related to language learning development, with an explained variance of about 33%. Interestingly, in a follow-up study with the same EEG data, Kliesch and colleagues (Kliesch et al., 2022) used a source-based approach to examine whether RS functional connectivity measures provide a suitable marker for foreign language attainment, and to what extent connectivity metrics are modulated by proficiency indices. Results indicated that functional connectivity in the beta band at baseline was predictive of linguistic complexity, fluency and accuracy, whereas connectivity in the alpha band was inversely related to the development of linguistic complexity. Furthermore, pre-post training comparisons showed an increase in beta connectivity that was paralleled by an improvement in foreign language accuracy and fluency.

Although these previous EEG studies paved the way toward a better understanding of RS brain activity related to foreign language learning, in the present study we measured forty participants and specifically focused on the predictive value of different RS metrics as well as on source-based network and functional connectivity reconfigurations (Kliesch et al., 2022) in association with a series of tasks which have previously been shown to facilitate the acquisition of new words, namely word discrimination, word-referent mapping and semantic generalization (Dittinger et al., 2016; Dittinger et al., 2017; Dittinger et al., 2019; Elmer et al., 2021a). With this purpose in mind, we first evaluated the sensitivity of RS scalp power spectra at baseline (RS1) in the delta (1-3 Hz), theta (4-7 Hz), lower alpha (8-10 Hz), upper alpha (10-12 Hz), lower beta (13-20 Hz) and upper beta (20-30 Hz) frequency range for predicting word discrimination skills, word-referent mapping and semantic generalization abilities using correlation analyses. In a next step, we separately tested whether short-term word discrimination and word learning led to a reconfiguration of RS neural networks. In particular, we compared scalp frequency spectra as well as three-dimensional source reconstructions of spectral density maps and functional connectivity metrics between the RS periods preceding and following the word discrimination (RS1 vs. RS2) and word learning tasks (RS2 vs. RS3). Furthermore, since RS2 and RS3 followed active tasks which are known to change brain activity in the default mode and the saliency network (Liang et al., 2016; Sidlauskaite et al., 2014), we additionally compared RS1 and RS3. This approach is particularly fruitful because the RS periods following the word discrimination and word learning tasks are tested against a common baseline reflecting a "default" RS condition. Finally, to test whether RS reconfigurations were related to word learning mechanisms per se, or mainly to the exposure to the new words of a foreign language, we additionally correlated the power difference between the different RS periods (RS2-RS1, RS3-RS2, RS3-RS1) with the three behavioral indices of the word discrimination and word learning tasks.

Based on previous EEG studies highlighting the predictive value of RS signals for foreign language learning (Kliesch et al., 2022; Kliesch et al., 2021; Küssner et al., 2016; Prat et al., 2016; Prat et al., 2019), we expected an association between scalp frequency spectra at baseline (RS1) and word discrimination, word-referent mapping and semantic generalization performance. Furthermore, we anticipated that both the word discrimination and word learning tasks are generally associated with changes in scalp power spectra as well as in sourcebased spectral density maps and functional connectivity patterns. Concerning the latter two source-based analyses, we hypothesized that word discrimination will mainly lead to functional changes in auditory and sensorimotor brain regions as well as in areas involved in shortterm and working memory (Callan et al., 2003; Raizada et al., 2010; Wong et al., 2007), whereas associative word learning was expected to additionally modulate brain regions involved in declarative memory (Breitenstein et al., 2005; Paulesu et al., 2009; Takashima et al., 2014, 2017). Finally, we predicted that the power difference between RS2 and RS1 correlates with word discrimination skills, whereas power differences between RS3 and RS2, or at least between RS3 and RS1, will be related to word-referent mapping and semantic generalization abilities.

2. Materials and methods

In the present study, we re-evaluated the EEG data of forty participants included in a previous work of our group (Elmer et al., 2021a) which aimed at tracking ERP dynamics during associative word learning, and at uncovering relationships between word discrimination skills and word-referent mapping abilities. However, here we conducted completely different analyses, and examined RS metrics as well as brainbehavior relationships instead of task-related ERPs. Furthermore, since part of the material used was the same as in the previous study, in some paragraphs we literally reiterated sections of our previous work (Elmer et al., 2021a). Also the description of the methods used for the source-based analyses was partially taken from previous studies of our group (Dittinger et al., 2018; Elmer et al., 2018).

2.1. Participants

From the forty subjects enrolled in the study, two had to be excluded from the analyses due to extensive EEG artefacts during the RS periods, resulting in a sample size of thirty-eight participants (mean age = 25.47 years, SD = 4.9 years). All individuals were consistently right-handed (Annett, 1970), native German speakers, and had an unremarkable audiological status in that all tested pure-tone frequencies (250-8000 Hz) could be heard below a threshold of 30 dB SPL (MAICO Diagnostic GmbH). None of the subjects was simultaneous or early bilingual or reported neurological or psychological complaints. The participants were paid for participation and gave informed written consent in accordance with the procedures of the local ethics committee (University of Zurich, No. 18.8.6) and the declaration of Helsinki.

2.2. Experimental procedure

During the experimental session, the forty participants were seated within a Faraday cage in a comfortable chair at about one meter from a computer screen. The auditory stimuli were presented through HiFi headphones (HD590, Sennheiser Electronic GmBH) at 70 dB sound pressure level. Visual and auditory stimuli presentation as well as the collection of behavioral responses was controlled by the Presentation software (Version 11.0, Neurobehavioral Systems). The experiment (Fig. 1) started with a baseline eyes-closed RS period of three minutes (RS1) which was followed, after a short instruction of a few minutes, by two successive word discrimination tasks consisting of detecting infrequent word repetitions (Figs. 1, 2A) and of judging whether word pairs were acoustically same or different (Figs. 1, 2B). The two word discrimination tasks were separated by a short pause which was required for instructing the participants. Afterwards, there was again a break of about 2 minutes, and RS2 was administered. After an additional pause of about 2 minutes, the participants completed two consecutive word learning tasks of increased complexity, namely a word-referent mapping task (Fig. 4A) and a semantic generalization task (Fig. 4B). The word-referent mapping task consisted of a learning condition where the participants had to acquire the meaning of new words through picture words associations as well as of a non-learning condition where pictures and words



Fig. 1. Overview of the experimental design and serial order of the tasks. The experiment started with a first resting-state (RS1) period (1) which was followed by two word discrimination tasks (2), namely word repetition detection (2A) and word discrimination (2B). In the repetition detection task the participants had to detect infrequent word repetitions (green box), whereas in the discrimination task they had to make same (green box) / different (red box) judgements. The word discrimination tasks were followed by a second resting-state (RS2) period (3), and afterwards the participants completed two word learning tasks (4), namely a word-referent mapping task (4A) and a semantic generalization task (4B). The word-referent mapping task (4A) consisted of a learning condition where the words were consistently associated with a specific picture (green box) as well as of a non-learning condition where words and pictures were inconsistently associated and learning was not possible (red box). Otherwise, in the following semantic generalization task (4B) the participants had to judge whether the pictures corresponded to the meaning of the words previously learned in the word-referent mapping task (green box, B), whether the pictures were semantically-related to the acquired meanings of the words (green box, D), whether the pictures did not correspond to the learned meanings (incongruent associations, green box, E) or whether the participants did not learn the meanings of the words (red boxes, A, C and F). After the two word learning tasks, the experiment ended with a third resting-state period (RS3).

were inconsistently associated, and hence word learning was not possible. The word-referent mapping task was followed, after a brief pause of about 2 minutes, by a forced-choice (FC) tasks that served to test learning performance. Next, after another break of about 2 minutes, the participants performed the semantic generalization task with the aim of testing semantic transfer of the learned words (see details below). Finally, after another break of about 2 minutes, the experiment ended with RS3. In the present study, we only evaluated the EEG data of the three RS periods. Moreover, we also integrated the behavioral data of the word discrimination and word learning tasks, and assessed brainbehavior relationships.

2.3. Experimental conditions

2.3.1. Word discrimination tasks

This experimental condition consisted of two successive parts, namely a word repetition detection and a word discrimination task. In the word repetition detection task, each of the 10 words was repeated once, and the participants had to identify word repetitions by pressing a response button (10 repetitions). The two pools of 10 Thai words (see Section 2.4 Auditory stimuli) were pseudo-randomly presented across participants. Furthermore, for both pools, each of the 10 words was presented 13 times, resulting in a total of 130 stimuli. Since the auditory stimuli differed in duration, stimulus-onset synchrony (SOA) was not jittered but kept constant at 1500 msec. The word repetition detection task had a duration of 3.25 min.

After a short break, the word repetition detection task was followed by the word discrimination task where the participants had to judge



Fig. 2. The average power spectra (μ V²) are shown separately for the frequency bands of interest as well as for the first (RS1), the second (RS2) and third (RS3) resting state-periods (three columns on the left). Furthermore, for each frequency band we computed spectral power differences by subtracting the first (RS1) from the second (RS2), the second (RS2) form the third (RS3), and the first (RS1) from the third (RS3) resting-state period (three columns of the right). The color scales depict spectral power for each condition and frequency band.

whether word pairs were acoustically same or different. Also in this experimental condition we used the same two pools of 10 Thai words. Each participant was exposed to 160 word pairs (80 same and 80 different) presented with an SOA of 2000 msec and a trial duration of 3500 msec, resulting in a total task time of 9.2. min. Each of the 10 words was presented 16 times, 8 in the same and 8 in the different condition. Furthermore, 25% of the different trials varied in duration, 25% in aspiration, 25% in pitch, and 25% in voicing. In particular, for trials containing changes in pitch, duration, or VOT, we used minimal pairs. Otherwise, since only the phoneme /Pha/ contained an aspiration cue, trials with changes in aspiration could also vary on another acoustic dimension. The behavioral data of the word repetition detection and word discrimination tasks were converted to d-prime scores (Stanislaw and Todorov, 1999), and these values were used for inference statistics and correlation analyses.

2.3.2. Word learning tasks

Word learning consisted of two successive tasks of increased complexity, namely a word-referent mapping task which was administered first, and a semantic generalization task. The first task only focused on word-referent mapping mechanisms, whereas in the second one word-referent mapping and word meaning generalization to new semantically-related pictures were intermixed. In the word-referent mapping task the participants were explicitly instructed to learn the meaning of the novel words based on picture-word associations. This task consisted of two successive blocks of 4.15 min each, and in each

block, half of the words of each pool (five) were consistently associated (learning condition) with variations of the same pictures (e.g., different pictures of a fork), whereas the other half was randomly coupled with different visual items (non-learning condition). The participants were not informed about the presence of a non-learning condition which was originally used to disentangle learning-specific and unspecific ERP manifestations along the anterior-posterior topographical axis (Elmer et al., 2021a). Furthermore, to exclude any influence of stimulus material on word-referent mapping, the words used in the learning and non-learning conditions were counterbalanced across participants. In particular, the words that in one version were consistently associated with the same pictures were presented with inconsistent ones across participants in the other version. Accordingly, for each of the two pools of stimuli, we created two different versions (Pool 1 Version 1: /ba1/, /ba:0/, /pa1/, /pa:0/, /p^ha:1/; Pool 1 Version 2: /ba:1/, /ba0/, /pa:1/, /pa0/, /p^ha:0/; Pool 2 Version 1: /ba1/, /ba:0/, /pa1/, /pa:0, /p^ha0/; Pool 2 Version 2: /ba:1/, /ba0/, /pa:1/, /pa0/, /p^ha1/).

In the word-referent mapping task, participants were exposed to 1 of the 10 pictures that was presented for 2000 msec and followed, 800 msec after picture presentation onset (SOA), by one of the words (trial duration = 2500 msec). Each of the two blocks consisted of 100 trials, with each word of the learning (five words) and non-learning (five words) conditions being presented 10 times in association with 10 variations of the same pictures (learning condition) or two variations of each of the five inconsistent pictures (non-learning condition). Immediately after the word-referent mapping task, performance was tested using a FC task. In the FC task, four pictures (two of the learning and two of the non-learning condition) were simultaneously presented side by side on the screen for 6500 msec (trial duration). Words were presented 800 msec after the onset of the pictures, and the participants had to select the picture that matched the meaning of the learned word by pressing the corresponding response button. Furthermore, the participants were instructed to press an additional response key when they thought that they did not learn the meaning of the presented word. This additional response option served as correct response for the words of the nonlearning condition. The FC task consisted of 30 trials, each of the five words of the learning and non-learning condition was presented 3 times, and each picture (including its variations) was presented 12 times. The test phase had a duration of 3.25 min.

The word-referent mapping task was followed, after a short delay, by the semantic generalization task. During the semantic generalization task, the participants had two decide via button press whether the pictures corresponded to the meaning of the words previously learned in the word-referent mapping task, whether the pictures were semantically-related to the acquired meaning of the words, whether the pictures did not correspond to the learned meaning (incongruent associations) or whether the participants did not learn the meaning of the words (FC task with 4 response alternatives). The semantic generalization task consisted of 4 blocks of 150 trials (i.e., N = 600 trials, 300 with the 5 words of the learning and 300 with the 5 words of the non-learning condition). In each block, the 5 Thai words of the learning condition were again consistently associated 5 times with a picture of the same item as in the previous word-referent mapping task (1/3 of)the trials), 5 times with semantically-related pictures to those previously learned (1/3 of the trials), and 5 times with semantically unrelated pictures (1/3 of the trials). Fifty percent of the incongruent pictures were taken from the pool used in the word-referent mapping task, whereas the other 50% were from the new pool of semantically-related pictures. Importantly, the pictures of the incongruent condition were selected pseudorandomly in order to avoid stimulus repetition effects and semantic relatedness between words and pictures. In addition to the 5 words of the learning condition, in the semantic generalization task we also presented the 5 words previously used in the non-learning condition. In particular, in each block, the 5 Thai words of the non-learning condition were associated 5 times with exactly the same pictures as in the word-referent mapping task, 5 times with pictures semantically related

to those presented in the word-referent mapping task, and 5 times with new pictures (i.e., 50% pictures used in the word-referent mapping task and 50% from the pool of semantically related pictures). In the semantic generalization task, the pictures were presented for 2000 msec and followed, 800 msec after picture presentation onset (SOA), by one of the words (trial duration = 4500 msec), resulting in a total duration of 45 minutes.

2.4. Auditory stimuli

The monosyllabic consonant-vowel Thai words used in the word discrimination and word learning tasks were taken from a corpus of twelve units (/ba0/, /ba:0/, /ba1/, /ba:1/, /pa0/, /pa:0/, /pa1/, /pa1/, /p^ha0/, /p^ha:0/, /p^ha1/, and /p^ha:1/) previously created by Dittinger et al. (Dittinger et al., 2016). In order to reproduce natural speech variability, four versions of each word were recorded by a native female Thai speaker. Sound pressure level was normalized across all items to a mean level of 70 dB using the Praat software (www.fon.hum.uva.nl/praat/).

The auditory stimuli consisted of natural Thai monosyllabic words with short (/ba1/, /pa1/, and /pha1/; 261 msec on average) and long vowel duration (/ba:1/, /pa:1/, /pha:1/, /ba:0/, /pa:0/, and /pha:0/; 531 msec on average), with low-tone (/ba1/, /pa1/, /pha1/, /ba:1/,/pa:1/, and /p^ha:1/; F0 = 175 Hz on average) and mid-tone vowels (/ba:0/, /pa:0/, and /pha:0/; F0 = 218 Hz on average) as well as with vowels varying in voicing (/ba1/, /ba:1/, and /ba:0/, VOT = -144msec vs. /pa1/, /pa:1/ and /pa:0/, VOT = 3 msec) and in aspiration contrasts (/pa1/, /pa:1/, and /pa:0/, VOT = 3 msec vs. /p^ha1/, /p^ha:1/, and $/p^{h}a:0/$, VOT = 77 msec). The monosyllabic Thai words presented in this experiment varied along four dimensions, duration, aspiration, pitch and voicing to reproduce the variability found in natural language. Based on pilot experiments, this corpus of 12 words was reduced to 10 to optimize the word learning curve. Since aspirated syllables exist in the German language, only two out of four of these stimuli were presented to each participant. However, to guarantee a certain degree of variability, we assigned the four aspirated words to two different pools of stimuli that consisted of the same eight words without aspiration but differed in two aspirated items, namely, /Pha1/ and /Pha0/ versus /Pha:1/ and /Pha:0/. These two pools of 10 stimuli were pseudorandomly counterbalanced across participants and used in the word discrimination and word learning tasks.

2.5. Visual stimuli of the word learning tasks

The word learning tasks consisted of two parts of increasing complexity. In the first part, the participants had to learn word-referent pairings (word-referent mapping task), whereas in the second one word-referent mapping and generalization of the meaning of the newly learned words to semantically-related pictures were intermixed (semantic generalization task, see below). Accordingly, for each of the 10 words used to examine word-referent mapping, we selected 10 similar variations of black and white pictures (e.g., 10 pictures of dogs). These pictures represented concrete living and nonliving objects with a high prototypicality for the following semantic categories: fruits (apple), animals (dog), weapons (pistol), office supplies (pencil), body parts (arm), clothes (trousers), vehicles (car), tools (hammer), buildings (house), kitchen equipment (fork), musical instruments (tambourine), and furniture (table). Furthermore, to test the generalization of the newly learned words to semantically-related pictures, for each prototypical item we selected 10 additional figural representations of the same semantic category, namely fruits (pineapple, banana, pear, strawberry, cherry, kiwi, orange, peach, prune and lemon), animals (elephant, donkey, giraffe, cat, leopard, lion, horse, sheep, tiger and zebra), weapons (dagger, gallows, gun, hand grenade, halberd, cannon, bow, saber, lance, and slingshot), office supplies (letter, paper-clip, folder, chalk, pen, rubber, typewriter, easel, stamp and compasses), body parts (eye, belly, leg, finger, foot, toe, hand, head, nose and ear), clothes (shirt, jacket, tie, coat,

pullover, skirt, shoe, sock, stockings and T-shirt), vehicles (bus, bicycle, airplane, helicopter, carriage, motorcycle, boat, tram, scooter and train), tools (drill, rasp, planer, screw nut, pin, saw, screw, screwdriver, clamp and tongs), buildings (castle, factory, garage, skyscraper, church, car park, barn, school, warehouse and hospital), kitchen equipment (bottle opener, burner, coffee machine, spoon, knife, rasp, sieve, plate, pot and lemon squeezer), musical instruments (flute, electric bass, violin, guitar, harp, clarinet, piano, harmonica, trumpet and Xylophone), and furniture (bench, bed, stool, commode, shelf, wardrobe, armchair, couch, chair and coffer). All black-and-white pictures were chosen from the Internet based on previous studies that evaluated objects' prototypicality of different semantic categories (Barbarotto et al., 2002; Maess et al., 2002), matched in size (width = 16 cm; height = 20 cm) and presented in the middle of a computer screen.

2.6. Behavioral data analyses

The behavioral data of the word repetition detection and word discrimination tasks were converted to d-prime scores (Stanislaw and Todorov, 1999), and these values were used for inference statistics and correlation analyses. In tasks with few response alternatives d-prime values are particularly fruitful because they enable to take into account response biases. Furthermore, the calculation of d-prime is appropriate in detection tasks in which not only correct and wrong responses are recorded but also misses and false alarms. The statistical analyses of the behavioral data of both the word-referent mapping and semantic generalization tasks focused on the percentage of correct responses instead of evaluating d-prime values because experimental conditions with several responses alternatives are relatively unaffected by biases (Green and Swets, 1966). In particular, for the word-referent mapping task we assessed the percentage of correct responses to the items of the learning as well as of the non-learning conditions. Otherwise, for the semantic generalization task we evaluated the percentage of correct responses to consistently associated word-picture pairs, to semanticallyrelated pictures, to incongruent pictures, and to associations that could not be learned.

2.7. Resting-state periods

As introduced above, in the present work we focused on three RS periods that were collected at the beginning of the experiment (baseline, RS1), after the two word discrimination tasks (RS2), and at the end of the two successive word learning tasks (RS3). RS data were acquired during 3 minutes of eyes-closed periods, and the participants were instructed to remain relaxed in a passive state and to not force any kinds of thoughts.

2.8. EEG data acquisition and preprocessing

The EEG was continuously recorded at a sampling rate of 1000 Hz with a high-pass filter of 0.1 Hz using an EEG amplifier (Brain Products, GmbH). Thirty-two active Ag/Cl electrodes were located at standard positions according to the international 10-20 system, the reference electrode was placed on the tip of the nose, and electrode impedance was kept below 10 kΩ. The EEG data were preprocessed using the Brain Vision Analyzer software (Version 2.1.0). In particular, the three-minute eyes-closed RS periods were re-referenced off-line to the averaged left and right mastoids and filtered with a bandpass filter of 0.1-30 Hz (slope of 48 dB/oct) and a Notch filter of 50 Hz. Furthermore, an independent component analysis was used to identify and correct vertical and horizontal ocular movements, and the remaining artifacts were automatically removed according to a maximum-minimum criterion of 100 μ V. For each participant, the three-minute RS periods were segmented into single epochs of 2 seconds, and subjected to topographical and sourcebased analyses.

Although in this study we did not focus on ERP analyses, we used the N100 ERP component elicited by all auditory stimuli of the word repetition detection task as a localizer to validate the three-dimensional eLORETA source reconstruction. Using this procedure, we wanted to provide evidence for a meaningful inverse solution with current-density maxima originating from the auditory cortex. Accordingly, for each participant single epochs time-locked to the onset of the auditory stimuli were extracted from -200 to 400 ms, baseline-corrected and averaged. In a next step, individual averages were assembled to compute a grand average waveform which was used for localizing the main sources associated with maximal N100 strength. Based on a vast electrophysiological literature, the purpose of the localizer was to corroborate previous finding showing a main origin of this ERP component from the auditory cortex (Liegeoischauvel et al., 1994; Picton et al., 1999; Scherg and Voncramon, 1986).

2.9. Scalp-based EEG frequency spectra

After having segmented the three RS periods into single epochs of 2 seconds with no overlap, the data were subjected to fast Fourier transforms (FFT) across the whole spectrum using a Hanning window with a length of 10%, resulting in a maximal FFT resolution of 0.488 Hz. Afterwards, the FFT-transformed segments were averaged for each participant and electrode to obtain power values (μV^2) for statistical analyses. In addition, power values at each electrode were averaged across the whole sample of participants to inspect the topographical distributions of the frequency bands of interest, namely delta (1-3 Hz), theta (4-7 Hz), lower alpha (8-10 Hz), upper alpha (10-12 Hz), lower beta (13-20 Hz) and upper beta (20-30 Hz). These specific frequency bands were selected according to previous EEG studies focusing on RS reconfigurations in association with learning (Kliesch et al., 2022; Kliesch et al., 2021; Küssner et al., 2016; Prat et al., 2016; Prat et al., 2019). Based on visual inspection of the grand averages of the selected frequency bands generally showing uniform power spectra distributions along the lateral-medial topographical axis, and due to additional maxima at anterior and posterior scalp sites (Fig. 2), we focused the FFT analyses on seven regions of interest (ROIs). An additional visual inspection of the individual data provided further confidence and indicated that the selection of the ROIs was adequate to capture the main effects. The ROIs were built by averaging the power spectra of the frequency bands of interest for each participant across several electrodes, resulting in anterior (Fp1 and Fp2), left (F7, Ft7, T7, Tp7 and P7), middle-left (F3, Fc3, C3, Cp3 and P3), middle (Fz, Fcz, Cz, Cpz and Pz), middle-right (F4, Fc4, C4, Cp4 and P4) right (F8, Ft8, T8, Tp8 and P8) and posterior (O1, Oz and O2) pools of electrodes.

2.10. Current-density source estimation of the N100 component: localizer

In a first step, we validated the eLORETA (http://www.uzh.ch/ keyinst/loreta.htm) source estimation approach using an auditory localizer. With this purpose in mind, we focused on the word repetition detection task, and estimated the main sources underlying the N100 ERP component which has consistently been shown to be generated in the auditory cortex (Liegeoischauvel et al., 1994; Picton et al., 1999; Scherg and Voncramon, 1986). Unlike conventional dipole fitting, the eLORETA approach does not require a-priori assumptions about the number and localization of dipoles. The eLORETA software calculates the three-dimensional distribution of electrically active neuronal generators in the brain as a current density value ($\mu A/mm^2$), and provides a solution for the inverse problem by assuming that the smoothest of all possible activity distributions is the most plausible one for explaining the data. The characteristic feature of this particular inverse solution approach is the low spatial resolution, which conserves the location of maximal activity, but with a certain degree of dispersion (Mulert et al., 2004).

The eLORETA toolbox relies on the Montreal Neurological Institute (MNI) 152 template (Mazziotta et al., 2001), with a three-dimensional

solution restricted to cortical gray matter, as determined by the probabilistic Talairach atlas (Lancaster et al., 2000). The intracranial volume is partitioned in 6239 voxels at 5 mm spatial resolution, and eLORETA images represent the electric activity at each voxel in the neuroanatomic MNI space as the magnitude of the estimated current density. Anatomical labels and Brodmann areas (BAs) are reported in the MNI space (Brett et al., 2002).

2.11. Voxel-by-voxel comparisons of spectral density maps in the source space

The eLORETA software package was also used to compare threedimensional whole-brain spectral density maps between RS1 and RS2, RS2 and RS3 as well as between RS1 and RS3. In particular, for all three RS we reconstructed spectral density maps corresponding to the delta, theta, lower alpha, upper alpha, lower beta and upper beta frequency bands, and compared them across RS conditions using voxel-byvoxel comparisons. All voxel-by-voxel analyses in the three-dimensional brain space were performed using a statistical non-parametric mapping (SnPM) procedure that enables to estimate the probability distribution by means of randomization statistics (5000 permutations) with correction for multiple comparisons (Nichols and Holmes, 2002). In particular, eLORETA images corresponding to the estimated neuronal generators of brain activity in the defined frequency bands were computed for each voxel (Frei et al., 2001), and compared between the RS periods using SnPM analyses. Due to the low spatial resolution of eLORETA, all results were reported using a rather conservative threshold of p < .01.

2.12. Functional connectivity analyses in the source space

In the present work, we additionally evaluated whole-brain lagged linear (coherence) and lagged non-linear (phase synchronization) functional connectivity (Pascual-Marqui, 2007) in the delta, theta, lower alpha, upper alpha, lower beta and upper beta frequency bands using the eLORETA toolbox. Lagged connectivity metrics are based on normalized Fourier transforms for each voxel, and corrected in order to represent the alignment between two signals after the instantaneous zerolag contribution has been excluded (Nolte et al., 2004; Stam and van Straaten, 2012). Such a correction is warranted because zero-lag connectivity in a given frequency band is normally due to non-physiological effects or intrinsic physical artifacts. The lagged connectivity metrics were calculated between all 84 bilateral BAs implemented in the eLORETA toolbox, and due to low spatial resolution, a method using a single voxel at the centroid of the ROIs was chosen (Dittinger et al., 2018; Elmer et al., 2018). For all analyses we used a conservative threshold of p < .01. Mathematical details on eLORETA functional connectivity algorithms can be found elsewhere (Pascual-Marqui et al., 2011).

2.13. Statistical analyses

The statistical analyses were conducted using the IBM SPSS Statistics 26 software package (SPSS, an IBM company, Armonk, New York, USA) and the eLORETA toolbox. In particular, the behavioral data and the scalp EEG metrics were evaluated by means of t-tests or omnibus analyses of variance (ANOVAs, repeated measures) with specific factors of interest for each model. Prior to the statistical analyses, all variables were tested for normal data distribution using the Kolmogorow-Smirnow test. Furthermore, for the sake of comparability between scalp and sourcebased EEG analyses, we performed separate ANOVAs to compare RS1 and RS2, RS2 and RS3 as well as RS1 and RS3. Such a procedure enables to isolate the general effects of word discrimination and word learning. Significant main and interaction effects were further inspected by post-hoc t-tests (two-tailed) or ANOVAs, and corrected for multiple comparisons using the Bonferroni procedure. Otherwise, brain-behavior relationships were assessed according to Pearson's r (two-tailed), and prior to correlation analyses, extreme outliers lying outside the range

of mean \pm 3 standard deviations were removed. Since the correlations were explorative in nature, we did not correct for multiple comparisons. However, to reduce the number of statistical tests and hence the falsepositive rates, we made a pre-selection of behavioral variables and only focused on three specific indices, namely d-prime values of the word discrimination task, percentage of correct responses to consistently associated picture-word pairs in the word-referent mapping task, and percentage of correct responses to semantically-related picture-word associations in the semantic generalization task. Moreover, to maximize interindividual variability for correlation analyses, we focused on the more difficult tasks which are less susceptible to ceiling effects. Accordingly, based on the behavioral results (see results section), d-prime indices of the word discrimination task were preferred over those of the word repetition detection task. Furthermore, since the learning curve is usually steeper at the beginning of the learning process and saturates with deliberate practice (Mirman et al., 2008), we prioritized the percentage of correct responses to consistently associated picture-word pairs of the word-referent mapping task instead of using the corresponding index of the semantic generalization task. The behavioral data of one participant in the word discrimination task and of one in the semantic generalization task were missing due to a technical problem with the response box.

3. Results

3.1. Behavioral data of the word discrimination tasks

A t-test for dependent sample (two-tailed) revealed significantly increased d-prime scores for the word repetition detection task (mean d-prime = 3.126) compared to the word discrimination task (mean d-prime = 1.925; $t_{(36)}$ = 5.090, p < .001, Cohen's d = 1.059, Fig. 3A). Hence, as expected, the word discrimination task was more demanding than the word repetition detection task.

3.2. Behavioral data of the word learning tasks

The behavioral data of the FC task that followed the word-referent mapping condition were examined using a t-test for dependent samples (two-tailed). Results showed that the percentage of correctly recognized words was higher in the learning (61.578 %) compared to the non-learning (34.035 %) condition ($t_{(37)} = 5.031$, p < .001, Cohen's d = 1.127, Fig. 3B). Nevertheless, a one-sample t-test against chance level (20%) showed that the participants were aware that they did not learn the items of the non-learning condition ($t_{(37)} = 3.074$, p = .004).

An univariate ANOVA was also performed to compare the percentage of correct responses between the four response alternatives of the semantic generalization task, namely same picture-word associations as in the word-referent mapping task, pictures that were semanticallyrelated to the acquired meanings of the words, pictures that did not correspond to the learned meanings (incongruent associations), and inconsistently associated items where the meaning of the words could not be inferred. Results revealed a main effect of response alternatives ($F_{(1,486,53,482)} = 6.452$, p = .007; partial eta² = .152, Fig. 3C), and post-hoc t-tests (Bonferroni-corrected p value for 6 tests = .0083) only reached significance for the comparison between the same pictureword associations as in the word-referent mapping task (% of correct responses = 78.432) and the condition with pictures that were semantically-related to the acquired meanings of the words (% of correct responses = 59.027, $t_{(36)}$ = 5.110, p < .001, Cohen's d = .904). Additional one-sample t-tests indicated a performance above chance level (25%, Bonferroni-corrected p value for 3 tests = .016) for pictures that were semantically-related to the acquired meanings of the words ($t_{(36)} = 8.162$, p < .001), pictures that did not correspond to the learned meanings (t_{(36)} = 11.990, p < .001, % of correct responses = 71.917), and for inconsistently associated items where the meaning of the words could not be inferred ($t_{(36)} = 13.172$, p < .001,



Fig. 3. Behavioral data of the word discrimination tasks (A), word-referent mapping task (B) and semantic generalization task (C). In the word discrimination tasks (A), the light brown violin plot indicates d-prime values of the word repetition detection condition, whereas the dark brown one depicts dprime values of word discrimination task. In the word-referent mapping task (B), the green violin plot refers to the percentage of correct responses to trials of the leaning condition, whereas the red one depicts the percentage of correct responses to items of the non-learning condition. In the semantic generalization task (C), the green violin plot shows the percentage of correct responses to the same picture-word associations as in the word-referent mapping task (learning condition), the blue violin plot refers to the percentage of correct responses to pictures that were semantically-related to the acquired meanings of the words, the orange violin plot depicts the percentage of correct responses to pictures that did not correspond to the learned meanings (incongruent associations), and the red violin plot indicates the percentage of correct responses to inconsistently associated items where the meaning of the words could not be inferred (nonlearning condition). *** p < .001; ** p < .01. The line in the middle of the distributions depicts the mean.

% of correct responses = 71.592). Accordingly, these results testify that learning performance was better for consistently associated items compared to semantically-related ones, but that new semantic associations could still be learned above chance level. Furthermore, the data indicate that in the semantic generalization task the participants were aware of incongruent picture-word associations as well as to not have learned inconsistently associated items.

3.3. Scalp-based EEG frequency spectra

We computed separate 2×7 ANOVAs (2 RS x 7 ROIs) to compare RS1 and RS2, RS2 and RS3 as well as RS1 and RS3 at the scalp level. Furthermore, we implemented separate ANOVAs for the six frequency bands of interest, and assessed brain-behavior correlations with the three variables of interest. In particular, the correlation analyses were computed with d-prime values (word discrimination task), percent-



Fig. 4. Significant correlations between scalpbased power spectra and behavior. A = negative correlation between power difference values in the theta frequency range obtained by subtracting the first (RS1) from the second (RS2) resting-state and the percentage of correctly recognized semantically-related pictures of the semantic generalization task. B = positive correlation between the power difference spectra in the upper alpha frequency-range obtained by subtracting the first (RS1) from the second (RS2) resting-state and d-prime values of the word discrimination task. C = negative

relationship between the power difference spectra in the upper alpha frequency-range obtained by subtracting the first (RS1) from the second (RS2) resting-state and the percentage of correctly recognized semantically-related items of the semantic generalization task. Outliers that were not included in the correlation analyses are marked by a red arrow.

age of correct responses to consistently associated picture-word pairs (word-referent mapping task) and percentage of correct responses to semantically-related picture-word associations (semantic generalization task). The statistical comparisons between RS1 and RS2 aimed at isolating frequency-band specific reconfigurations related to word discrimination, whereas the contrasts between RS2 and RS3 as well as between RS1 and RS3 were used to infer possible neural reconfigurations as a function of word learning. In all spectral power analyses, we reported the main effects of RS and ROI as well as the interaction between these two factors. Significant ROI x RS interactions were further inspected by means of post-hoc analyses using separate t-tests for dependent samples for the two RS conditions (Bonferroni-corrected p value for 21 tests = .0023), or by comparing the ROIs between the two conditions (Bonferroni-corrected p value for 7 tests = .00714). However, to simplify the presentation of the results, we abstained from decomposing main effects of ROI because they were not of interest for the purpose of the study. In addition, in the case of a significant main effect of RS, we also performed exploratory brain-behavior correlation analyses. Nevertheless, it is important to mention that in the case of a main effect of RS in the comparison between RS1 and RS3, the correlations between mean power of RS1 and behavior were not calculated as they were already reported when comparing RS1 and RS2.

3.3.1. First vs. second resting-state

Delta frequency band. The analysis of the delta frequency band (1-3 Hz) yielded main effects of ROI ($F_{(6, 222)} = 11.854$, p < .001; partial eta² = .243) and RS ($F_{(1, 37)}$ = 64.608, p < .001; partial eta² = .636) as well as a significant ROI x RS interaction effect ($F_{(1.518, 56.167)} = 3.606$, p = .045; partial eta² = .089). The main effect of RS was associated with increased delta power in RS1 (mean power = $8.210 \ \mu V^2$) compared to RS2 (mean power = $4.739 \,\mu V^2$). Separate t-tests for dependent samples for the two RS conditions used to inspect the significant ROI x RS interaction yielded a complex pattern of results. In fact, in RS1 posterior > left, middle-right, and right, middle-left > left and right, middle > left, middle-left, middle-right and right, and middle-right > left and right (all p values < .001). In contrast, in RS2 we revealed that anterior > left and right, posterior > left and right, middle-left > left and right, middle > left, middle-left, middle-right and right, and middle-right > left and right (all p values < .001, Fig. 2). Finally, due to the main effect of RS, we computed additional exploratory correlation analyses. In particular, we tested whether RS1 at baseline as well as the power difference between RS2 and RS1 were predictive of behavior (mean power across all ROIs). However, none of the correlations reached significance (all p values > .50).

Theta frequency band. The 2×7 ANOVA computed for the theta frequency band (4-7 Hz) yielded main effects of RS ($F_{(1, 37)} = 6.339$, p = .016; partial eta² = .146) and ROI ($F_{(6, 222)} = 29.254$, p < .001; partial eta² = .442) as well as a significant RS x ROI interaction ($F_{(2,46,91,014)} = 3.62$, p = .023; partial eta² = .089). The main effect of RS

was associated with increased theta power in RS1 (mean power = 1.404 μ V²) compared to RS2 (mean power = 1.223 μ V², Fig. 2). T-tests for dependent sampled used to capture the origin of the RS x ROI interaction by comparing the ROIs of the two RS reached significance for the posterior (t₍₃₇₎ = 2.848, p = .00713), left (t₍₃₇₎ = 4.279, p < .001) and right (t₍₃₇₎ = 3.996, p < .001) ROIs, with increased values for RS1 compared to RS2 (Fig. 2).

Due the main effect of RS, we correlated theta power of RS1 and the power difference between RS2 and RS1 with the three usual behavioral variables (mean power across all ROIs). The three correlations computed for RS1 did not reach significance (all p values > .85). However, the power difference between the two RS showed a negative association with the percentage of correctly identified semantically-related items of the semantic generalization task (r = -.444, p = .007, Fig. 4A, for all other correlations p > .68). This means that the more strongly theta power decreased from RS1 to RS2, the higher was the percentage of correct responses to semantically-related items.

Lower alpha frequency band. The 2×7 ANOVA for the lower alpha frequency band (8-10 Hz) revealed main effects of RS ($F_{(1, 37)} = 18.234$, p < .001; partial eta² = .330) and ROI ($F_{(6, 222)} = 16.726$, p < .001; partial eta² = .311) as well as an interaction between the two variables ($F_{(2.125, 78.643)} = 7.701$, p = .001; partial eta² = .172). The main effect of RS was associated with an overall increased lower alpha power in RS2 (mean power = 3.007 μ V²) compared to RS1 (mean power = .874 μ V²) RS (Fig. 2). Otherwise, according to post-hoc t-tests for dependent samples, all 7 ROIs significantly differed between the two conditions (all p values < .003, Fig. 2). Hence, the origin of the RS x ROI interaction remained unclear.

Nevertheless, based on the main effect of RS, also for the lower alpha band we correlated power of RS1 and well as the power difference between RS2 and RS1 with the three behavioral indices of interest (mean power across all ROIs). Lower alpha power in RS1 did not correlate with behavioral indices (all p values > .07), and also the correlations computed by subtracting power values between RS2 and RS1 did not reach significance (all p value > .093).

Upper alpha frequency band. The 2×7 ANOVA computed with power values corresponding to the upper alpha frequency band (10-12 Hz) yielded main effects of RS ($F_{(1, 37)} = 24.471$, p < .001; partial eta² = .398) and ROI ($F_{(6, 222)} = 14.885$, p < .001; partial eta² = .287) as well as a RS x ROI interaction ($F_{(6, 222)} = 12.301$, p < .001; partial eta² = .250). The main effect of RS originated form significantly increased upper alpha power in RS2 (mean power = 4.890 μ V²) compared to RS1 (mean power = .806 μ V², Fig. 2). The RS x ROI interaction was further analyzed using t-tests for dependent samples aiming at comparing the ROIs of the two RS. However, since all post-hoc comparisons reached significance (all p values < .003) the exact origin remains unknown (Fig. 2).

Also for the upper alpha band we correlated power of RS1 as well as the power difference value between RS2 and RS1 with the three preselected behavioral indices (mean power across all ROIs). None of the correlations computed for RS1 turned to be significant (all p value > .058). In contrast, the correlations calculated with the difference value of the two RS revealed a positive relationship with d-prime values of the word discrimination task (r = .355, p = .031, Fig. 4B) as well as a negative one with the percentage of correctly recognized semanticallyrelated items in the semantic generalization task (r = .334, p = .043, Fig. 4C; p value of the third correlation = .279).

Lower beta frequency band. The 2×7 ANOVA computed for the lower beta band (13-20 Hz) resulted in a main effect of ROI ($F_{(6, 222)} = 15.235$, p < .001; partial eta² = .292) as well as in a RS x ROI interaction ($F_{(2.216, 82.003)} = 4.553$, p = .011; partial eta² = .110). Post-hoc t-tests for dependent samples used to compare the ROIs of the two RS with the aim of capturing the origin of the interaction did not survive the correction for multiple comparisons. However, at an uncorrected p value, RS1 demonstrated increased lower beta power in the left ($t_{(37)} = 2.229$, p = .032) and right ($t_{(37)} = 2.163$, p = .037) ROIs (Fig. 2). Since the omnibus ANOVA did not reveal a main effect of RS, we abstained from computing additional correlation analyses.

Upper beta frequency band. The 2×7 ANOVA analysis for the upper beta band resulted in main effects of RS ($F_{(1, 37)} = 10.394$, p = .003; partial eta² = .219) and ROI ($F_{(2.428, 89.819)} = 4.073$, p = .014; partial eta² = .099) as well as in a RS x ROI interaction ($F_{(3.251, 120.275)} = 5.458$, p = .001; partial eta² = .129). The main effect of RS originated form overall increased power values in RS1 (mean power = .3104 μ V²) compared to RS2 (mean power = .1968 μ V², Fig. 2). T-tests for dependent samples used to decompose the RS x ROI interaction by comparing the ROIs of the two RS reached significance at the anterior ($t_{(37)} = 3.574$, p = .001), left ($t_{(37)} = 3.789$, p = .001) and right ($t_{(37)} = 3.815$, p = .001) ROI, with increased power values in RS1 compared to RS2 (Fig. 2). None of the correlations (mean power across all ROIs) computed with RS1 (all p values > .424) or with the power difference values between RS2 and RS1 (all p values > .350) reached significance.

3.3.2. Second vs. third resting-state

All 2×7 ANOVA analyses for the delta ($F_{(6, 222)} = 15.803$, p < .001; partial eta² = .299), theta ($F_{(6, 222)} = 31.543$, p < .001; partial eta² = .460), lower alpha ($F_{(6, 222)} = 13.443$, p < .001; partial eta² = .266), upper alpha ($F_{(6, 222)} = 14.481$, p < .001; partial eta² = .281), lower beta ($F_{(6, 222)} = 15.994$, p < .001; partial eta² = .302)

and upper beta ($F_{(6, 222)} = 7.339$, p < .001; partial eta² = .166) only revealed main effects of ROIs. Since these main effects were not of main interest for the study, their origins were not further inspected by posthoc comparisons.

3.3.3. First vs. third resting-state

Delta frequency band. The 2×7 ANOVA computed for the delta band (1-3 Hz) revealed main effects of RS ($F_{(1, 37)} = 25.549$, p < 001; partial eta² = .408) and ROI ($F_{(1.539, 56.933)}$ = 11.262, p < 001; partial eta² = .233) as well as a significant RS x ROI interaction $(F_{(1.721, 63.670)} = 3.925, p = .030; partial eta^2 = .096)$. The main effect of RS was associated with increased delta power in RS1 (mean power = $8.210 \,\mu\text{V}^2$) compared to RS3 (mean power = $5.342 \,\mu\text{V}^2$, Fig. 2). The significant RS x ROI interaction was further inspected using separate t-tests for dependent samples for the two RS conditions. This procedure revealed that in RS1 anterior > left and right, posterior > left, middleright and right, middle-left > left and right, middle > left, middle-left, middle-right and right, middle-right > left and right (all p values < .004). Otherwise, the same procedure applied to RS3 showed that anterior > left and right, posterior > left and right, middle-left > left and right, middle > left, middle-left and right, and middle-right > left and right (all p values < .001). Finally, due to the main effect of RS, we correlated the power difference between RS3 and RS1 (mean power across all ROIs) with the pre-selected behavioral indices. However, none of the correlations computed with the three behavioral variables reached significance (all p values > .50).

Theta frequency band. The 2×7 ANOVA computed for the theta band (4-7 Hz) yielded a main effect of ROI ($F_{(1.936, 71.624)} = 31.856$, p < 001; partial eta² = .463) as well as a RS x ROI interaction ($F_{(2.853, 105.559)} = 3.688$, p = .016; partial eta² = .091), whereas the main effect of RS did not reach significance ($F_{(1, 37)} = 3.092$, p = .087; partial eta² = .077). Post-hoc t-tests for dependent samples between the ROIs of the two RS with the aim of capturing the origin of the interaction reached significance for the posterior ($t_{(37)} = 2.937$, p = .006) and the left ROIs ($t_{(37)} = 3.290$, p = .002), with increased power in RS1 compared to RS3. Since the omnibus ANOVA did not reveal a main effect of RS, we abstained from computing additional correlation analyses. Tables 1 and 2

Lower alpha frequency band. The 2×7 ANOVA computed for the lower alpha band (8-10 Hz) revealed main effects of RS ($F_{(1, 37)} = 21.688$, p < .001; partial eta² = .370) and ROI ($F_{(2.596, 96.064)} = 17.529$, p < .001; partial eta² = .321) as well as a significant RS x ROI interaction

Table 1

Summary of the ANOVA results of the scalp-based power spectra analyses for the comparisons between the first (RS1) and the second (RS2) resting-state (RS) periods. For reasons of simplicity, the origins of the effects are only listed for the main effects of RS. ROI = region of interest.

Frequency	Contrast	Effects	F value	p value	Origin of the effects
Delta	RS1 vs. RS2	Main effect of RS	64.608	< .001	RS1 > RS2
Delta	RS1 vs. RS2	Main effect of ROI	11.854	< .001	
Delta	RS1 vs. RS2	RS x ROI	3.606	0.045	
Theta	RS1 vs. RS2	Main effect of RS	6.339	0.016	RS1 > RS2
Theta	RS1 vs. RS2	Main effect of ROI	29.254	< .001	
Theta	RS1 vs. RS2	RS x ROI	3.620	0.023	
Lower alpha	RS1 vs. RS2	Main effect of RS	18.234	< .001	RS2 > RS1
Lower alpha	RS1 vs. RS2	Main effect of ROI	16.726	< .001	
Lower alpha	RS1 vs. RS2	RS x ROI	7.701	0.001	
Upper alpha	RS1 vs. RS2	Main effect of RS	24.471	< .001	RS2 > RS1
Upper alpha	RS1 vs. RS2	Main effect of ROI	14.885	< .001	
Upper alpha	RS1 vs. RS2	RS x ROI	12.301	< .001	
Lower beta	RS1 vs. RS2	Main effect of ROI	15.235	< .001	
Lower beta	RS1 vs. RS2	RS x ROI	4.553	0.011	
Upper beta	RS1 vs. RS2	Main effect of RS	10.394	0.003	RS1 > RS2
Upper beta	RS1 vs. RS2	Main effect of ROI	4.073	0.014	
Upper beta	RS1 vs. RS2	RS x ROI	5.458	0.001	

Table 2

Summary of the ANOVA results of the scalp-based power spectra analyses for the comparisons between the first (RS1) and the third (RS3) resting-state (RS) periods. For reasons of simplicity, the origins of the effects are only listed for the main effects of RS. ROI = region of interest.

Frequency	Contrast	Effects	F value	p value	Origin of the effects
Delta	RS1 vs. RS3	Main effect of RS	25.549	< .001	RS1 > RS3
Delta	RS1 vs. RS3	Main effect of ROI	11.262	< .001	
Delta	RS1 vs. RS3	RS x ROI	3.925	0.030	
Theta	RS1 vs. RS3	Main effect of ROI	31.856	< .001	
Theta	RS1 vs. RS3	RS x ROI	3.688	0.016	
Lower alpha	RS1 vs. RS3	Main effect of RS	21.688	< .001	RS3 > RS1
Lower alpha	RS1 vs. RS3	Main effect of ROI	17.529	< .001	
Lower alpha	RS1 vs. RS3	RS x ROI	8.322	< .001	
Upper alpha	RS1 vs. RS3	Main effect of RS	27.770	< .001	RS3 > RS1
Upper alpha	RS1 vs. RS3	Main effect of ROI	16.040	< .001	
Upper alpha	RS1 vs. RS3	RS x ROI	13.581	< .001	
Lower beta	RS1 vs. RS3	Main effect of ROI	16.068	< .001	
Lower beta	RS1 vs. RS3	RS x ROI	5.375	0.003	
Upper beta	RS1 vs. RS3	Main effect of RS	6.033	0.019	RS1 > RS3
Upper beta	RS1 vs. RS3	Main effect of ROI	3.916	0.016	
Upper beta	RS1 vs. RS3	RS x ROI	6.081	< .001	

 $(F_{(2,210, 81,758)} = 8.322, p < .001; partial eta² = .184)$. The main effect of RS was associated with increased power in RS3 (mean power = 3.195 μV^2) compared to RS1 (mean power = 0.874 μV^2 , Fig. 2). Furthermore, separate t-tests for dependent samples for the two RS conditions were used to disentangle the RS x ROI interaction. Accordingly, in RS1 anterior > left and right, posterior > left, middle-left, middle-right and right, middle-left > left and right, middle > left, middle-left, middle-right and right, and middle-right > left and right (all p values < .001). Otherwise, in RS3 anterior > left and right, posterior > left, middle-right and right, middle-left > left and right, middle > left, middle-left, middle-right and right, and middle-right > left and right (all p values < .002). Finally, based on the main effect of RS, we additionally correlated the power difference between RS3 and RS1 with the three behavioral indices (mean power across all ROIs). According to this procedure, mean power difference between RS3 and RS1 positively correlated with d-prime values of the word discrimination task (r = .326, p = .049, Fig. 5, all other p value > .055).

Upper alpha frequency band. The 2×7 ANOVA computed for the upper alpha band (10-12 Hz) resulted in main effects of RS ($F_{(1, 37)} = 27.770$, p < .001; partial eta² = .429) and ROI ($F_{(1.440, 53.288)} = 16.040$, p < .001; partial eta² = .302) as well as in a significant RS x ROI interaction ($F_{(1.368, 50.634)} = 13.581$, p < .001; partial eta² = .269). The main effect of RS originated from increased power in RS3 (mean power = $5.531 \,\mu$ V²) compared to RS1 (mean power = $0.805 \,\mu$ V², Fig. 2). Separate t-tests for



Fig. 5. Significant correlations between scalp-based power spectra and behavior. Positive correlation between power difference values in the lower alpha frequency range obtained by subtracting the first (RS1) from the third (RS3) resting-state and d-prime values of the word discrimination task.

dependent samples for the two RS conditions were used to disentangle the RS x ROI interaction. The comparisons of RS1 showed that posterior > anterior, left, middle-left, middle, middle-right, and right, anterior > left and right, middle-left > left and right, middle > left, middle-left, middle-right and right, and middle-right > left and right (all p values < .001). In contrast, the analyses of RS3 revealed that posterior > anterior, left, middle-left, middle, middle-right and right, middle-left > left and right, middle > left, middle, middle-right and right, and middleright > left and right (all p values < .001). Based on the main effect of RS, we additionally correlated the power difference values between RS3 and RS1 with the three pre-selected behavioral indices (mean power across all ROIs). None of the correlations computed with the power difference values reached significance (all p values > .06).

Lower beta frequency band. The 2×7 ANOVA computed for the lower beta band (13-20 Hz) yielded a main effect of ROI ($F_{(2.405, 88.997)}$) = 16.068, p < .001; partial eta² = .303) as well as a significant RS x ROI interaction ($F_{(2.589, 95.781)}$) = 5.375, p = .003; partial eta² = .127). The interaction was further disentangled using separate t-tests for dependent samples for the two RS conditions. In RS1 the analyses revealed that posterior > left, middle-left, middle, middle-right, and right, middle-left > left and right, middle > left and right, and middle-right > left and right (all p values < .001). The same analyses of RS3 showed that anterior > left and right, posterior > left, middle-left, middle-right, and right, middle-left > left and right, middle > left, right and middle-right, and middle-right > left and right. Since the main effect of RS did not reach significance we did not compute additional correlations with the behavioral data.

Upper beta frequency band. The 2×7 ANOVA computed for the upper beta band (20-30 Hz) revealed significant main effects of RS ($F_{(1, 37)} = 6.033$, p = .019; partial eta² = .140) and ROI ($F_{(2.491, 92.160)} = 3.916$, p = .016; partial eta² = .096) as well as a RS x ROI interaction ($F_{(3.327, 123.095)} = 6.081$, p < .001; partial eta² = .141). The main effect of RS was associated with increased power in RS1 (mean power = 0.310 μ V²) compared to RS3 (mean power = 0.210 μ V², Fig. 2). Post-hoc t-tests for dependent samples between the ROIs of the two RS conditions with the aim of capturing the origin of the RS x ROI interaction reached significance at the anterior ($t_{(37)} = 3.238$, p = .003), left ($t_{(37)} = 3.203$, p = .003) and right ($t_{(37)} = 3.227$, p = .003) ROIs. Based on the main effect of RS, we performed additional correlation analyses between the mean power difference obtained by subtracting RS1 from RS3 and the three pre-selected behavioral variables. None of the three correlations reached significance (all p values > .50).

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3.4. Current-density source estimation of the N100 component: localizer

To validate the inverse-space solution of the eLORETA toolbox, we localized the maximal N100 amplitude elicited by all auditory stimuli of the word repetition detection task. Since this component is well known to be mainly generated by the auditory cortex (Liegeoischauvel et al., 1994; Picton et al., 1999; Scherg and Voncramon, 1986), we expected a corresponding source localization. In line with this assumption, we indeed found main sources in the auditory cortex with maxima in BA 42 (MNI coordinates, x = 60, y = -25, z = 10) and 22 (MNI coordinates, x = 65, y = -20, z = 0).

3.5. Voxel-by-voxel comparisons of spectral density maps and functional connectivity in the source space

3.5.1. First vs. second resting-state: spectral density maps

Separate voxel-by-voxel comparisons for the six frequency bands of interest (p < .01, corrected for multiple comparisons) between RS1 and RS2 only revealed significant results in the lower (Table 3 and Fig. 6A) and upper (Table 4 and Fig. 6B) alpha range. In particular, RS2 was associated with increased spectral density values in the proximity of occipital and parahippocampal regions, posterior cingulate cortex, insula, inferior parietal lobe and of the auditory cortex (Fig. 6).

Interestingly, and in line with previous neuroimaging studies that evaluated functional changes in association with phonetic discrimination training protocols (Callan et al., 2003; Raizada et al., 2010; Wong et al., 2007), the voxel-by-voxel analyses consistently indicated increased auditory cortex activity after foreign word discrimination in both the lower and upper alpha frequency bands (Fig. 6). Hence, to provide complementary information, for each of these two frequency bands as well as for RS1 and RS2, we extracted mean spectral density values from the bilateral auditory cortex (BA 41) and performed additional correlation analyses. In particular, we correlated the usual pre-selected behavioral indices with mean spectral density values of RS1, and tested possible associations between the same behavioral metrics and difference values obtained by subtracting spectral density of RS1 from RS2. The correlations computed with the data of the first RS period were not significant for either the lower (all p values > .13) or the upper alpha band (all p values > .23). However, for the correlations calculated with the difference values in the lower alpha band, we found a significant

positive relationship between auditory cortex modulation and d-prime indices of the word discrimination task (r = .387, p = .018, Fig. 6C, all other p values > .13; all p values in the upper alpha band > .055).

3.5.2. First vs. second resting-state: functional connectivity

The whole-brain source-based functional connectivity analyses reached significance in the theta, lower alpha and upper alpha frequency bands (Fig. 7), and generally showed an up- or down-regulation of RS networks as a function of word discrimination. In particular, RS1 was associated with increased lagged linear (Fig. 7A) and nonlinear (Fig. 7C) connectivity in the theta frequency range compared to RS2, whereas in the upper alpha frequency range the same connectivity metrics were overall higher in RS2 (Fig. 7B and 7E). Also the analysis in the lower alpha band yielded increased nonlinear connectivity in RS2 compared to RS1 (Fig. 7D). Based on the high number of significant connections, and due to the generally low spatial resolution of source-based approaches, the functional connectivity results are reported on a gross anatomical scale with no claim to anatomical accuracy.

The increased connectivity patterns in the theta frequency band during RS1 were mainly restricted to connections between bilateral visual and posterior cingulate areas and ventral-anterior temporal and parahippocampal brain regions. In contrast, increased upper alpha linear and nonlinear connectivity in RS2 compared to RS1 was principally found between visual areas and ventral-anterior temporal and parahippocampal brain regions, between visual areas and inferior and superior parietal lobe structures, between the parietal and the frontal lobe, between the inferior parietal lobe and the anterior cingulate cortex as well as between the parietal lobe and anterior temporal lobe regions. Finally, the evaluation of lagged nonlinear connectivity in the lower alpha frequency band also revealed a single significant connection between the left supramarginal gyrus (BA 40) and the right anterior cingulate (BA 25) that was increased after word discrimination (RS2) compared to baseline (RS1).

3.5.3. Second vs. third resting-state: spectral density maps and functional connectivity

In line with the results of the scalp EEG data, for all frequency bands examined none of the spectral density maps or functional connectivity metrics reached significance, not even at a less conservative threshold of p < .05.

Table 3

Significant results of the voxel-by-voxel comparisons of spectral density maps in the lower alpha (8-10 Hz) frequency range for the contrast first (RS1) vs. second (RS2) resting-state. Due to the low spatial resolution of eLORETA, only the maximal supra-threshold voxel of each Brodmann area is listed. p < .01, corrected for multiple comparisons.

MNI coordinates			Brodmann area Brain lobe Brain structure		Brain structure	Log of F-ratio
x	Y	Z				
15	-45	0	30	Limbic	Parahippocampal gyrus	-2.04
10	-45	5	29	Limbic	Posterior cingulate	-2.03
20	-45	-5	19	Limbic	Parahippocampal gyrus	-2.03
20	-55	0	18	Occipital	Lingual gyrus	-2.01
15	-35	0	27	Limbic	Parahippocampal gyrus	-2.01
20	-40	-10	36	Limbic	Parahippocampal gyrus	-2.01
25	-45	-10	37	Limbic	Parahippocampal gyrus	-2.00
20	-35	-10	35	Limbic	Parahippocampal gyrus	-1.99
10	-55	15	23	Limbic	Posterior cingulate	-1.99
20	-65	15	31	Limbic	Posterior cingulate	-1.95
20	-30	-10	28	Limbic	Parahippocampal gyrus	-1.95
30	-40	-20	20	Temporal	Fusiform gyrus	-1.92
20	-75	10	17	Occipital	Cuneus	-1.88
30	-35	20	13	Sub-lobar	Insula	-1.81
35	-35	15	41	Temporal	Superior temporal gyrus	-1.75
35	-60	25	39	Temporal	Superior temporal gyrus	-1.74
-35	-55	20	22	Temporal	Superior temporal gyrus	-1.71
20	-65	30	7	Parietal	Precuneus	-1.64
15	-10	-20	34	Limbic	Parahippocampal gyrus	-1.60
40	-50	35	40	Parietal	Supramarginal gyrus	-1.53
0	0	-5	25	Limbic	Anterior cingulate	-1.43



Fig. 6. The significant results of the voxel-by-voxel t-tests computed with the eLORETA software package for the lower (A) and upper (B) alpha band are shown superimposed on a three-dimensional Van Essen template. The blue colors indicate lower spectral density values during the first (RS1) compared to the second (RS2) resting-state. First column = lateral view of the left hemisphere, second column = later view of the right hemisphere, third column = medial view of the left hemisphere, fourth column = medial view of the right hemisphere. C = significant positive correlation between spectral density difference values in the lower alpha frequency band extracted from the bilateral auditory cortex (RS2 minus RS1) and d-prime values of the word discrimination task. D = Nonsignificant positive correlation between spectral density difference values in the upper alpha frequency band extracted from the bilateral auditory cortex and d-prime values of the word discrimination task.

3.5.4. First vs. third resting-state: spectral density maps

Separate voxel-by-voxel comparisons for the six frequency bands of interest (p < .01, corrected for multiple comparisons) between RS1 and RS3 yielded similar results as those found for the comparison between RS1 and RS2. In particular, RS1 was associated with smaller current-density values in the lower and upper alpha frequency bands compared to RS3 in occipital and parahippocampal regions, in the posterior cingulate cortex, in the insula, in the inferior parietal lobe and in the auditory cortex (Table 5).

3.5.5. First vs. third resting-state: functional connectivity

The source-based analyses consistently revealed significant lagged linear and nonlinear connectivity differences between RS1 and RS3 in the theta, lower alpha and upper alpha frequency ranges (Fig. 8). RS1 was associated with increased lagged linear and nonlinear connectivity in the theta frequency range compared to RS3 (Fig. 8A and D), whereas RS3 was characterized by increased linear and nonlinear connectivity in the lower (Fig. 8B and E) and upper (Fig. 8C and F) alpha range. Increased linear and nonlinear connectivity in the theta fre-

Table 4

Significant results of the voxel-by-voxel comparisons of spectral density maps in the upper alpha (10-12 Hz) frequency range for the contrast first (RS1) vs. second (RS2) resting-state. Due to the low spatial resolution of eLORETA, only the maximal supra-threshold voxel of each Brodmann area is listed. p < .01, corrected for multiple comparisons.

MNI coordinates		Brodmann area	Brain lobe	Brain lobe Brain structure		
Х	Y	Z				
10	-45	5	29	Limbic	Posterior cingulate	-2.11
10	-45	0	30	Limbic	Parahippocampal gyrus	-2.11
15	-50	0	19	Occipital	Lingual gyrus	-2.09
10	-35	0	27	Limbic	Parahippocampal gyrus	-2.08
15	-55	0	18	Occipital	Lingual gyrus	-2.08
20	-40	-10	36	Limbic	Parahippocampal gyrus	-2.06
10	-55	15	23	Limbic	Posterior cingulate	-2.05
20	-35	-10	35	Limbic	Parahippocampal gyrus	-2.04
25	-45	-10	37	Limbic	Parahippocampal gyrus	-2.04
20	-65	15	31	Limbic	Posterior cingulate	-2.01
20	-30	-10	28	Limbic	Parahippocampal gyrus	-2.00
20	-75	10	17	Occipital	Cuneus	-1.98
30	-40	-20	20	Temporal	Fusiform gyrus	-1.95
-30	-60	25	39	Temporal	Sub-gyral	-1.80
30	-35	20	13	Sub-lobar	Insula	-1.77
20	-65	30	7	Parietal	Precuneus	-1.76
-35	-55	20	22	Temporal	Superior temporal gyrus	-1.72
35	-35	15	41	Temporal	Superior temporal gyrus	-1.68
15	-10	-20	34	Limbic	Parahippocampal gyrus	-1.63
50	-60	45	40	Parietal	Inferior parietal lobule	-1.60
0	0	-5	25	Limbic	Anterior cingulate	-1.48
45	-35	55	2	Parietal	Postcentral gyrus	-1.47
40	-35	65	3	Parietal	Postcentral gyrus	-1.46
40	-30	65	4	Frontal	Precentral gyrus	-1.45
45	-30	60	1	Parietal	Postcentral gyrus	-1.44

Table 5

Significant results of the voxel-by-voxel comparisons of spectral density maps in the lower (8-10 Hz) and upper (10-12 Hz) alpha frequency range for the contrast first (RS1) vs. third (RS3) resting-state. Due to the low spatial resolution of eLORETA, only the maximal supra-threshold voxel of each Brodmann area is listed. p < .01, corrected for multiple comparisons.

Frequency band	MNI coordinates		Brodmann area	Brain lobe	Brain structure	Log of F-ratio	
	х	Y	Z				
Lower alpha	15	-45	0	30	Limbic	Parahippocampal gyrus	-2.14
	20	-45	-5	19	Limbic	Parahippocampal gyrus	-2.14
	10	-45	5	29	Limbic	Posterior cingulate	-2.13
	15	-35	0	27	Limbic	Parahippocampal gyrus	-2.12
	20	-40	-10	36	Limbic	Parahippocampal gyrus	-2.12
	20	-55	0	18	Occipital	Lingual gyrus	-2.12
	25	-45	-10	37	Limbic	Parahippocampal gyrus	-2.12
	20	-35	-10	35	Limbic	Parahippocampal gyrus	-2.10
	10	-55	15	23	Limbic	Posterior cingulate	-2.07
	20	-30	-10	28	Limbic	Parahippocampal gyrus	-2.06
	20	-65	15	31	Limbic	Posterior cingulate	-2.04
	30	-40	-20	20	Temporal	Fusiform gyrus	-2.03
	20	-75	10	17	Occipital	Cuneus	-1.99
	30	-35	20	13	Sub-lobar	Insula	-1.92
	35	-35	15	41	Temporal	Superior temporal gyrus	-1.85
	35	-60	25	39	Temporal	Superior temporal gyrus	-1.82
	-35	-55	20	22	Temporal	Superior temporal gyrus	-1.76
	15	-10	-20	34	Limbic	Parahippocampal gyrus	-1.71
	20	-65	30	7	Parietal	Precuneus	-1.70
Upper alpha	10	-45	5	29	Limbic	Posterior cingulate	-2.18
	15	-45	0	30	Limbic	Parahippocampal gyrus	-2.18
	15	-45	-5	19	Occipital	Lingual gyrus	-2.170
	10	-35	0	27	Limbic	Parahippocampal gyrus	-2.170
	15	-55	0	18	Occipital	Lingual gyrus	-2.16
	20	-40	-10	36	Limbic	Parahippocampal gyrus	-2.15
	10	-55	15	23	Limbic	Posterior cingulate	-2.13
	20	-35	-10	35	Limbic	Parahippocampal gyrus	-2.13
	25	-45	-10	37	Limbic	Parahippocampal gyrus	-2.12
	20	-65	15	31	Limbic	Posterior cingulate	-2.10
	20	-30	-10	28	Limbic	Parahippocampal gyrus	-2.09
	20	-75	10	17	Occipital	Cuneus	-2.07
	30	-40	-20	20	Temporal	Fusiform gyrus	-2.03
	20	-65	30	7	Parietal	Precuneus	-1.86
	35	-80	30	39	Temporal	Superior occipital gyrus	-1.86
	30	-35	20	13	Sub-lobar	Insula	-1.85
	35	-35	15	41	Temporal	Superior temporal gyrus	-1.76
	-35	-55	20	22	Temporal	Superior temporal gyrus	-1.74
	15	-10	-20	34	Limbic	Parahippocampal gyrus	-1.74
	50	-60	45	40	Parietal	Inferior parietal lobule	-1.66
	0	0	-5	25	Limbic	Anterior cingulate	-1.63

quency range during RS1 was mainly observed between visual areas, the posterior cingulate cortex, the ventral-anterior part of the temporal lobe and parahippocampal regions. Otherwise, increased lagged linear connectivity in RS3 compared to RS1 in the lower alpha frequency range was reflected by a complex pattern of connections between the posterior cingulate cortex / parietal regions and bilateral medial temporal areas, between bilateral inferior parietal areas, as well as between temporal and orbitofrontal regions. In contrast, increased lagged nonlinear connectivity in RS3 in the lower alpha frequency band was restricted to connections between bilateral inferior parietal and posterior temporal regions. Furthermore, increased lagged linear connectivity in the upper alpha frequency range during RS3 included a vast network of connections between visual, parietal, posterior cingulate, medial-lateral temporal and frontal areas. Finally, increased lagged nonlinear connectivity in the upper alpha frequency band in RS3 included connections between the posterior cingulate cortex, inferior parietal areas, visual regions, and medial-lateral temporal areas.

4. Discussion

4.1. General discussion

In the present EEG study, we examined associations between scalp power spectra, word discrimination abilities and word learning skills, and tested possible task-related RS reconfigurations in multiple frequency bands. Furthermore, we included source-based analyses, and evaluated whole-brain spectral density and functional connectivity changes. Obviously, although we used an auditory localizer to verify the reliability of eLORETA source estimates, the data cannot be interpreted in an fMRI-like manner, and should therefore not be over-interpreted. Nevertheless, such an RS-based approach bears the advantage of monitoring functional reorganization processes which are related to specific tasks, and benefit the consolidation of learned features through the regulation of information flow in the brain (van den Heuvel et al., 2008). In the present study, we expected (1) to find relationships between scalp frequency spectra at baseline (RS1) and word discrimination, word-referent mapping and semantic generalization performance. Furthermore, (2) we predicted that the word discrimination as well as the word learning tasks would be associated with changes in scalp power spectra as well as in source-based spectral density maps and functional connectivity metrics. Concerning the latter two source-based analyses, (3) we postulated that word discrimination will be associated with functional changes in auditory and sensorimotor brain regions as well as in areas involved in short-term and working memory (Callan et al., 2003; Raizada et al., 2010; Wong et al., 2007), whereas word learning should also modulate brain activity in regions supporting declarative memory (Breitenstein et al., 2005; Paulesu et al., 2009; Takashima et al., 2014, 2017). Finally, (4) we anticipated that the power difference between



Fig. 7. The significant eLORETA-based linear (A and B) and nonlinear (C, D and E) connectivity results are shown superimposed on a three-dimensional Van Essen template. The blue colors indicate increased connectivity in the second (RS2) compared to the first (RS1) resting-state, whereas red colors depict increased connectivity values in the first (RS1) resting-state compared to the second one (RS2). First column = lateral view of the left hemisphere, second column = medial view of the left hemisphere, third column = lateral view of the right hemisphere, fourth column = medial view of the right hemisphere, fifth column = bottom view.



Fig. 8. The significant eLORETA-based linear (A, B and C) and nonlinear (D, E and F) connectivity results for the contrast between the first (RS1) and the third (RS3) resting-states are shown superimposed on a three-dimensional Van Essen template. The blue colors indicate increased connectivity in the third (RS3) compared to the first (RS1) resting-state, whereas red colors depict increased connectivity values in the first (RS1) resting-state compared to the third one (RS3). First column = lateral view of the left hemisphere, second column = medial view of the left hemisphere, fifth column = bottom view.

RS2 and RS1 will correlate with word discrimination skills, whereas power differences between RS3 and RS2, or between RS3 and RS1, will be associated with word-referent mapping and semantic generalization abilities.

Results showed that spectral-density changes (difference between RS2 and RS1) in the bilateral auditory cortex correlated with word discrimination abilities, and that both the word discrimination (RS1 vs. RS2) and word learning (RS1 vs. RS3) tasks were associated with functional changes in RS networks at multiple scales. However, this was only the case when RS2 and RS3 were compared to a common baseline reflecting a "default" RS condition (RS1) which was not influenced by a previous experimental condition. Hence, it is plausible that the contrast RS2 vs. RS3 did not yield significant outcomes because RS2 was influenced by the previous word discrimination tasks (Liang et al., 2016; Sidlauskaite et al., 2014). Furthermore, correlation analyses computed with the difference values between RS2 and RS1 revealed several relationships between RS changes, word discrimination and semantic generalization performance. In particular, theta and upper alpha power changes were negatively correlated with semantic generalization, and upper alpha modulations were predictive of word discrimination abilities. Finally, correlation analyses additionally brought to light a positive association between lower alpha power values obtained by subtracting RS1 from RS3 and word discrimination skills. Taken together, these results emphasize that learning to discriminate foreign speech sounds as well as word learning have the potential to fast reconfigure RS networks. In the next sections, all results will be discussed in a more comprehensive manner.

4.2. Behavioral data

The behavioral data indicated that the participants generally performed better on the word repetition detection than on the word discrimination task, leading to suggest that the latter was more difficult. Hence, the second metric was preferentially used for correlation analyses. Even though in both experimental conditions the participants had principally to distinguish between equal and unequal stimulus attributes in order to solve the task, at least three interpretations may account for the asymmetric processing costs. The first argument is that the word repetition detection and the word discrimination tasks relied on different attentional functions (Oken et al., 2006). In fact, the former task consisted of detecting target words which were sporadically presented over time with a low probability of occurrence. In contrast, in the latter experimental condition the target frequency was much higher because subjects had to judge on a trial-to-trial basis whether word pairs were same or different. Accordingly, we might speculate that the word repetition detection task more strongly loaded on vigilance, whereas the word discrimination task was mainly rooted in sustained attention functions (Oken et al., 2006). The second interpretation is related to task completion time which was much longer for the word discrimination compared to the word repetition detection task. Hence, it is truly possible that the longer task duration had a negative influence on motivational factors or general attentional capacities. The third aspect that should be considered is that the word discrimination task placed additional demands on sensory-to-motor coupling mechanisms, which in turn required more extensive control and monitoring mechanisms and rendered the task more difficult (Torgesen et al., 1999).

The analysis of the behavioral data of the word-referent mapping condition showed that the participants were better at correctly recognizing the words of the learning compared to those of the non-learning condition. However, since the participants were not explicitly informed about the presence of a non-learning condition, this result is not at all surprising. Furthermore, as testified by a t-test against change level, the participants were aware that they failed to learn the meaning of some words, which may possibly have served as a motivating factor for the subsequent semantic generalization task. Otherwise, in the semantic generalization task we examined the percentage of correct responses to the same picture-word associations as in the word-referent mapping task, to pictures that were semantically-related to the acquired meanings of the words, to pictures that did not correspond to the learned meanings (incongruent associations), and to inconsistently associated items where the meaning of the words could not be inferred. According to this procedure, we found a significant difference between trials with same picture-word associations as in the word-referent mapping task and the ones with pictures that were semantically-related to the acquired meanings of the words, whereas the other contrasts failed to reach significance. Nevertheless, the percentage of correct responses differed from chance level, indicating that the participants were able to generalize the meaning of the new words to semantically-related concepts, and that they were aware to not have learned the inconsistently associated items.

Repetition is an important component of learning that enables to consolidate memory traces in declarative memory systems (Axelsson and Horst, 2014; Schwab and Lew-Williams, 2016). Hence, it is not astonishing that performance was better for consistently associated items compared to semantically-related ones, and that incongruent associations were at the higher end of the achievement spectrum. It is also important to denote that the inconsistently associated trials were associated with a relatively high level of performance that was even more pronounced (\sim 70 %) than in the previous word-referent mapping task (\sim 35 %, Fig. 3). This may possibly indicate that in the course of the learning process the participants became more and more aware of the experimental manipulation.

4.3. Resting-state reconfigurations

In line with our hypotheses, we consistently revealed scalp power spectra changes as a function of the word discrimination (RS1 vs. RS2) and word learning (RS1 vs. RS3) tasks in the delta, lower alpha, upper alpha and upper beta frequency bands. In particular, delta and upper beta power was increased in RS1 compared to RS2 and RS3, whereas lower and upper alpha power was more pronounced in RS2 and RS3 compared to RS1. Furthermore, the comparison between RS1 and RS2 also indicated functional modulations in the theta frequency range, with higher power in RS1.

4.3.1. Delta frequency band

The precise role of delta oscillations in phonetic discrimination and word learning remains elusive. Nevertheless, this frequency band has been shown to modulate cortical excitability in response to speech stimuli (Kayser et al., 2015; Lakatos et al., 2008; Meyer, 2018; Park et al., 2015), to align with the envelope of the speech signal (Doelling et al., 2014; Meyer, 2018), and to be relevant for the extraction of prosodic information (Ghitza et al., 2013; Giraud and Poeppel, 2012; Meyer, 2018; Soltesz et al., 2013). Furthermore, influential models of speech and language processing have proposed that delta as well as theta oscillations contribute to the parsing of acoustic information into segmental, phonological and syllabic units (Ghitza et al., 2013; Giraud and Poeppel, 2012; Poeppel, 2003). A reduction in the delta frequency band has also been related to encoding and retrieval processes (Van Strien et al., 2005), and to inhibitory mechanisms which are necessary for down-regulating task-irrelevant neural networks (Harmony, 2013).

Based on our data, delta power significantly decreased from RS1 to RS2 as well as from RS1 to RS3. However, since neither this change nor delta power at baseline was related to behavior, the physiological significance of this effect remains speculative. Also the source-based analyses did not provide any additional information that would have been useful to interpret the observed delta power modulations as a function of word discrimination and word learning. For these reasons, we speculate that the task-related changes we noticed in the delta band might possibly reflect neural adaptation induced by the repeated presentation of the words (Besson et al., 1992; Radeau et al., 1998), a fine-tuning of a neural oscillator involved in processing phonetic information (Batterink and Paller, 2017, 2019; Elmer et al., 2021b), or even the construction of phonological memory traces for the Thai words (Di Liberto et al., 2015; Soltesz et al., 2013).

4.3.2. Theta frequency band

The comparison of RS1 and RS2 revealed a down-regulation of theta power after the word discrimination tasks. Although the functional significance of neural oscillations is difficult to deduce, particularly when considered decoupled from physical stimulation, the theta frequency band has been repeatedly proposed to play a pivotal role in declarative memory formation and retrieval (Bastiaansen and Hagoort, 2003; Kragel et al., 2020). Basically, theta oscillations have been associated with the encoding of novel information in the hippocampal-entorhinal memory system as well as with consolidation processes which are mediated by interactions between the hippocampal system and the neocortex (Bastiaansen and Hagoort, 2003; Kragel et al., 2020). Theta band activity has also been shown to support semantic retrieval processes (Bastiaansen et al., 2005; Marko et al., 2019), and to play a critical role in speech encoding (Hyafil et al., 2015), speech change detection (Jin et al., 2014) as well as in tracking syllabic units (Ghitza et al., 2013; Giraud and Poeppel, 2012; Meyer, 2018; Poeppel, 2003; Wagner et al., 2022).

The evaluation of spectral density maps in the three-dimensional brain space did not reveal significant results, but functional connectivity analyses additionally showed decreased linear and nonlinear connectivity between bilateral visual and posterior cingulate areas, and ventral-anterior temporal and parahippocampal brain regions in RS2 and RS3 compared to RS1. In addition, the correlation analyses computed with the difference values obtained by subtracting the power of RS1 from RS2, revealed a negative association between this variable and the percentage of correctly recognized semantically-related items in the semantic generalization task. In principle, this could indicate that the exposure to unfamiliar speech sounds led to the formation of new phonological or declarative memory traces that facilitated the retrieval of the new words, and consequently their mapping onto already established semantic representations. Finally, it is noteworthy to mention that the explorative correlation analyses did not reveal a relationship between theta power at baseline, or between the modulation of theta across RS1 and RS2, and word discrimination abilities. Nevertheless, this would be compatible with the view that theta plays a pivotal role in the formation of declarative memory traces (Bastiaansen and Hagoort, 2003; Kragel et al., 2020) rather than supporting basic acoustic processes and phonetic analyses (Dittinger et al., 2021; Elmer et al., 2021a; Kuhl, 2004) which are needed to perceptually distinguish the foreign speech sounds.

4.3.3. Lower and upper alpha frequency bands

The evaluation of the lower alpha frequency band yielded a consistent pattern of results with overall increased power, spectral density and functional connectivity in RS2 and RS3 compared to RS1. In particular, the source-based analysis revealed increased spectral density values in the proximity of the following brain regions: occipital and parahippocampal areas, posterior cingulate cortex, insula, inferior parietal lobe and auditory cortex. Furthermore, the comparison between RS1 and RS2 yielded an increment of nonlinear connectivity between the left supramarginal gyrus (BA 40) and the right anterior cingulate (BA 25) after word discrimination compared to baseline. Otherwise, the comparison between RS1 and RS3 revealed increased linear connectivity between the posterior cingulate cortex / parietal regions and bilateral medial temporal areas, between bilateral inferior parietal areas, as well as between temporal and orbitofrontal regions. In contrast, increased nonlinear connectivity in the lower alpha band in RS3 compared to RS1 was restricted to connections between bilateral inferior parietal and posterior temporal regions. It is also noteworthy to mention that post-hoc sourcebased analyses also showed a positive relationship between task-related spectral density changes in the bilateral auditory cortex from RS1 to RS2

and d-prime indices of the word discrimination task (explained variance \sim 15%). Furthermore, lower alpha power changes between RS1 and RS3 positively correlated with word discrimination skills (explained variance \sim 10%).

Alpha is the dominant frequency in the human scalp EEG (Klimesch, 1999), has classically been associated with inhibitory functions (Klimesch et al., 2007; Strauss et al., 2014), and been shown to inversely correlate with hemodynamic responses (Goldman et al., 2002; Moosmann et al., 2003; Mukamel et al., 2005). In recent years, tonic alpha oscillations have also been proposed to reflect brain maturity, and have been linked to cognitive performance, with higher power values reflecting increased memory span and processing speed (Klimesch, 1999; Surwillo, 1971). Alpha oscillations have also been ascribed a significant role in auditory processing (Teng et al., 2017), and been shown to correlate with auditory attention (Wostmann et al., 2016; Wostmann et al., 2017), auditory working memory (Obleser et al., 2012; Wilsch and Obleser, 2016) as well as listening effort (Strauss et al., 2014; Wostmann et al., 2015). Drawing on the background of auditory processing, the significantly increased lower alpha metrics we revealed as a function of word discrimination and word learning might be a byproduct of in-depth phonological analyses of the new words, increased allocation of attentional resources, or even of memory encoding processes. Such a perspective would also be compatible with the increased spectral density values we revealed in the auditory cortex after the word discrimination tasks as well as with the positive correlation we found between auditory cortex activity changes from RS1 to RS2 and d-prime indices of the word discrimination task. Finally, the sensitivity of the lower alpha band to auditory-related perceptual or cognitive processes was also corroborated by the fact that lower alpha power changes from RS1 to RS3 correlated with d-prime metrics of the word discrimination task.

Also the analyses of the upper alpha frequency band yielded consistent results at multiple levels of signal processing, with overall increased values in RS2 and RS3 compared to RS1. Although the upper alpha band has been shown to be related to lexical-semantic processing (Klimesch, 1999), it is unlikely that the increased alpha values we observed after the word discrimination and word learning tasks mirrored this specific mnemonic functions. In fact, current evidence indicates that neural desynchronization but not synchronization in the upper alpha band facilitates semantic memory performance (Klimesch, 1999), and that this process is mediated by thalamo-cortical loops (Larson et al., 1998; Lopesdasilva et al., 1973). Furthermore, after the semantic generalization task which placed additional demands on semantic processing, we revealed increased and not decreased upper alpha values, making it unlikely that the upper alpha band was selectively involved in accessing semantic information in memory. Hence, as already discussed above, the consistently increased upper alpha values we revealed in RS2 and RS3 compared to RS1 might more likely reflect neural changes related to phonological analyses, the allocation of attentional resources to the unfamiliar stimuli, or even to verbal working memory functions. Interestingly, the perspective of a relationship between the upper alpha frequency band and auditory-related functions would also be compatible with the positive correlation we found between power difference values obtained by subtracting RS1 from RS2 and d-prime parameters of the word discrimination task (explained variance ~ 12%). However, it is important to mention that we also revealed a negative correlation between the same power difference index and the percentage of correctly recognized semantically-related items in the semantic generalization task (explained variance \sim 11%) which is difficult to explain. In fact, although this relationship suggests that upper alpha synchronization is detrimental for semantic processing as previously proposed by Klimesch (1999), the underlying operating principles are difficult to grasp, mainly because after RS2 the new words have not yet been associated with a meaning. Finally, source-based functional connectivity analyses in the upper alpha frequency band also brought to light complex patterns of increased linear and nonlinear connectivity between visual, medial-lateral and anterior temporal, parahippocampal, inferior and superior parietal as well as frontal and anterior-posterior cingulate areas. Although an accurate interpretation of these results is difficult, they demonstrate the potential of word discrimination to alter network configurations at rest.

4.3.4. Lower and upper beta bands

A handful of previous EEG studies mined the link between beta activity at baseline and foreign language learning aptitudes (Kliesch et al., 2022; Kliesch et al., 2021; Küssner et al., 2016; Prat et al., 2016; Prat et al., 2019). For example, Prat and colleagues could show that in a sample of young adults who learned French as a second language, pre-training RS power in the beta band correlated with the attained degree of French proficiency (Prat et al., 2016; Prat et al., 2019). Also Kliesch and co-workers (Kliesch et al., 2021) provided evidence that beta power at baseline was predictive of second language development in older adults, whereas Küssner and colleagues (Küssner et al., 2016) revealed that beta power measurements prior to a vocabulary learning session was positively associated with recall scores. Furthermore, Kliesch and colleagues (Kliesch et al., 2022) examined source-based connectivity at rest, and reported that the functional architecture in the beta frequency band predicted several parameters of second language learning. In a similar vein, Kepinska et al. (Kepinska et al., 2017) brought to light that learners who exhibited increased functional connectivity in the beta band during the learning phase were also better able to learn an artificial grammar.

Interestingly, our results are somewhat in contrast to these previous reports in that we did not find evidence for a predictive value of the lower or upper beta frequency bands for word-referent mapping or semantic generalization abilities. However, in both frequency ranges scalp power significantly decreased after foreign word discrimination and word learning, leading to suggest an involvement of these two specific EEG metrics in perceptual processes, phonetic discrimination or phonological learning mechanisms. Even if the exact role of beta oscillations in speech processing is still far away from being understood (Meyer, 2018), our interpretation fits with a previous study of Bidelman and colleagues who showed a connection between beta activity and the categorization of speech sounds (Bidelman, 2015). Specifically, beta power was increased for those native vowels with a well-defined phonetic identity compared to ambiguous items situated in the middle of the continuum, and the same neural marker was positively related to the slope of the psychometric identification function. Even though our data indicated a decrease rather than an increase in beta power, it is truly possible that the task-related beta changes we observed contributed to establish the new phonetic categories of the foreign speech sounds

Neural oscillations in the beta frequency range have also repeatedly been associated with selective attention to task-relevant stimuli (Waldhauser et al., 2012; Womelsdorf and Fries, 2007) as well as with declarative memory encoding and retrieval (Hanslmayr et al., 2012; Waldhauser et al., 2012). In particular, decreased beta power at rest has generally been shown to be accompanied by reduced alertness (Coben et al., 1985; Ishii et al., 2017), and to benefit long-term memory encoding and retrieval (Hanslmayr et al., 2012; Pfurtscheller and Aranibar, 1977). Since foreign speech sound discrimination is unlikely to reduce attentional functions, it is more plausible to assume a functional role of beta oscillations in the construction of episodic memory traces for the new words.

5. Limitations

A first limitation of this study is that the evaluation of scalp power spectra data does not allow to draw any conclusions about the brain regions which were predictive of behavior or were modulated by the different tasks. A second shortcoming is that the intrinsic meaning of RS brain rhythms is still largely unknown. Accordingly, clear associations between EEG parameters and specific cognitive functions remain purely elusive. Finally, it is important to mention that although our sample size was relatively large, the variance explained by our correlation analyses was generally lower compared to previous studies (Kliesch et al., 2022; Kliesch et al., 2021; Küssner et al., 2016; Prat et al., 2016; Prat et al., 2019). However, this might have been driven by the fact that most previous studies used ecologically valid language interventions over relatively long time periods, whereas we focused on a laboratory-based test procedure with a limited set of stimuli.

6. Conclusions

In the present EEG study, we exploited the potential of RS power metrics at baseline to predict behavioral indices of word discrimination and word learning, and examined possible task-related reconfigurations of neural networks at multiple levels of signal processing. As a main result, we showed that both foreign speech sound discrimination as well as word learning resulted in rapid RS changes in multiple frequency bands at both the scalp and the source level. However, this was only the case if RS2 and RS3 were contrasted to RS1 reflecting a "default" RS condition which was not blurred by a previous task. Correlation analyses also showed that scalp-based RS power changes related to the word discrimination tasks (difference between RS2 and RS1) were associated with word discrimination and semantic generalization skills, whereas functional changes related to the word learning tasks (difference between RS3 and RS1) correlated with word discrimination scores. Taken together, these results provide a framework for better understanding the physiological role of RS rhythms in association with word learning, and help to rationalize which of the multistep processes have the potential to rapidly reconfigure RS networks. For future studies it might be interesting to examine whether the paradigm we used is sensitive enough for predicting specific aspects of language development deficits in children, whether it can be used as a potential intervention for ameliorating recovery from aphasia, and whether the task-related RS changes we observed are comparable with real-life language learning scenarios.

Data and code availability statement

The EEG data of this study are available from SE upon request. Due to ethical considerations the data cannot be made openly available. However, the data will be shared upon request without any restrictions.

Declaration of Competing Interest

The authors declare no competing interests.

Credit authorship contribution statement

Stefan Elmer: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft. Mireille Besson: Conceptualization, Writing – review & editing. Antoni Rodriguez-Fornells: Conceptualization, Writing – review & editing. Nathalie Giroud: Writing – review & editing.

Data availability

Data will be made available on request.

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