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SHORT REPORT

Resting gamma power is linked to reading ability in adolescents Adam Tierney,¹ Dana L. Strait^{1,2} and Nina Kraus^{1,2,3,4,5}

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Abstract

Infants who have more power within the gamma frequency range at rest develop better language and cognitive abilities over their first 3 years of life (Benasich et al., 2008). This positive trend may reflect the gradual increase in resting gamma power that peaks at about 4 years (Takano & Ogawa, 1998): infants further along the maturational curve may exhibit both increased resting gamma power and more advanced language and cognitive function. Similar to other neural characteristics such as synaptic density, resting gamma power subsequently decreases with further development into adulthood (Tierney, Strait, O'Connell & Kraus, 2013). If previously reported relationships between resting gamma power and behavioral performance reflect variance in maturation, at least in part, negative correlations between resting gamma and behavior may predominate in later developmental stages, during which resting gamma activity is decreasing. We tested this prediction by examining resting gamma activity and language-dependent behavioral performance, reflected by a variety of reading-related tests, in adolescents between the ages of 14 and 15 years. Consistent with our predictions, resting gamma power inversely related to every aspect of reading assessed (i.e. reading fluency, rapid naming, and basic reading proficiency). Our results suggest that resting gamma power acts as an index of maturational progress in adolescents.

Research highlights

- It is known that resting gamma power is linked to linguistic ability in infants.
- Resting gamma increases with age in early childhood but decreases with age in later childhood through adulthood.
- We show that adolescents with less resting gamma have better reading skills.
- The gamma-reading relationship may, therefore, be driven by neural maturation.

Introduction

Stimulus-induced increases in neural activity within the gamma frequency range (here defined as 31–50 Hz) have been linked to a variety of cognitive and perceptual abilities, including object recognition (Rodriguez,

George, Lachaux, Martinerie, Renault & Varela, 1999; Csibra, Davis, Spratling & Johnson, 2000; Gruber, Muller & Keil, 2002; Uhlhaas, Roux, Singer, Haenschel, Sirenteanu & Rodriguez, 2009), memory (Tallon-Baudry, Bertrand, Peronnet & Pernier, 1998; Tallon-Baudry, Kreiter & Bertrand, 1999; Fell, Klaver, Lehnertz, Grunwald, Schaller, Elger & Fernández, 2001), and attention (Tiitinen, Sinkkonen, Reinikainen, Alho, Lavikainen & Näätänen, 1993; Fan, Byrne, Worden, Guise, McCandliss, Fossella & Posner, 2007). Stimulus-induced gamma activity's relationship to these processes has led to studies addressing whether the amount of gamma activity in the absence of a stimulus (i.e. during a resting state) likewise relates to individual differences in behavioral performance. Accordingly, Benasich, Gou, Choudhury and Harris (2008) found that resting power within the gamma range positively associates with individual performance on standardized language measures in preschoolers. Moreover, children with more resting gamma activity performed better on subsequent

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language tests conducted 2 years later (Gou, Choudhury & Benasich, 2011). This indicates that differences in resting gamma power during infancy have the power to predict the subsequent development of language abilities.

The underlying cause of the relationship between resting gamma power and linguistic ability is unknown. Here, we considered two possibilities, the first being that correlations between resting gamma power and language abilities in early childhood reflect their covariance with neural maturation (the maturation hypothesis). Synaptic density (Huttenlocher, 1979), gray matter volume (Pfefferbaum, Mathalon, Sullivan, Rawles, Zipursky & Lim, 1994), and resting gamma power (Takano & Ogawa, 1998) all increase until about age 4 as the brain builds up a surplus of synapses. Throughout infancy, language abilities also rapidly develop as their underlying neuronal circuitry matures (Bates, Thal & Janowsky, 1992; Paus, Zijdenbos, Worsley, Collins, Blumenthal, Giedd, Rapoport & Evans, 1999; Thomson, Giedd, Woods, MacDonald, Evans & Toga, 2000, Schmithorst, Wilke, Dardzinski & Holland, 2002; Nagy, Westerberg & Klingberg, 2004). As a result, children under the age of 4 who are further along the neural maturational trajectory may show both increased resting gamma power and stronger language skills compared to same-aged children who are maturing at a slower pace.

A second potential explanation is that gamma activity reflects neural characteristics that facilitate language acquisition (the neural coordination hypothesis). Given that gamma oscillations take place when neuronal activity is bound together both within and across brain regions (Gray & Singer, 1989; Gray, Koenig, Engel & Singer, 1989; Engel, Kreiter, Konig & Singer, 1991a; Engel, Konig, Kreiter & Singer, 1991b; Engel, Konig & Singer, 1991c; Freiwald, Kreiter & Singer, 1995; Roelfsema, Engel, Konig & Singer, 1997), resting gamma power may reflect the extent to which processing in distant brain regions can be coordinated. Given that language processing relies on neural resources that are spread throughout the brain, coordination of disparate brain regions - reflected in resting gamma power - could be vital for language acquisition.

These two theories can both account for the relationship between resting gamma power and language abilities in early childhood. How, then, can we decide between them? One way to test these theories would be to examine resting gamma power in an older population of children: adolescents. Between childhood and early adolescence, after the initial buildup of synapses has halted, frequently used synapses are retained while others are pruned, leading to an overall decrease in synaptic density and gray matter volume (Huttenlocher, 1979, 1990; Pfefferbaum *et al.*, 1994; Reiss, Abrams, Singer,

Ross & Denckla, 1996; Huttenlocher & Dabholkar, 1997; Sowell, Thompson, Holmes, Batth, Jernigan & Toga, 1999; Sowell, Thompson, Tessner & Toga, 2001; Sowell, Peterson, Thompson, Welcome, Henkenius & Toga, 2003; Gogtay, Giedd, Lusk, Hayashi, Greenstein, Vaituzis, Nugent, Herman, Clasen, Toga, Rapoport & Thompson, 2004; Blakemore & Choudhury, 2006; Whitford, Rennie, Grieve, Clark, Gordon & Williams, 2007). Resting power within the gamma range follows a similar maturational trajectory, peaking at age 4 and decreasing thereafter (Takano & Ogawa, 1998; Tierney et al., 2013). If the link between resting gamma power and language abilities is driven by neural maturation, the relationship between gamma power and language ability should be negative during adolescence, when more advanced neural maturation is linked to less resting gamma power and, presumably, enhanced language skills. If, on the other hand, resting gamma power reflects neural characteristics vital for language processing at any developmental period, the relationship between gamma power and language ability should be positive. We examined these two possibilities by recording resting gamma power and assessing one aspect of language ability, reading, in adolescents.

Methods

Subjects

All experimental procedures were approved by the Northwestern University Institutional Review Board. Ninety-nine high-school freshman (44 female) ages 14–15 from the Chicago metropolitan area participated in this study (mean age = 14.6, SD = 0.36). All participants had normal hearing (air-conduction binaural hearing thresholds ≤ 20 dB HL at octave frequencies from 125 to 8000 Hz) and no participants reported a history of neurological deficits or learning disabilities. Informed assent and parent consent were obtained for all testing procedures and subjects were compensated for their participation. All participants had IQ scores within the normal range (Weschler Abbreviated Scale of Intelligence (Weschler 1999) 2-scale IQ ≥ 76).

Data collection

Resting cortical electroencephalographic (EEG) activity was recorded using NeuroScan Acquire 4.3 (Compumedics) with a 31-channel tin electrode cap (Electrocap International, Eaton, OH, USA). Reference electrodes were placed on the earlobes and blink-monitoring electrodes were placed on the superior and outer canthi of the left eye. Contact impedance for all electrodes was kept below 10 k Ω . Subjects were asked to sit quietly, without moving, in a lighted soundproof booth for 3 minutes. Subjects were instructed to keep their eyes open except when blinking and to fixate on a point on the wall in front of them to avoid excessive eye movement.

Three composite measures of reading were assessed. Single word-reading fluency was measured using the Test of Oral Word Reading Efficiency (Torgesen, Wagner & Rashotte, 1999), which contains subtests requiring subjects to read words (Sight subtest) and nonwords (Phonemic Decoding subtest) aloud as rapidly as possible. Rapid naming was assessed using two subtests from the Comprehensive Test of Phonological Processing (Wagner, Torgesen & Rashotte, 1999) in which subjects are asked to read aloud lists of letters and numbers as rapidly as possible. Finally, untimed word-reading proficiency was assessed using the Woodcock Johnson Test of Achievement's Basic Reading score (Woodcock, McGrew & Mather, 2001), which comprises untimed single word- and nonword-reading subtests (Letter-Word ID and Word Attack subtests, respectively). All measures analyzed were age-normed standardized scores.

Data analysis

Continuous EEG recordings were bandpass-filtered offline from 1 to 100 Hz with a 12-dB rolloff to emphasize cortical contributions to the signal. The removal of eye-blink artifacts was conducted with the NeuroScan Edit 4.3 spatial filtering algorithm. The spatial filter, by comparing the data with a hand-made 'clean file' free of eye blinks and other artifacts, first generates an average eye blink. It then extracts the first covariance and component values using a spatial singular value decomposition based on principal component analysis. Finally, it develops a filter specifically sensitive to eye blinks using those covariance values. This results in continuous EEG data in which eye blinks have been removed, permitting the analysis of data uncontaminated by eye blinks without the loss of large portions of data. Visual inspection confirmed that this procedure successfully removed all eye blinks.

The spatially filtered 3-minute recording was then segmented into 180 1-second non-overlapping epochs. Epochs containing amplitude spikes greater than 75 µV were rejected as artifacts. The frequency spectrum of each epoch was then measured using a fast Fourier transform in MATLAB (The Mathworks, Natick, MA). The resulting 180 frequency spectra were averaged to create an average frequency spectrum for each channel in each participant. Following Benasich et al. (2008), gamma-band frequencies were limited to 31-50 Hz. To confirm the specificity of relationships between gamma and reading ability, power within theta (3-7 Hz), alpha (8-12 Hz), and beta (20-30 Hz) frequency bands was assessed as well. Absolute power within this frequency range was calculated using the equation $20*\log 10(x)$ at each electrode site. We divided the 31 channels into five groups: frontal (F3, F4, FZ, FP1, FP2, and FPZ), temporoparietal (FC3, FC4, FCZ, C3, C4, CZ, CP3, CP4, CPZ, P3, P4, and PZ), left (F7, FT7, TP7, and T5), right (F8, FT8, TP8, and T6), and occipital (O1, O2, and OZ). A sixth grouping comprised all 31 channels. Resting gamma power was averaged across electrodes within each electrode grouping. Outliers were corrected to two standard deviations from the mean to ensure that correlations were not driven by outliers. This procedure had a minimal effect on the data; for the channel grouping consisting of all 31 channels, for example, only one outlier was corrected.

Results

We hypothesized that resting gamma power relates to linguistic ability due to a common link with maturational progress. To test this hypothesis, we ran Pearson's partial correlations between each channel grouping and raw scores on the behavioral tests, covarying for age (Table 1). Descriptive statistics for each behavioral test can be found in Table 2. For every group of channels and every behavioral test, the relationship between performance and resting gamma power was negative, i.e. lower gamma was associated with better performance. Resting gamma power significantly correlated with all aspects of reading-

Table 1 Pearson's partial correlations between resting gamma power and behavioral performance, covarying for age at time oftesting

Correlation with resting gamma (Pearson's r, p-values)	Frontal	Temporoparietal	Occipital	Left	Right	All
Rapid naming Reading fluency Untimed naming IQ	$\begin{array}{c} -0.31, \ 0.0020 \\ -0.25, \ 0.013 \\ -0.25, \ 0.0119 \\ -0.04, \ 0.6731 \end{array}$	$\begin{array}{c} -0.39, 0.0001 \\ -0.29, 0.0039 \\ -0.27, 0.0067 \\ -0.10, 0.3254 \end{array}$	$\begin{array}{c} -0.32, 0.0012\\ -0.24, 0.015\\ -0.18, 0.073\\ -0.11, 0.2995\end{array}$	$\begin{array}{c} -0.40, 0.0001\\ -0.30, 0.0025\\ -0.24, 0.016\\ -0.04, 0.6674\end{array}$	$\begin{array}{c} -0.36, 0.0002\\ -0.28, 0.0050\\ -0.25, 0.0133\\ 0.02, 0.8560\end{array}$	$\begin{array}{r} -0.39, 0.0001 \\ -0.30, 0.0027 \\ -0.27, 0.0076 \\ -0.06, 0.5568 \end{array}$

related language performance across all channels. Of the 31 channels analyzed, 28 showed a significant negative correlation (p < .05) between resting gamma power and rapid naming ability, 25 showed a significant negative correlation between resting gamma power and reading fluency, and 22 showed a significant negative correlation between resting gamma power and untimed naming. When covarying for both age and IO or for IO alone, relationships between reading ability and resting gamma power in all channels remained significant for all three reading tests (p < .01). This, together with the lack of any correlation between resting gamma power and IQ (Table 1), indicates that the relationship between gamma and reading was not driven by factors related to general intelligence. Figure 1 displays relationships between resting gamma power across all channels and performance on behavioral measures. Figure 2 displays the Pearson's r value for the relationship between resting gamma power and rapid naming ability for each channel across the scalp. When analyzing the data using the electrode groups, of the 18 correlations between resting gamma power and reading ability assessed, all but one were significant (p < .05) and all were in the same direction (i.e. less resting gamma power corresponded to better reading ability). Figure 3 displays the topological distribution of resting gamma power, while Figure 4 displays the average frequency spectrum from 1 to 50 Hz across all channels and subjects.

While we also considered relationships between reading and resting oscillatory activity within the theta (3– 7 Hz), alpha (8–12 Hz) and beta (20–30 Hz) frequency ranges, significant relationships were largely limited to the gamma frequency range. Table 3 lists correlations between reading ability and resting power in these other three frequency bands; all relationships were insignificant except for a negative relationship between beta power and rapid naming as well as between theta power and untimed naming.

Discussion

We investigated the question of why resting gamma power is linked to language ability in young children.

Table 2 Descriptive statistics for IQ and reading measures

Descriptive statistics	Mean	SD	Range
Rapid naming	98.7	13.2	67–127
Reading fluency	96.6	12.5	65–129
Untimed naming	98.2	9.8	73–128
IQ	101.0	10.9	76–127

One possibility, the neural coordination hypothesis, is that resting gamma power is an index of the extent to which different brain regions can coordinate. An alternative possibility, the maturation hypothesis, suggests that children who mature earlier show both improved language skills and greater resting gamma power, as in the first few years of life resting gamma increases with age (Takano & Ogawa, 1998).

We find that reading ability inversely relates to resting gamma power in young adolescents. Correlations between resting power within theta, alpha, and beta bands and reading ability were weaker and less consistent, suggesting that the relationship between resting oscillatory power and reading skill is largely limited to the gamma range. Since resting gamma power gradually decreases during adolescence (Tierney et al., 2013), this finding supports the maturation hypothesis: relationships between resting gamma and language skill exist because both are affected by neural changes occurring as children mature. On the other hand, these results do not support the neural coordination hypothesis: if resting gamma power reflected neural characteristics vital for language processing across the life span, one would expect positive relationships between resting gamma and language ability to predominate regardless of the age range tested.

Resting gamma power's relationship to neural maturation may be driven by the fact that, during adolescence, synaptic pruning gradually decreases synaptic density and, therefore, gray matter volume, which correlates with resting oscillatory power (Thomson et al., 2000). A number of changes in neural structure occur during adolescence that could facilitate the development of language skills, tying language ability to maturation. These neural changes include an increase in white matter density within the arcuate fasciculus (Paus et al., 1999; Schmithorst et al., 2002; Giorgio, Watkins, Chadwick, James, Winmill, Douaud, De Stefano, Matthews, Smith, Johansen-Berg & James, 2010), the neuronal tract connecting receptive and productive language areas, and an enlargement of the posterior section of the corpus callosum, which connects language areas (Thomson et al., 2000; Snook, Paulson, Roy, Phillips & Beaulieu, 2005). White matter maturation continues throughout adolescence within prefrontal (Barnea-Goraly, Menon, Eckert, Tamm, Bammer, Karchemskiy, Dant & Reiss, 2005) and parietal (Whitford et al., 2007: Ashtari, Cervellione, Hasan, Wu, McIlree, Kester, Ardekani, Roofeh, Szeszko & Kumra, 2007) cortices, both of which are involved in language functions, including reading (Price, Moore & Frackowiak, 1996). These changes could underscore language performance; Nagy et al. (2004), for example, found



Figure 1 Subjects with less resting gamma power displayed superior linguistic abilities. Correlation between resting gamma and rapid naming, r = -0.39, p = .0001; correlation between resting gamma and reading fluency, r = -0.30, p = .0027; correlation between resting gamma and untimed naming, r = -0.27, p = .0076.



Figure 2 Topographic plot of the relationship between resting gamma power and rapid naming performance. Darker colors indicate higher Pearson's r-values, and therefore stronger relationships, while lighter colors indicate lower rvalues and weaker relationships.

that white matter development within the left temporal lobe correlated with reading ability.

In adults, increases in gamma power induced by a stimulus accompany many cognitive and perceptual tasks, including object recognition (Rodriguez *et al.*, 1999; Csibra *et al.*, 2000; Gruber *et al.*, 2002; Uhlhaas *et al.*, 2009), attention (Tiitinen *et al.*, 1993; Fan *et al.*, 2007), memory (Tallon-Baudry *et al.*, 1998; Tallon-Baudry *et al.*, 1999; Fell *et al.*, 2001), and learning

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Resting gamma power



Figure 3 Topographic plot of resting gamma power. Lighter colors indicate regions with greater power, while darker colors indicate regions with less power.

(Miltner, Braun, Arnold, Witte & Taub, 1999). Nevertheless, we find that, in adolescents, less resting gamma power is linked to greater reading ability. These findings can be reconciled. Studies of stimulus-induced gamma power commonly examine an increase in gamma over baseline. Thus, an overall decrease in the level of ongoing gamma activity would not, all else being equal, lead to a decrease in gamma induced by a stimulus. In fact, decreased resting gamma could lead to increases in



Figure 4 Average power spectrum of resting EEG across subjects.

Table 3 Pearson's partial correlations between resting powerin theta, alpha, and beta bands and behavioral performance,covarying for age at time of testing

Correlation with resting oscillatory power, all channels (Pearson's <i>r</i> , <i>p</i> -values)	Theta	Alpha	Beta
Rapid naming Reading fluency Untimed naming IQ	$\begin{array}{r} -0.15, 0.1272\\ -0.01, 0.9360\\ -0.23, 0.0203\\ -0.20, 0.0491\end{array}$	$\begin{array}{c} 0.01, 0.8934\\ 0.03, 0.7694\\ -0.07, 0.4883\\ -0.11, 0.2680\end{array}$	$\begin{array}{r} -0.26, 0.0094\\ -0.15, 0.1521\\ -0.18, 0.0800\\ -0.01, 0.8878\end{array}$

induced gamma if the absolute response to a stimulus stays constant.

Future directions

If language abilities are affected by the progress of neural maturation, identifying adolescents who are maturationally delayed could help diagnose one potential cause of language processing difficulties. An adolescent with both low language skills and abnormally high resting gamma power for his or her age may be maturationally delayed with respect to peers. On the other hand, an adolescent with low language skills and resting gamma power within the normal range for his or her age could have problems with language that stem from some other source. The facility with which resting gamma activity is acquired makes it particularly attractive as a measure of neural maturation when compared with another recently proposed measure of neural maturation, the density of theta and delta oscillations during sleep, which requires many hours of data collection that take place over multiple nights (Campbell & Feinberg, 2009). In contrast, resting gamma activity can be collected in only 3 minutes. Still, future work identifying and quantifying other potential factors that can affect resting gamma power and the collection of age norms is needed before resting gamma power can be considered to serve this purpose.

Relationships between maturational progress and behavioral and cognitive abilities are not likely to be limited to the language domain but may extend to skills such as attention and memory. Future work could examine this proposal by investigating relationships in adolescent subjects between resting gamma power, working memory, and attention. Negative correlations between resting gamma power and these abilities would provide further support for our claim that the development of cognitive abilities in adolescence is driven in part by the rate of neural maturation.

Future work might also consider relationships between resting gamma power and other language measures. While our measures consist of reading-related tests, the measures used by Benasich et al. (2008) and Gou et al. (2011) comprise tests of receptive and expressive language skills, phonological awareness, and the comprehension and use of morphological and syntactical rules. We cannot rule out the possibility that the inverse correlation we find is specific to language processes underlying the ability to read. Future work could investigate this possibility using a test such as the Clinical Evaluation of Language Fundamentals (CELF; Wiig, Secord & Semel, 1992), which assesses language skills not specific to reading ability and is normed from ages 3 to 21. Gou et al. (2011) found positive correlations between resting gamma power in preschool and CELF performance at age 5. The finding of a negative correlation between gamma and CELF performance in adolescents would confirm that the inversion of the relationship between resting gamma and language abilities between preschool and adolescence is not limited to reading.

Conclusions

Here, we report that resting gamma power in adolescents inversely correlates with reading ability. We suggest that resting gamma can be used as an index of neural maturation during early adolescence and that differences in neural maturation account for some of the variance in reading ability within normal readers.

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