Electroencephalographic Coherence and Learning: Distinct Patterns of Change During Word Learning and Figure Learning Tasks

Peter Collins[1], Michael Hogan[1], Liam Kilmartin[2], Michael Keane[1], Jochen Kaiser[3], and Kurt Fischer[4]

ABSTRACT—One likely mechanism in learning new skills is change in synchronous connections between distributed neural networks, which can be measured by coherence analysis of electroencephalographic patterns. This study examined coherence changes during the learning of two tasks, a word association task and a figure association task. Although learning curves were similar for both tasks, distinct patterns of coherence change were observed. Coherence tended to increase as learning progressed in the figure association task. In contrast, coherence tended to decrease in the word association task, especially within hemisphere. Word learning was coupled with negative intrahemispheric and positive interhemispheric performance–coherence relations in the gamma frequency. Unique to the figure learning task was an increase in the number of positive coherence–performance relations in both delta and theta frequencies across blocks. Results are discussed in light of ongoing efforts to identify the mechanisms that coordinate distributed brain activities during the process of learning. Further research is needed to define patterns of coherence change for different tasks, goals, and brain regions.

Human activity—inherently dynamic and context sensitive—emerges as a function of connected brain activity. Connections among brain regions seem to change frequently as networks adjust in response to learning and variations in tasks and goals (Immordino-Yang, McColl, Damasio, & Damasio, 2009; Poldrack, Halchenko, & Hanson, 2009; Raichle et al., 2001). One challenge for researchers is to understand how distributed brain regions communicate with one another during the coordination of action in context and how that communication changes with learning. This study focuses on electroencephalographic (EEG) coherence as a measure of connection and communication and specifically examines the ways in which functional networks of electrical activity change in different ways in word learning and figure learning tasks.

Neural Assemblies and EEG Coherence

One of the primary candidates for mechanisms of learning when people master a new skill is change in the coordination of distributed brain areas, called *neural assemblies or networks*. Researchers have been working to identify the mechanisms that select and coordinate distributed brain activities—distributed networks of neurons transiently linked by reciprocal dynamic connections. The assumption is that particular behaviors are associated with a relatively stable activation pattern of the relevant assemblies and that synchronous oscillations mediate both local interactions between neural networks and long-distance interactions between cortical areas (Schnitzler & Gross, 2005). The millisecond temporal resolution of EEG makes possible coherence analysis, which can be used to examine synchronous oscillations of electrical activity across scalp locations to assess the operation of neural assemblies.

EEG Coherence

Coherence between two EEG signals, which is the squared cross-correlation in the frequency domain between two EEG time series measured simultaneously at different scalp locations (Nunez, 1981; Nunez & Srinivasan, 2005), provides a measure of the degree of synchronization between brain signals of diverse brain regions. Research suggests that patterns of high coherence between EEG signals recorded at different scalp sites have functional significance, indicating stronger or weaker connections between sites and correlating with different kinds of cognitive information processing, such as memory, language, concept retrieval, and music processing (Petsche, Etlinger, & Filz, 1993; Petsche, Kaplan, Stein, & Filz, 1997; Sarnthein, Petsche, Rappelsberger, Shaw, &

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[1] School of Psychology, NUI
[2] College of Engineering and Informatics, NUI
[3] Institute of Medical Psychology, Johann Wolfgang Goethe-University
[4] Harvard Graduate School of Education, Harvard University

Address correspondence to Michael J. Hogan, School of Psychology, NUI, Galway, Ireland; e-mail: michael.hogan@nuigalway.ie.

Stein, 1998; Schack, Grieszbach, & Krause, 1999; Schack, Rappelsberger, Weiss, & Moller, 1999; Weiss, Chromecek, & Rappelsberger, 1998; Weiss, Muller, & Rappelsberger, 1999; Weiss & Rappelsberger, 1998, 2000).

Patterns of coherence also change as a result of learning. For example, Bell and Fox (1996) examined the relationship between EEG coherence and the emergence of crawling in infants. Specifically, intrahemispheric coherence in the 6–9 Hz band was calculated for four groups: prelocomotor infants, novice crawlers with 1–4 weeks' experience, novice crawlers with 5–8 weeks' experience, and long-term crawlers with 9+ weeks' experience. Novice crawlers with 1–4 weeks' experience were shown to have greater levels of coherence than the prelocomotor or experienced crawlers. The authors suggested that there is a genetic disposition for the abundant production of cortical connections at the onset of crawling, and as the infant becomes more skilled the superfluous synapses are pruned; hence, those with more experience exhibited lower levels of coherence. In this way, learning can be reflected by dynamic short-term changes in coherence, not simply sustained increases or decreases.

Animal research suggests that the coherence–performance relation varies depending on the context of learning. For example, Kay recorded theta band oscillations of the local field potential of the olfactory bulb and the dorsal hippocampus in rats and found that coherence magnitude was positively correlated with performance in a two-odor discrimination condition, but not in a single odor condition. This finding was interpreted as consistent with the established role of the hippocampus in the formation of associations. However, the positive correlation between coherence and odor discrimination performance was contrary to an earlier study (Macrides, Eichenbaum, & Forbes, 1982) showing a negative correlation between hippocampal theta coherence and sniffing performance in rats during contingency reversal learning. Kay hypothesized that during contingency reversal learning both task and stimuli were less well known to the rats; therefore, the inverse correlation between performance and coherence reflected a shift toward greater stimulus specificity observable as a response of lesser coherence.

In general, coherence changes during learning are most likely dynamic and nonlinear, in the sense that both positive and negative performance–coherence relations emerge and dissolve as different neural networks or assemblies are established and disestablished. This view is consistent with the framework and research findings of Silberstein, Neuper, & Klimesch (2006), who describe a process of "functional connectivity sculpting," and argue that it may constitute an important functional component of the neural substrate of learning. They found that patterns of coherence were *both* positively and negatively correlated with task proficiency during different phases of a mental rotation task. Specifically, Silberstein and colleagues found that functional connectivity changed dramatically over the time course of a mental rotation trial, with a largely negative coherence–performance relation observed during the encoding of objects, a mixture of negative early-stage and positive late-stage coherence–performance relations observed during a retention phase, and largely negative coherence–performance relations emerging again during the mental rotation phase of the task. Silberstein argued that performance ability is related to a capacity to strengthen coherence between cortical regions that are relevant to current cognitive demands while attenuating irrelevant connections, and thus patterns of coherence–performance relations change as cognitive demands change. This view is consistent with cross-sectional research demonstrating a complex and yet specific cyclical pattern of long- and short-range left and right hemisphere coherence changes associated with the growth of intellectual skills throughout development (Hanlon, Thatcher, & Cline, 1999).

Gamma and Associative Learning: Toward a Model of Coherence Change in Learning

Electrophysiological recordings in both humans and animals have provided support for neuronal synchronization in the gamma band underlying feature binding, which seems to be central to many kinds of learning (Gray, König, Engel, & Singer, 1989; Kaiser, Bühler, & Lutzenberger, 2004; Lutzenberger, Pulvermüller, Elbert, & Birbaumer, 1995; Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1996). More recent research has associated gamma synchronization with a variety of cognitive processes including attention and both short- and long-term memory (Herrmann, Frund, & Lenz, 2009; Jensen, Kaiser, & Lachaux, 2007; Kaiser & Lutzenberger, 2005). An influential hypothesis proposes a role for synchronized neuronal activity at gamma frequency in cortical long-distance communication (Fries, 2005; Jensen et al., 2007). Distributed networks should be activated when cortical representations of familiar objects are processed. Familiar compared with novel stimuli have been shown to elicit increased gamma power and synchronization, putatively reflecting the activation of existing networks (Gruber, Malinowski, & Müller, 2004; Pulvermüller et al., 1996). Repeated exposure to initially unfamiliar objects increases gamma synchronization possibly indicating the formation of new neural assemblies (Gruber & Müller, 2005). However, direct evidence for increases in gamma synchronization or coherence as a result of learning has remained scarce. Miltner, Braun, Arnold, Witte, and Taub (1999) have demonstrated enhanced coherence between occipital and central electrode sites resulting from visual–somatosensory classical conditioning. Closer to this study are findings of broadly distributed gamma coherence increases in response to a visual paired-associate learning paradigm (Gruber, Keil, & Müller, 2001).

At the same time, coherence in frequencies other than gamma may also be critical for understanding learning. One limitation of the studies by Miltner et al. (1999) and Gruber et al. (2001) is that frequencies other than gamma were not reported and thus we are uncertain as to the effect of other frequencies in this context. Although current theory and research suggest that gamma synchronization may be more critical than other frequencies during the formation of new neural assemblies that undergird associative learning, theta is known to be involved in memory processing and has been related to gamma (gamma appearing during particular phases within the theta cycle) in studies using intracortical recordings (Mormann et al., 2005) and EEG recording (Demiralp et al., 2007). Both gamma and alpha modulation have been reported in studies of working memory, where alpha has been related to both memory and active inhibition (Jokisch & Jensen, 2007).

Also, consistent with Silberstein et al. (2006), it is possible that coherence in different frequency bands is *both* positively and negatively correlated with learning, and this in turn may depend on the nature of the task and the phase or level of learning. Serrian and Brown (2003) used a learning task requiring participants to move one hand at twice the frequency of the other and they found that learning was associated with a decrease in coherence between the primary sensorimotor regions in the alpha and beta bands and an increase in coherence between prefrontal areas in the gamma band range. In order to better understand the influence of gamma coherence relative to other frequencies, this study explores coherence changes associated with learning in the delta, theta, alpha, beta, and gamma range.

Also, there are surprisingly few process-oriented studies that examine coherence changes during the learning of different tasks in the same subjects. Different types of learning tasks may draw upon distinct regions and distinct coherence frequency bands. For example, activation of the left but not the right Broca's area during semantic processing is a robust finding (Bookheimer, 2002). Also, during visuospatial attention tasks, predominant activation in the right but not the left parietal areas has been observed (Fink et al., 2000). In a study comparing verbal and nonverbal auditory processing, Härle (2004) used a magnetoencephalogram to record oscillations in response to a comprehensible sentence and to a tone, a scale, and a melody. Intrahemispheric gamma coherence was larger in the left than the right hemisphere for comprehensible sentences and larger in the right than the left for the tone, scale, and melody conditions.

This study was designed to examine how patterns of coherence vary across learning blocks in a verbal learning task and a visuospatial learning task. As noted, the research by Miltner et al. (1999) highlighted the central role of gamma coherence in learning. However, their study used a classical conditioning paradigm with electric shock stimulation. It is unclear whether or not gamma coherence, and growth in gamma coherence over trials, is functional in all learning contexts. Also, no study has compared verbal and visual associative learning in this context. Given that verbal and visual processing is often assumed to rely on distinct brain networks in the left and right sides of the brain, it is possible that the pattern of growth in gamma coherence, or in other frequency bands, is unique for verbal and visual associative learning tasks.

In this study, participants completed two tasks, a word learning and a figure learning paired-associate task, each composed of four blocks of trials and each with an encoding and recognition phase included as part of each block. This allowed for progressive improvements in learning to be tracked across blocks and for corresponding changes in brain coherence to be measured. It also allowed for an analysis of the relationship between progressive changes in brain coherence and progressive improvement in paired-associate learning. On the basis of previous research, it was hypothesized that gamma coherence changes would be a key marker of learning. However, it was also hypothesized that the pattern of coherence change associated with learning would be distinct for word and figure learning tasks. Two alternative hypotheses were proposed in this context.

First, based on research demonstrating predominant left hemisphere activation during semantic processing (Bookheimer, 2002) and predominant right hemisphere activation during visuospatial tasks (Fink et al., 2000), we hypothesized that word learning will selectively activate left hemisphere networks and figure learning will selectively activate right hemisphere networks. Consistent with the idea that gamma coherence is the critical marker of associative learning, a more refined version of this hypothesis is that left hemisphere gamma networks will emerge as a more prominent correlate of word paired-associate learning performance, whereas right hemisphere gamma networks will emerge as a more prominent correlate of figure paired-associate learning performance. Furthermore, consistent with theory and research that highlight a role for gamma synchronization in cortical long-distance communication (Fries, 2005; Jensen et al., 2007), we hypothesized that slower frequencies (delta, theta, alpha, and beta), if they emerge as correlates of learning, will be more localized in performance–coherence maps when compared with gamma coherence networks.

The alternative hypothesis to the gamma hemispheric specialization hypothesis above is that learning involves broad distributed networks of activity in the context of coherence analysis and that patterns of coherence observed during associative learning are a function of the (un)familiarity of the stimuli used. This hypothesis is based on the work of Thomas Gruber and colleagues (Gruber & Müller, 2005). More specifically, Gruber and Müller (2005) examined poststimulus gamma coherence and found repetition suppression for familiar objects but repetition enhancement for unfamiliar objects. In particular, they found that for familiar objects, which presumably have a cortical representation, gamma coherence becomes more localized and more global networks are deactivated when the same object is repeated. In contrast, for unfamiliar objects there are no cortical representations (i.e., weak gamma response to initial presentation) but stimulus repetition leads to learning/memory and elicits increased gamma coherence, possibly reflecting the development of new representations. This distinction can be applied to this study, because the words used were familiar and meaningful, whereas the figures used were unfamiliar and abstract. Therefore, in opposition to the gamma hemispheric specialization hypothesis, we hypothesized that the learning of unfamiliar figures would be associated with increased gamma coherence, whereas the learning of words would be associated with a reduction in gamma coherence.

METHODS

Design

A 2 (task) × 4 (block) within-subject design was used to examine behavioral performance and coherence changes in two tasks, a word learning task and a figure learning task. Coherence changes associated with learning across six frequency bands (delta, theta, lower alpha, upper alpha, beta, and gamma) were analyzed using a 2 (task) × 4 (block) × 6 (frequency) repeated measures analysis of variance (ANOVA). We also tested for differences across the right and left hemispheres in patterns of coherence change across blocks and frequencies. Pearson's product moment correlations were used to map performance–coherence relations during each block and for each electrode pairing, thus allowing us to construct functional connectivity maps describing changes in the nature of the relationship between performance and coherence as learning progressed (cf. Silberstein et al., 2006).

Participants

Twenty-four participants took part in the study (14 females and 10 males, mean age = 21.95 years, *SD* = 4.73). All participants were psychology students who received course credit for their participation. Only right-handed native English speakers were used. Informed consent was obtained from all participants and the study protocol was approved by the National University of Ireland, Galway research ethics committee.

Apparatus

The computer program E-prime was used to design and run the two learning tasks. E-prime was run on a Dell desktop computer with Windows XP. Responses were made by participants on a standard keyboard. Custom software developed within the cross platform MATLAB environment, which utilized the EEGLAB toolbox (Delorme and Makeig, 2004), was run to perform coherence analysis on the data. SPSS software was used to carry out all other statistical analyses.

A Quick-amp 40 EEG amplifier purchased from Brain Product Ltd. was used in conjunction with Brain Vision Recorder (v. 1.03.0001) and Brain Vision Analyser software (Brain Products, GmbH, München, Germany). This software was run on a Dell desktop computer with Windows XP. Silver/silver-chloride (Ag/AgCl) recessed ring electrodes were used. All electrode cables were individually shielded (ActiShield™) and all channels were amplified against the average of all connected inputs.

Experimental Tasks

Two tasks were developed for the purpose of this study, a word and a figure paired-associate learning task. The order of task completion was counterbalanced across participants. Each task included four learning blocks, with each block containing an encoding phase and a recognition phase. Trial list order was counterbalanced across participants. The encoding phase always appeared first, during which time participants were asked to learn the paired stimuli that appeared on screen. The recognition phase required participants to respond to stimulus pairs that appeared on screen by indicating if the pair had appeared in the encoding phase or whether it was a novel pair not seen before. All the pairings presented during encoding phase, 22 pairings for the word task and 16 pairings for the picture task, were presented again during the recognition phase, along with an equal number of novel distractor pairings (22 word and 16 figure). Stimuli were presented in random order. No novel pairing was ever repeated. An iterative pilot study phase, including various task manipulations (e.g., increasing the number of word pairs), ensured that both figure learning and word learning tasks produced similar learning curves (see following text).

The words for the word learning task were sourced from the MRC Psycholinguistics Database and selected on the basis of word frequency and imageability. The final set of words used had an imageability score between 200 and 400 (from a database range of 100–700) and a frequency between 300 and 500 (from a database range of 100–700). Target pairs and novel recognition test pairs were matched on both imageability and frequency. Samples of pairs used include CONSIST–WOULD, CONTEXT–VALUE, and ELSE–TOLD.

The abstract figures used in this study had been created for and used in a previous experiment on the EEG of visuospatial learning (Moore, Cassidy, & Roche, in press) and were reproduced with permission (Figure 1).

Procedure

Upon arrival in the test laboratory, participants were seated in a dimly lit room in a comfortable chair. Participants were

Fig. 1. Sample figures used in the figure paired-associate learning task.

told that the setup would take approximately 50 min and the performance of both tasks approximately 45 min.

Head measurements were taken to ensure that a cap corresponding to the participant's head size was used and to ensure its correct placement. Once in place a chin strap secured the placement of the cap. In accordance with the international 10–20 system, activity was recorded from 32 electrode sites—Fp1, Fp2, F3, F4, C3, C4, P3, P4, O1, O2, F7, F8, P7, P8, Fz, Cz, Pz, FC1, FC2, CP1, CP2, FC5, FC6, CP5, CP6, T7, T8, TP9, TP10, PO9, Iz, and PO10—using a commercially available cap (EASY CAP EC40; EASYCAP GmbH, Herrsching-Breirbrun, Germany). Before connecting the electrodes to the cap, the hair at each site was separated, and with the use of a cotton bud, a small amount of 70% proof alcohol solution was used to clean the scalp at the electrode site. The electrodes were then connected up and a chloride-free abrasive electrolyte gel was delivered with a syringe to bridge the gap between the electrode and the scalp. Two vertical electrooculogiam (VEOG) and horizontal electrooculogiam (HEOG) electrodes were also used to record and control for eye blink artifacts. Impedance, measured with the Brain Vision Recorder, was kept below 10 kΩ. When the participant felt ready to begin, a 3-min baseline for eyes closed and a 3-min baseline for eyes open were recorded. Following this the task recording began.

All task responses were made with the right hand's index finger using the "B" key colored blue and the "V" key colored yellow. Participants were instructed to learn the pairs presented during the encoding phase. The encoding phase consisted of 16 pairings for the figure learning task and 22 pairings for the word task. Each pairing was presented once and no response was required. The presentation structure was identical for the encoding and recognition phases, except that the recognition phase had twice as many stimulus presentations and required a response. Specifically, a fixation cross appeared in the center of the screen for 500 ms, followed by a prompt to "blink" lasting 500 ms, encouraging participants to blink if needed. Then the screen was blank for a period of 750 ms before the pairs appeared on screen to the left and right of the central fixation marker. The pairs remained on screen for 1,500 ms. During the encoding phase participants were instructed to study the pairs. During the recognition phase participants responded with a blue key press if the presented pair had appeared in the encoding phase or with a yellow key press if the pair had not appeared in the encoding phase. No feedback was given for a correct or incorrect response. The recognition response time did not affect the duration of stimulus presentation, which always lasted for a period of 1,500 ms regardless of the reaction time. A period of 1,000 ms then followed before the next fixation point appeared and the next trial unfolded.

Triggers identifying the type of stimulus presented were sent via the amplifier to the EEG recorder upon their presentation in E-prime. Triggers were also sent identifying participants' responses and the timing of the response. On completion of the task, participants were debriefed and thanked.

Behavioral Data Processing

Hits, misses, false alarms, and correct rejections were recorded automatically by E-prime. These data were exported to SPSS where d' (discriminability index), based on signal detection theory (Wickens, 2002), was computed for each block for each participant as a marker of overall learning. To calculate d' the following formula was used:

$$d' = z(H) - z(\mathrm{FA})$$

where z is the z-score, and FA and H are the false alarm and hit rates, respectively.

EEG Data Processing

EEG signals were sampled at 1000 Hz and were band pass filtered using an analogue filter of 0.1–100 Hz. Encoding phase data were used for the assessment of coherence, as encoding data were uncontaminated by response artifacts. The Gratton and Coles ocular correction algorithm was implemented using BrainVision Analyzer software to remove eye blink artifact, and the data for all encoding trials were then segmented into 1,500 ms segments, 200 prestimulus to 1,300 poststimulus. The semiautomatic artifact rejection function of the BrainVision Analyzer was used to identify artifact-free segments based on voltage criteria of −40 to +40 μV. Artifact-free segments were then exported with the criteria of at least 10 clean segments per encoding block applied. If there were fewer than 10 clean segments during any block, then all the EEG and behavioral data relating to that participant were excluded from the study. These criteria led to the exclusion of data from three participants.

The exported data were analyzed using functionality from EEGLAB (cf. Detorme and Makeig, 2003) within the MATLAB environment. Individual coherence values were calculated using an EEG sample frame duration of 0.512 s (i.e., 512 samples). A Hanning window was applied to the EEG samples prior to coherence calculation. A mean coherence value was then calculated by applying this frame coherence analysis to 200 different frames of EEG samples, each centered at a different poststimulus time ranging from +250 ms to +750 ms poststimulus.

The particular coherence metric used in this study was the event-related linear coherence (ERLCOH) which is a measure of the synchronization in activity between two electrode sites. This linear coherence value was computed for all electrode pairings using Equation (1).

$$\mathrm{ERLCOH}_{a,b}(f,t) = \frac{\sum_{k=1}^{n} F_k{}^a(f,t) F_k{}^b(f,t)^*}{\sqrt{\sum_{k=1}^{n} \left|F_k{}^a(f,t)\right|^2 \sum_{k=1}^{n} \left|F_k{}^b(f,t)\right|^2}} \tag{1}$$

where n is the number of trials or epochs, $F_k{}^a(f,t)$ is the short-time Fourier Transform of the Hanning windowed EEG samples for trial k on channel a at time t and frequency f and $F_k{}^a(f,t)^*$ is the complex conjugate of $F_k{}^a(f,t)$.

This cross-channel coherence metric has a value in the range of 0–1 (where a value of 0 represents the complete absence of synchronization between channels a and b at frequency f during the time window centered on time t and a value of 1 represents perfect synchronization between these channels).

As part of the process of calculating the ERLCOH, the intertrial linear coherence (ITLC) as calculated by Equation (2) is removed.

$$\mathrm{ITLC}_a(f,t) = \frac{1}{n} \frac{\sum_{k=1}^{n} F_k{}^a(f,t)}{\sqrt{\frac{1}{n} \sum_{k=1}^{n} \left|F_k{}^a(f,t)\right|^2}} \tag{2}$$

The ITLC is a *phase locking factor* (cf. Tallon-Baudry et al., 1996), which represents a measure of synchronization on a channel of the activity at time t and frequency f which is time locked to the experimental stimulus across the data trials. The subtraction of ITC during the calculation of ERLCOH should result in an *intrinsic* synchronization between the two electrode sites being reported. The linear coherence with ITC subtracted was computed for six frequencies: delta 0.5–3 Hz, theta 3–5 Hz, lower alpha 5–9 Hz, upper alpha 9–12.5 Hz, beta 12.5–30 Hz, and gamma 30–50 Hz, and for each block for a total of 111 electrode pairings representative of links across all major brain areas. The data were then exported to SPSS for further analysis.

RESULTS

Descriptive statistics for both performance and coherence measures averaged across all electrode pairs are summarized in Table 1. A 2 (task) × 4 (block) repeated measures ANOVA was carried out on the computed d' values to examine learning across blocks in the figure and word association tasks. There was a significant effect of block, $F(3,60) = 36.10$, $p < .001$, $\eta = 0.643$, with a clear learning effect for both the figure and word association conditions (Figure 2). No other main or interaction effects were observed.

A 2 (task) × 4 (block) × 6 (frequency) repeated measures ANOVA was carried out on the computed coherence values. There was a main effect of task, $F(1,20) = 10.19$, $p = 0.005$, $\eta = 0.338$, with word coherence greater than figure coherence when averaged across all frequency bands. There was a main effect of frequency, $F(5,100) = 11.548$, $p < .001$, $\eta = 0.366$, with lower alpha having the highest overall coherence levels and gamma having the lowest. There was a borderline task × block interaction effect, $F(3,60) = 2.72$; $p = .052$. As can be

Table 1

Descriptive Statistics for Performance and Coherence Measures Across Blocks for Word Learning and Figure Learning Tasks

	Block 1		*Block 2*		*Block 3*		*Block 4*	
	M	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*
Word task								
d′	0.76	0.64	1.93	1.17	2.15	1.36	2.79	1.44
Delta	0.43	0.06	0.41	0.03	0.42	0.03	0.42	0.03
Theta	0.44	0.06	0.42	0.04	0.42	0.04	0.42	0.04
Lower alpha	0.44	0.07	0.43	0.04	0.43	0.04	0.42	0.04
Upper alpha	0.42	0.07	0.40	0.03	0.41	0.03	0.41	0.04
Beta	0.38	0.07	0.36	0.03	0.36	0.03	0.36	0.03
Gamma	0.36	0.06	0.36	0.04	0.36	0.04	0.36	0.05
Figure task								
d′	0.83	0.99	1.80	1.19	2.16	1.39	2.53	1.49
Delta	0.39	0.03	0.40	0.03	0.41	0.04	0.43	0.08
Theta	0.39	0.03	0.40	0.03	0.39	0.03	0.42	0.08
Lower alpha	0.39	0.03	0.40	0.03	0.40	0.03	0.43	0.08
Upper alpha	0.39	0.03	0.39	0.03	0.39	0.04	0.41	0.07
Beta	0.34	0.03	0.34	0.04	0.35	0.05	0.37	0.08
Gamma	0.34	0.04	0.34	0.05	0.35	0.06	0.35	0.08

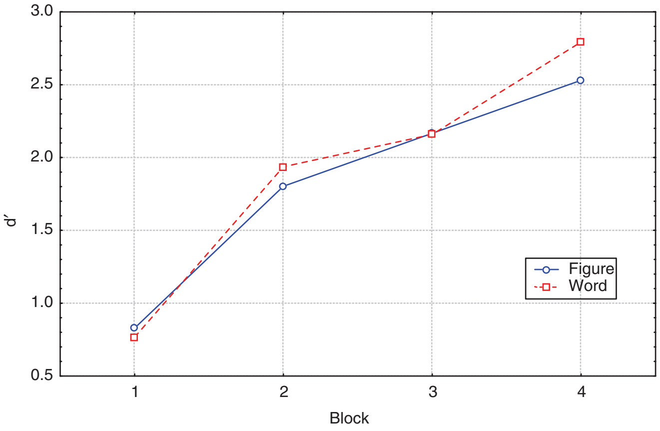

Fig. 2. Learning curves for figure and word learning tasks.

seen in Figure 3 there was a trend for an increase in coherence in the figure learning task and a decrease in coherence in the word learning task. Additional analyses examining effects across the right and left hemispheres revealed no other main or interaction effects.

To examine the relationship between coherence and performance in more detail, a series of bivariate correlations were carried out for both word and figure tasks. Specifically, Pearson's product moment correlations between *d*′ and coherence values were computed for each electrode pairing separately for each block and for each frequency band. The significant correlations are illustrated in the coherence maps in Figure 4. Red lines indicate positive correlations and blue lines indicate negative correlations ($p < .05$). Patterns of coherence–performance relations are clearly different across tasks. For example, one striking effect is the emergence of negative intrahemispheric and positive interhemispheric correlations between gamma coherence and performance during the later stages of word learning. In contrast, there was no substantive relationship between gamma coherence and performance in the figure learning task. Another interesting pattern observed for word learning is a generalized decrease in the number of positive performance–coherence relations in upper alpha, coupled with a generalized increase in positive performance–coherence relations in beta, particularly for blocks 1–3. In the figure learning task, in contrast, there is an increase in the number of positive coherence–performance relations in delta and theta across blocks, and a curious pattern in both upper alpha and beta, whereby positive performance–coherence relations present in block 1 vanish during blocks 2 and 3, only to be replaced by a new set of positive performance–coherence relations in block 4.

DISCUSSION

This study examined coherence changes during two learning tasks, a word paired-associate task and a figure paired-associate task. Coherence was greater for slower frequencies (e.g., lower alpha, theta, and delta) relative to faster frequencies (gamma, beta, and upper alpha). Different patterns of

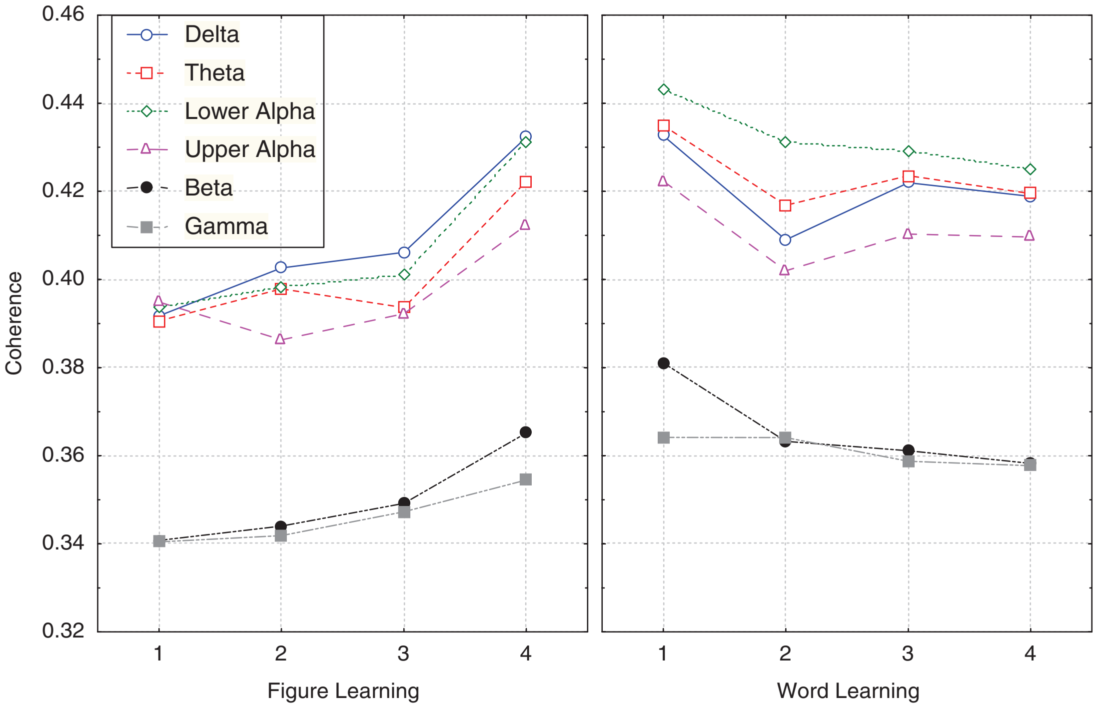

Fig. 3. Growth and decline in coherence across six frequency bands for figure and word learning tasks.

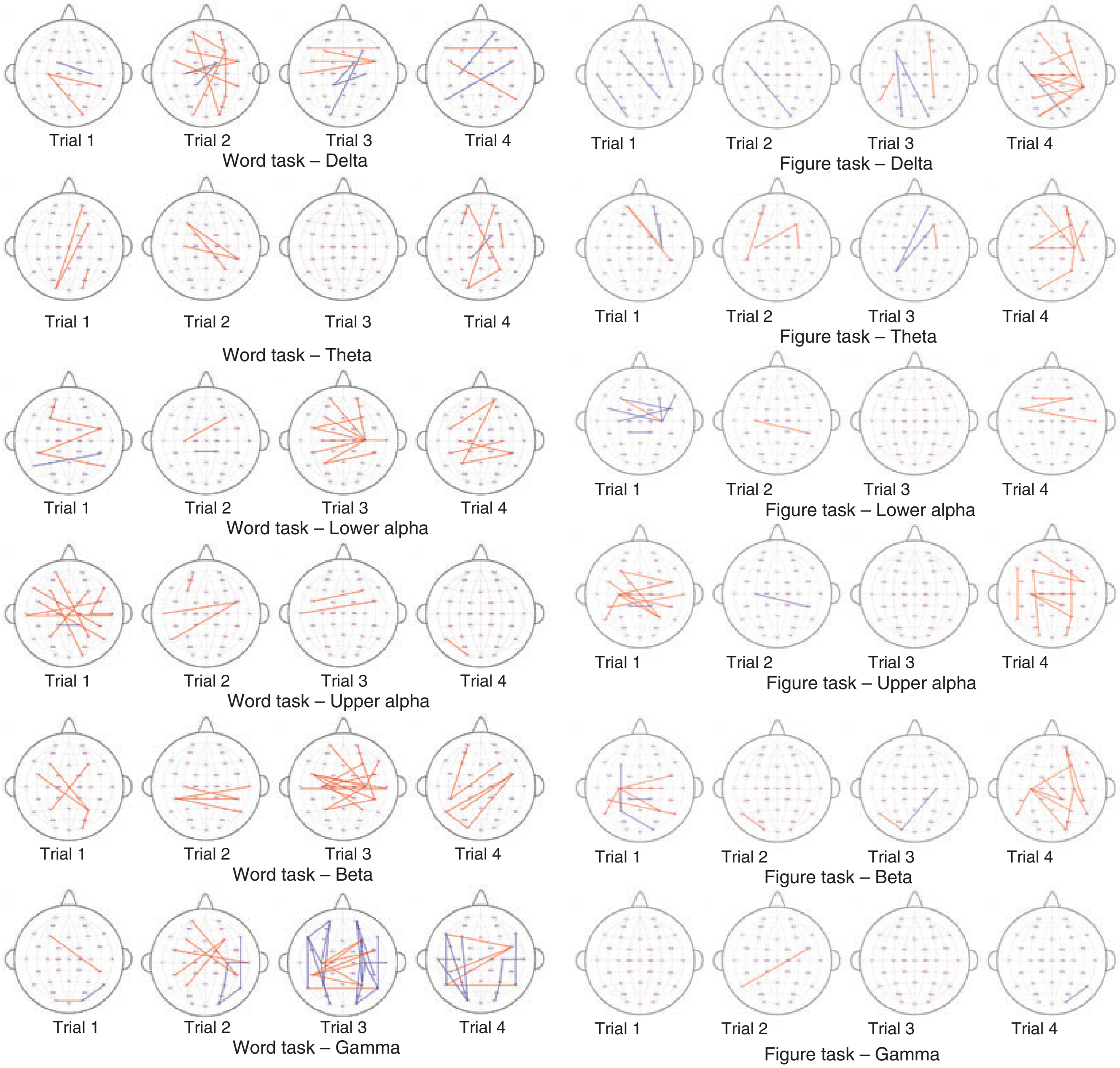

Fig. 4. Functional maps describing positive (red) and negative (blue) correlations between coherence and performance across blocks in the figure and word learning tasks.

coherence change were observed during the learning of the two tasks, even though the rate of learning was comparable across tasks. Coherence was greater overall during the encoding of words when compared with the encoding of figures, and coherence tended to decrease over the course of learning in the word task and increase over the course of learning in the figure task. These findings provide some limited support for our second hypothesis, which stated that the learning of unfamiliar figures would be associated with increased coherence, whereas the learning of familiar words would be associated with a reduction in coherence. However, the effect was not specific to gamma coherence, and gamma coherence did not show the strongest effects in this regard.

On closer inspection, for some frequencies (e.g., upper alpha), the pattern of coherence change across blocks appeared to describe a quadratic function or a U-shaped curve, with coherence effects greater at the outset of learning (block 1) before dropping off during block 2 and increasing again during either block 3 or block 4. However, this quadratic function did not emerge as a statistically significant effect. It is notable that gamma coherence, unlike all other bands, was relatively stable across blocks, particularly in the word learning task, only showing a slight and steady increase from block 1 to block 4 in the figure learning task. These differences across frequency bands and tasks are suggestive and warrant further study. One possibility here is that coherence changes during learning are different for slow and fast waves. However, the functional significance of these trends has yet to be revealed and it is likely that more fine-grained componential analysis of task changes and associated coherence changes will be necessary.

Having said that, this study did reveal some interesting patterns in the way coherence was related to performance across learning blocks, and the results of these analyses clearly suggest that coherence–performance relations change as learning progresses. Some network connections appear to be more important during the early stage of learning and other connections seem more important during the later stages of learning. Consistent with previous research, the results of this study also suggest that coherence can be both positively and negatively correlated with performance (Silberstein et al., 2006). However, in light of the number of comparisons conducted in this context, we draw attention here to the exploratory nature of our coherence–performance analysis and we interpret our findings with caution.

The Figure Task

As noted, significant performance improvements were observed across blocks indicating that learning did occur during the figure learning task. Overall, levels of coherence were low and stable in most frequencies until trial 4 when they increased dramatically. The figure stimuli that participants had to learn were both novel and abstract. It is therefore likely that much of the related processing involved feature analysis and grouping. The sudden shift in the level of coherence observed in block 4 may reflect an increase in communication between brain networks because of the establishment of higher order feature groupings that supported clearer discrimination between figures. There also seems to be some correspondence between this pattern of gross coherence change and the pattern of performance–coherence relations observed across blocks, in the sense that block 4 performance–coherence relations are more prominently positive for many frequency bands, including delta, theta, and beta. Lower alpha also shows a relative shift in positive performance–coherence relations when block 1 and block 4 are compared. The emergent pattern of performance–coherence relations in the theta frequency is also interesting, in the sense that the functional network is primarily localized in the right hemisphere. The lateralization of activity to the right hemisphere may reflect the visuospatial nature of the processing involved (Fink et al., 2000). The observed pattern is also consistent with the findings of Guderian and Duzel (2005), who found that theta coherence between the prefrontal, mediotemporal, and occipital regions is related to successful face recognition.

But what accounts for the negative theta coherence–performance correlations observed in block 1? Perhaps because of the fact that the figures were largely novel at this stage, theta coherence, signifying an attempt to draw on existing figural representations, may have hindered the required feature processing of novel representations. By block 4 participants have consolidated their representations of the novel figures, and with increased recognition there is an accompanying increase in positive theta correlation between frontal and mediotemporal regions.

The increase in the levels of positive beta correlations seen across figure learning blocks may also reflect the visual recognition aspect of the task. Specifically, research suggests that increased beta coherence between the lateral prefrontal cortex, lateral occipital complex, and the hippocampal formation is critically activated during visual recognition processes (Sehatpour et al., 2008). Thus, the increase in beta coherence–performance relations by block 4 may reflect more effective communication within a visual processing network necessary for recognition of figure paired associates.

The Word Task

Much like in the figure association task, there were significant performance improvements in the word association task across blocks indicating that learning did occur. The patterns of coherence change observed, with higher levels of coherence earlier in the task followed by a reduced and relatively stable level of coherence from block 2 onward are broadly consistent with our hypothesis that familiar stimuli activate high levels of coherence in the early stages of learning, perhaps reflecting higher levels of activation that result from the many semantic associations generated when studying word pairs. Unlike the figure learning task, where fewer semantic associations were presumably available from the outset, the word association task may have generated a confluence of associations that were gradually pruned down during later stages of learning. This hypothesis fits nicely with the pattern of gamma performance–coherence relations observed over the course of learning. Specifically, the gamma pattern of change across blocks was marked by an increase in the number of positive interhemispheric coherence–performance relations from block 1 to block 3, coupled with an increase in the number of negative intrahemispheric coherence–performance relations. This pattern of results suggests some degree of inhibition of intrahemispheric gamma networks in the context of increased interhemispheric gamma network activation relevant for successful performance.

Overall, the results of this study suggest that the relationship between EEG coherence and learning is perhaps more complex than has been previously assumed. It is unlikely that there is any simple one-to-one relationship between growth in coherence and learning gain. Consistent with Silberstein et al. (2006) and consistent with the idea that cycles of growth and learning are dynamic and nonlinear (Fischer & Bidell, 2006), it is more likely that the relationship between coherence and performance is nonlinear, showing patterns of both growth and decline, positive and negative network associations, depending on the tasks used and the level of experience that participants have with stimuli and learning conditions. Nevertheless, it is also possible that relatively consistent coherence–performance patterns will emerge across tasks, participant groupings, and learning conditions. For example, as noted above, word association tasks might, during the early stages of learning, draw upon many well-established neural assemblies that become redundant or that need to be inhibited as learning progresses (Gruber & Müller, 2005). Thus, when compared with novel learning tasks using novel stimuli, we might expect to see more negative coherence–performance relations in tasks where participants have some familiarity with the stimuli, as established networks may need to be inhibited while new, specialized networks are established. One way to test this hypothesis more directly is to use a learning task that requires a shift in the pattern of relations that a participant must respond to, that is, by simply altering response contingencies after participants have acquired some level of expertise responding to one set of contingencies.

There are also a number of methodological issues worth considering. For example, this study analyzed coherence using a large time window. Multiple windows of shorter duration would allow for a more detailed analysis of coherence changes within trails as well as across blocks. This level of microdevelopmental analysis might reveal new insights into the way neural assemblies are established for novel versus well-learnt stimuli and also help to bridge the divide between mapping changes at the millisecond level and those observed over the course of minutes and hours as new skills are acquired. More generally, a major challenge for developmental researchers is to understand the relationship between change at different timescales of microdevelopmental analysis (from milliseconds to weeks) and different timescales of macrodevelopmental analysis (from months to years). Also, if we are to develop more complex statistical tests, for example, of coherence pattern analysis or complementary strategies of micro–macrodevelopmental mapping, it will be important to increase the sample size of future studies. One limitation of this study is the small sample size, which limits the power of statistical models.

Coherence–performance analysis has the potential to provide insight into dynamic changes in functional networks during learning and development, including advancing understanding of a range of disorders, such as attention deficit disorder, dyslexia, and Alzheimer's disease. A focus on coherence changes associated with learning can inform optimal pedagogical strategies associated with promoting neural network plasticity, flexibility, relational complexity, and adaptive capacity in a diverse range of information processing scenarios. The study of connections among brain regions in learning and development promises to illuminate the fundamental brain mechanisms that underlie growth and change in networks as students learn new skills and adjust to the diverse demands that they encounter in school, work, and everyday life. This study suggests that changes in EEG coherence provide important information about how networks function and how they adapt to the demands of learning environments across variety of performance domains.

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