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Intelligence and the tuning-in of brain networks

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Abstract

The phase-synchronization of Gamma-band oscillations has been postulated as a mechanism of "network binding" and implicated in various aspects of perception, memory, and cognition. The current study investigates a possible link between Gamma synchrony and individual differences in intelligence within the theory of fluid and crystallized intelligence, with due reference to Hebbian theory. The hypothesis is that there are significant correlations between cognitive performance and synchronous Gamma activity across diverse brain regions. EEG data were recorded from 35 healthy participants, and the peak magnitude and latency of early and late Gamma Synchrony were extracted using a method for quantifying phase synchronization across multiple sites. Participants also completed 11 diverse cognitive ability tests tapping fluid and crystallized intelligence. Overall, moderate-sized correlations were obtained between accuracy and speed composite scores, derived from the ability tests, and magnitude and latency indices of Gamma synchrony. Phase-synchronous Gamma activity provides a plausible physiological mechanism that might account for individual differences in cognitive abilities.
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The main aims of the present study are two-fold. First, a recently developed procedure for the assessment of high frequency *synchronous oscillations* over diverse brain regions is employed, as a measure of binding. Second, this physiological index of binding is linked to the mediating processes that are captured by typical tests of intelligence. In this regard, synchronization was viewed as a physiological process, whereas the outcome of synchronization (variation in intelligence) was seen to be psychological. The present study addressed the proposition that it is plausible to assume that those scoring high on tests of cognitive abilities do so because their brain functions are better synchronized than in those with low intelligence.

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1. Hebbian accounts of brain processes

In his seminal work on the *Organization of Behavior*, Donald O. Hebb (1949) introduced the idea of cell assemblies and the associated mechanisms underlying human intelligence. These proposals remain relevant today, despite the intervening years and noteworthy advances in understanding of the brain and its structures, as an account of a postulated *mediating process*. This process, in Hebbian theory, is clearly distinguished from *sense-dominated* behavior and refers to "ideas" and thinking as captured, for example, by standardized tests of intelligence. The focus of the current investigation is to examine new measurement techniques and ideas concerning the linking these cell assemblies; specifically the notion of binding, and its relationship to the mediating processes that are captured by typical tests of intelligence.

According to Hebb, a mediating process, in contrast to *sense-dominated* behavior, is a psychological phenomenon produced by activity in a group of neurons arranged as a set of pathways (or cell assemblies). These underlying cell assemblies are postulated to be physiological in nature. Hebb assumed that cell assemblies are established slowly, initially during development in infancy, as a result of the repetition of particular kinds of sensory events. The synaptic connections between cells that are repeatedly active at the same time strengthen, leading to groups of functionally related neurons forming cell assemblies. Biological evidence supporting Hebb's theory has since been presented in the process of long-term potentiation (Bliss & Lomo, 1973).

In ensuing years, research into neural plasticity has shown that there exist biological mechanisms that can lead to physical changes in neurons in response to environmental stimulation (e.g., dendritic arborizations), not just strengthening of the excitatory links between existing neurons. Furthermore, with advanced understanding of the functions of glial cells, it is conceivable that new neurons may emerge under similar conditions (see Bennett, Gibson, & Lemon, 2002). One of the puzzles of the Hebbian position is the nature of the relationship between the functioning of cell assemblies that may be involved in the same mediating process, but are communicating from geographically distinct, sometimes far-removed, parts of the brain. The question of what mechanism allows the integration of diverse brain networks to form coherent perceptions and output, with minimal (or even zero) time lag, is commonly referred to as the "binding problem".[3] Evidence from both animal and human studies, reviewed below, indicates that the *phase synchrony* of high frequency brain activity is a central mechanism in the integration and binding of geographically distinct brain activities (Phillips & Singer, 1997).

In the present study, the relationship between individual differences in high frequency synchronous brain activity across the whole brain (using scalp-recorded EEG activity) and individual differences in measured intelligence is examined. The term *tuning-in* refers to the synchronization of different cell assemblies, which may be engaged as a person works on items in tests of intelligence, and which may produce outcomes (answers) that differ in quality (i.e., they may be right or wrong, faster or slower). In other words, it seems plausible that at the level of the whole brain (i.e., collective populations of cells), parameters of synchronization, which can differ from person to person, may account for individual differences in measured cognitive ability. The assumption is that those parameters indicative of better tuning-in among cell populations characterize individuals scoring high on tests of cognitive ability, and vice versa (i.e., poor tuning-in is synonymous with imprecision and noise within the system).[4]

2. Synchronized Gamma-band activity and the tuning-in of cognitive processes

Joliot, Ribary, and Llinas (1994), Basar-Eroglu, Stuber, Schurmann, Stadler, and Basar (1996), and Engel, Roelfsema, Fries, Brecht, and Singer (1997) were among the first researchers to note that high frequency, oscillatory activity in the Gamma band may have an important role in network binding. Gamma oscillations in electrical brain activity typically center on 40 Hz, but vary from 30–90 Hz. In particular, it is the *phase synchrony* of Gamma activity that is postulated to be relevant for the integration of geographically distinct brain activities (e.g., Phillips & Singer, 1997).

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[3] In some accounts of binding, the emphasis is on the triggering mechanism that calls into action other cell populations engaged in the same tuning-in process. Within Hebb's theory, this can be handled by assuming that the system operates in a way that is similar to the auditory system. That is, that there is sensitivity to differences in phase sequences produced by the pathways that reach the same synapse.

[4] A metaphor that comes to mind, of course, is the idea of a good brain that functions as a "well-tempered klavier".

Synchronous Gamma activity may be observed at various levels of analysis, from the microscopic (e.g., a single neuron, typically examined in animal studies) to the mesoscopic level (e.g., scalp recorded EEG and MEG, commonly used in human studies). At the mesoscopic scale, the collective synchronization of neural assemblies, rather than single neurons, is captured (Lee, Williams, Breakspear, & Gordon, 2003). The mesoscopic scale EEG method developed by Haig and colleagues (Haig, 2001; Haig & Gordon, 1998; Haig, Gordon, Wright, Meares, & Bahramali, 2000) is the first method to consider Gamma synchrony across multiple brain sites at one time. Haig (2001) distinguishes two peaks of Gamma synchrony that are of particular importance in fundamental processing of task-relevant stimuli. First, an early (G1) synchrony, at −150 to 150 ms, is directly locked to the presentation of the stimulus. A later (G2) synchrony, at 200 to 550 ms, following the presentation of the stimulus, is interpreted as being involved in the elaboration of the stimulus input and context. It is possible to interpret the two time windows in terms of Hebb's theory; that is, as indicants of sensory-dominated and mediating processes, respectively. The sensory-dominated process captured by the G1 window reflects both anticipatory and detection processes. As indicated in Fig. 3, task-relevant stimuli in an auditory oddball paradigm primarily produce a significant increase in synchrony within the G2 window. Two alternative processes can be captured by the G2 window within the oddball task, namely, *motor activity* (i.e., button press) and "*contextual processing*"; the latter reflecting cognitive evaluations of stimulus novelty relative to background frequencies (Lee et al., 2003). Stimuli that last a second or more are likely to engage both G1 and G2 processes.

Lee et al. (2003) reviewed the literature on Gamma methodology, as well as theories regarding the functional significance of Gamma activity in relation to perception, cognition, and memory. They also review evidence that suggests that Gamma activity is related to selective attention and motor responses, and that it is modulated by arousal. Furthermore, Gamma synchrony in distributed fronto-central and parieto-occipital regions of both hemispheres has been observed in response to the perception of ambiguous stimuli (Klemm, Li, & Hernandez, 2000; Rodriguez et al, 1999).[5] With regard to cognition and memory, Bhattacharya and Petsche (2000) suggest that the enhanced Gamma synchrony observed in musicians, when listening to music, might represent the coordination of working memory processing with perception.

3. Fluid (Gf) and crystallized (Gc) ability and Hebb's intelligences A and B

Because cognitive processes of perception, attention, learning, memory, and information processing all play a significant part in tests of intelligence, it is reasonable to expect that Gamma-band synchronous activity may be related to performance on tests of intelligence in the ways suggested above. Given Hebb's interest in the way we form new associations, it is understandable that he proposed a theory of intelligence that consisted of two components: Intelligence A and Intelligence B. Intelligence A cannot be measured directly because it reflects the innate potential that, in interaction with the environment, contributes to the development of Intelligence B (which, within this model, can be measured). By coincidence, Hebb first presented his theory at the 1941 APA Annual Meeting, the same forum at which Cattell introduced the theory of fluid (Gf) and crystallized (Gc) intelligence. It was quickly realized by Cattell that Intelligence A is synonymous with Gf, and Intelligence B with Gc.[6] Even Cattell's (e.g., Cattell, 1987) later elaborations of "investment" theory retained the essential aspects of Hebb's Intelligence A (i.e., the notion of an "historical" Gf that cannot be measured directly).

Subsequent research on the nature of Gf, largely through the writings of John L. Horn (see e.g., Horn, 1998), has shifted the emphasis from "historical" aspects of Gf. It is now accepted that there exists a broad ability of Gf that can be adequately measured. However, rather than being purely innate, measured Gf reflects incidental learning experiences. Gc, on the other hand, reflects processes of education and acculturation. Although both Gf and Gc capture aspects of attention, learning, and information processing, it is likely that synchronous functioning of cell assemblies and the notion of binding, within Hebb's theory, is somewhat more closely linked to the current interpretation of Gf, rather than

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[5] The coherence function is the most basic and widely used index of interdependent activity between two time series in EEG studies. However, coherence provides a general measure of covariance in activity, and with this measure it is not possible to distinguish between the relative contributions of phase and magnitude to this covariance (Friston, Stephan, & Frackowiak, 1997). By contrast, the technique for determining Gamma phase synchrony employed in this paper allows for the exclusive analysis of phase covariance. Moreover, while coherence provides a measure of covariance between only pairs of electrode sites, our Gamma phase synchrony measures index synchrony across multiple (i.e., two or more) sites.

[6] Indeed, Cattell remarks that "Hebb has independently stated very clearly what constitutes two thirds of the present theory (i.e., Gf/Gc theory)" (Cattell, 1943, p. 179). Further discussion of the relationship between Hebb's and Cattell's theories, alongside Halstead's (1947) constructs of biological and psychometric intelligences, is presented by Pallier, Roberts, and Stankov (2000).

Gc. This is because measured Gf appears more closely related to the physiological basis of cognitive functioning than does Gc. In order to test the veracity of these various accounts of fluid and crystallized intelligence, measures of both constructs were included in the current design.

Three additional features of the present study are related to still more recent elaborations of Gf/Gc theory. Firstly, current versions of Gf/Gc theory point to the importance of broad visual (Gv) and auditory (Ga) perceptual abilities ("provincial powers" in Cattell's terminology), which possess qualities similar to Intelligence A (in the sense of being more related to innate potential). Given plausible links to the brain processes currently under investigation, measures of Gv and Ga were also employed. Secondly, certain work within the framework of Gf/Gc theory has been inspired by the use of competing tasks—simultaneous presentation of two intelligence tests, usually through different modalities (see Stankov, 1988). It can be presumed that, because of the different processing demands of the ingredient tasks, competing presentation would naturally capture distinct cell assemblies and would therefore be suited for any research linking Gamma synchrony to intelligence. In particular, competing tasks would be expected to correlate with measures of synchrony for regions encompassing a relatively large number of scalp sites (e.g., one whole hemisphere) in comparison to single tasks. A competing task was therefore employed in the study to assess this hypothesis.

Finally, several measures of cognitive speed were included in the study. Although distinct types of speed of processing factors have been identified (Danthiir, Wilhelm, Schulze, & Roberts, 2005; Roberts & Stankov, 1999) for the purposes of this study three types of mental speed were distinguished. The first type is measures of test-taking speed that are obtained from computerized tests of cognitive abilities. Although these measures may not define the same factors as those that arise from the analyses of accuracy scores (Carroll, 1993; however, see Danthiir, Wilhelm, & Schacht, 2005), in order to preserve parallelism between accuracy and speed, consideration is given to speed composites that correspond to the accuracy composites (i.e., speed measures derived from tests of Gf, Gc, Gv, Ga, and the competing task). The second type of speed measure is obtained from performance on the "auditory oddball" task, employed to collect the EEG data for the investigation of Gamma synchronicity. Finally, the third type of mental speed measure is a reaction time task, modeled after the Odd-Man-Out task developed by Frearson and Eysenck (1986).[7]

4. Aims

While Gamma synchrony has been related to aspects of cognition, perception, and memory, there is no empirical evidence, at present, to suggest that individual differences on tests of intelligence may be related to the quality of tuning-in of cell assemblies at the whole-brain level (as indexed by Gamma synchrony). In this study, we focused on comparisons between contiguous areas of Gamma synchrony, since the aim of this initial study was to examine whether there is *any* noteworthy relationship between indices of Gamma synchrony and measures of intelligence. We emphasize that our measures of Gamma synchrony are mesoscopic scale indexes of synchronous brain activity obtained from multiple sites across the scalp. It is presumed that these measures reflect the synchronous functioning of cell assemblies at the cellular and neural network levels. It was expected that both windows, but especially G2, should be related to measures of intelligence. This is because, as the name of the oddball test suggests, the participants have to react to rare events only (i.e., tones that occur on only 15% of trials). It is therefore implied that selective attention is required, and judgments about the novelty of the stimulus have to be made. This process, in effect, implies a post-discrimination contextual processing, involving a comparison between subjective expectancy of the stimulus being a target, and whether in actuality the stimulus was a background (or target) tone. This procedure is thought to involve the evaluation and updating of the memory stored expectation of a target.

The present study first sought to establish whether Gamma-synchrony measures are correlated with reaction time to target tones on the oddball task, as a framework for examination of the relationships with more complex psychometric ability tasks. It is important to note that the comparator and performance processes captured by the oddball paradigm are fundamental components of information processing. Therefore, it might be expected that Gamma-band synchrony observed during the oddball task would be related to accuracy, and possibly speed of performance, on more complex

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[7] It is important to mention that accuracy scores on the Odd-Man-Out task, as expected, approached the ceiling level (the mean for these scores is 94% of the total number of items). Nevertheless, they have reasonably low correlation ($r = -.33$) with the speed scores from the same test, indicating that these two types of scores measure different things. We mention this in order to alert the reader to the fact that accuracy scores did have some noteworthy correlations with the synchrony measures in this study. We do not present these correlations in Tables 4 and 5 in order avoid clutter. However, this finding should be checked in future studies.

psychometric tasks that may require a greater degree of brain network synchronization, but nonetheless still rely on fundamental performance processes.

5. Method

5.1. Participants

Data from 37 participants (16 females), with a mean age of 55.73 years (SD = 13.12, range = 30–74) were obtained for this study. Two had missing data for some of the ability tests, therefore some of the results reported here are based on $N = 35$. The participants were recruited from the volunteer pool at Westmead Hospital, Sydney, Australia (and the surrounding community), with no known history of psychiatric or neurological disorders, or of substance abuse — as assessed using the Westmead Hospital's clinical information questionnaire. They were originally recruited for the purpose of validating procedures for assessing synchronicity. Only right-handers were included in this study. Subsequently, they were asked to take cognitive tests. The time period that elapsed between EEG recordings and cognitive testing was on average 12 months.

5.2. Data acquisition: physiological measures

EEG data were recorded within the auditory oddball paradigm, consisting of 15% "target" (1500 Hz) tones and 85% "background" (1000 Hz) tones. The tones (50 ms duration, 10 ms rise and fall time) were presented binaurally through headphones, at 80 dB above threshold (determined individually prior to recording), with a fixed inter-stimulus interval of 1.3 s. Tones were presented pseudorandomly, with the constraint that no two target stimuli were presented in succession. Participants were instructed to respond to the target tones via button press, with the middle finger of each hand (to counterbalance motor effects), as quickly and accurately as possible, and to ignore the background tones. This provided a measure of RT for each target stimulus. Only correctly identified target epochs for which a button press was obtained within one second of the target tone were analyzed. The recording session continued until 40 correctly identified target epochs were acquired. All participants had their eyes open and were instructed to look at a colored dot in the center of a computer screen, in order to minimize eye movements. It is noted that the oddball paradigm employed in this study involves predictable stimulus presentation, and therefore early Gamma synchronization will reflect anticipatory responses as well as integration of sensory input.

Participants were seated in a sound- and light-attenuated room. Electrical activity was recorded from the Fp1, Fp2, F7, F3, Fz, F4, F8, T3, C3, Cz, C4, T4, T5, P3, Pz, P4, T6, O1, and O2 sites, according to the international 10–20 system, using an electrode cap (Blom & Anneveldt, 1982) with linked earlobes as reference (see Fig. 1). Horizontal eye movements were recorded using two electrodes, placed 1 cm lateral to the outer canthus of each eye. Vertical eye movement potentials were recorded using two electrodes placed on the middle of the supraorbital and infraorbital regions of the left eye. A continuous acquisition system was employed at a sampling rate of 250 and a 50 Hz low-pass filter was applied to the signal prior to digitization.

5.3. Data analysis: Gamma-band synchrony

The procedure for the calculation of Gamma phase synchrony used in the present study was developed by Haig and colleagues (Haig, 2001; see also Haig & Gordon, 1998; Haig et al., 2000; Lee et al., 2003). High-frequency Gamma activity is extracted from the EEG data as a time-locked response to auditory stimuli presented in the oddball task. Narrow Gamma band activity (37–41 Hz) was examined, as this frequency range contains the specific synchronous Gamma response elicited by the auditory oddball task (Haig et al., 2000; see also, Miltner, Braun, Arnold, Witte & Trub, 1999), and also encompasses the key frequency of 40 Hz.

The EEG is recorded continuously throughout the oddball task. To extract stimulus-locked Gamma responses, the EEG data were segregated into single-trial epochs associated with each target stimulus. Each epoch comprised 512 EEG segments that were centered on the stimulus onset. Linear trends were removed from each single-trial epoch by subtracting the line of best fit over the 512 samples.

Gamma-band phase information was extracted by means of a fast Fourier transform (FFT) from each time series. The phase synchrony was estimated at every time point from 500 ms pre-stimulus to 750 ms post-stimulus.
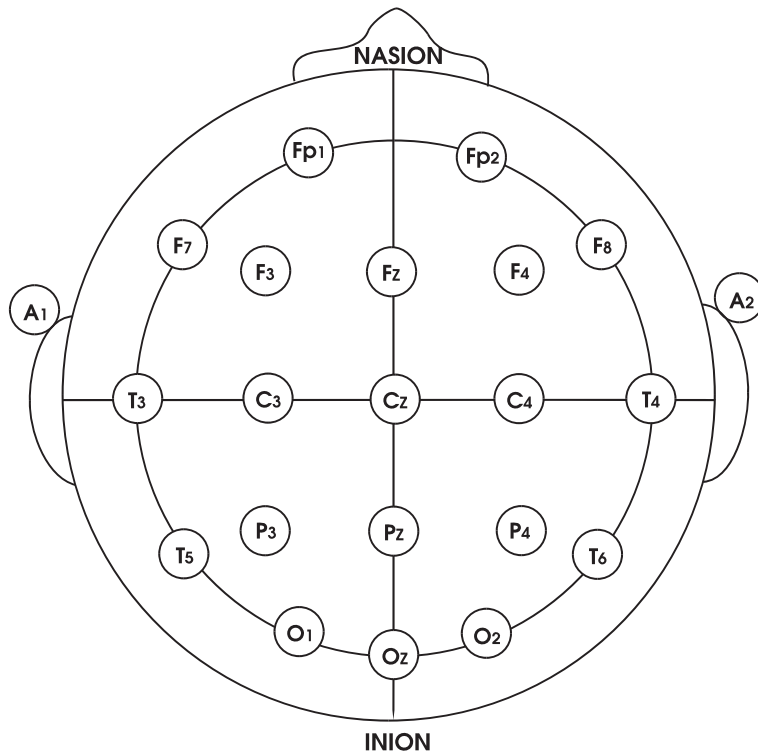
Fig. 1. The international ten-twenty electrode system. Adapted and redrawn from Jasper (1958).

At each sample position (from −500 to 750 ms), a 64 sample Welch window was moved along sample by sample (with a sampling rate of 250 Hz), and the phase of the Gamma frequency component was computed by means of the fast Fourier transform. This procedure produced a time series of Gamma phase from each electrode site. It should be noted here that the procedure was not used to filter the data to the 37 to 41 Hz bandwidth. Rather, the moving Welch window and short time FFT was used to estimate the phase of Gamma, in that bandwidth, as a function of time. Our method allows an examination of the temporal dynamics of phase synchrony across the scalp.

The measure used to calculate the magnitude of phase synchrony across two or more electrode sites was based on Fisher's (1993) index of *circular variance*. Phase synchronicity was computed by first taking the phase estimates from the various sites at a given time, and computing the circular variance of these phase estimates (Haig & Gordon, 1998). This procedure produces a normalized value, for every point in time, ranging between one and zero, which is independent of the magnitude of Gamma activity and represents the degree of phase-locking across sites. This measure of phase synchronicity is plotted as a time series against latency. Since circular variance is low when the phases are similar (top panel in Fig. 2), and high when they are not (bottom panel in Fig. 2), phase synchronicity was inverted (calculated using one minus the circular variance) for ease of interpretation, such that 1 represents maximum synchrony.

The waveforms of Gamma synchrony for each trial were then averaged over the correct target-response trials. Gamma phase synchrony waveforms were calculated for 12 regions: global (all sites), frontal (Fp1, Fp2, Fz, F3, F4, F7, and F8 sites), centero-temporal (Cz, C3, C4, T3, T4, T5, and T6), parieto-occipital (Pz, P3, P4, O1, and O2), posterior (T5, P3, Pz, P4, T6, O1, and O2), left hemisphere (Fp1, F3, F7, C3, T3, T5, P3, and O1), midline (Fz, Cz, and Pz), right hemisphere (Fp2, F4, F8, C4, T4, T6, P4, and O2), left frontal (Fp1, F3, and F7), right frontal (Fp2, F4, and F8), left temporal (T3 and T5), right temporal (T4 and T6), left posterior (C3, P3, and O1), and right posterior (C4, P4, and O2).

Within the averaged Gamma synchrony responses, phase locking was revealed at two latency windows, as found in an earlier study (Haig et al., 2000): An early (Gamma 1 or G1) synchrony at −150 to 150 ms and a later (Gamma 2 or G2) synchrony at 200 to 550 ms. For each averaged waveform, the peak magnitude and the latency of the peaks, within both the Gamma 1 and Gamma 2 latency windows, was derived relative to a pre-stimulus baseline level. Example
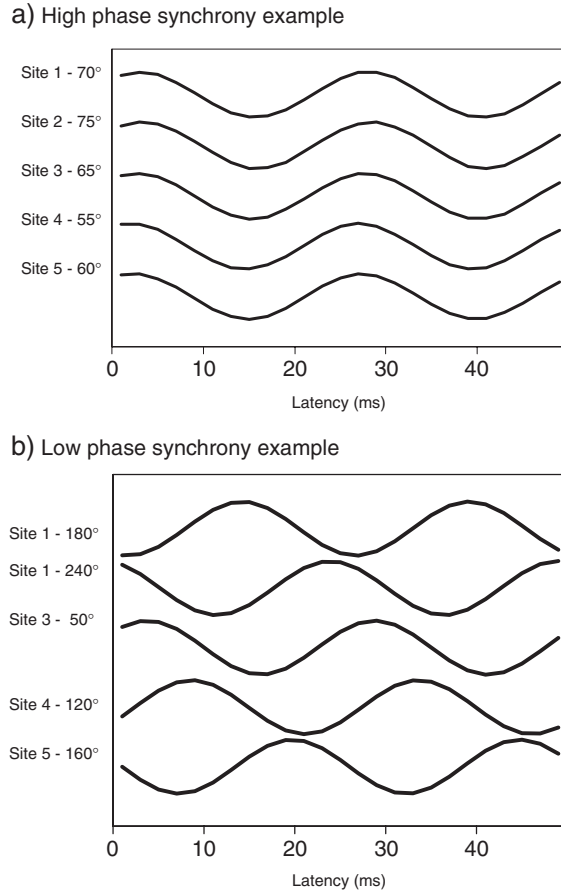
Fig. 2. Examples of high (a) and low (b) Gamma synchrony with simulated data (Haig, 2001).

waveforms are presented in Fig. 3, representing the average Gamma synchrony for 100 participants (the larger sample used to validate the Gamma measure).

5.4. Test description: psychometrics measures

Participants completed eleven tests, chosen to demarcate a number of broad abilities postulated within Gf/Gc theory. The broad abilities represented by the tasks were fluid reasoning (Gf), acculturated knowledge (Gc), auditory reception
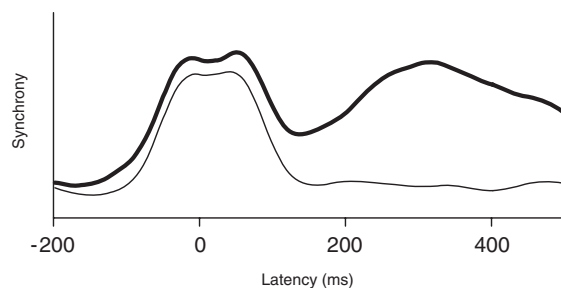

Fig. 3. Group averages of global (all sites) Gamma phase synchrony from the 100 normal participants. Target (thick line) and background (thin line) waveforms are shown. The vertical axis is synchrony, which is a normalized measure with no associated units of measurement. (Haig, 2001).

(Ga), visual processing (Gv), and processing speed (Gs) (see e.g., Horn, 1998). All tests were presented on computer and are tests that have been employed in many previous studies in our laboratory, selected from Sydney University's Individual Differences and Computerized Assessment Unit (IDCAU) Gf/Gc Computerized Test Battery (Stankov & Roberts, 2000). The number of items in each test is displayed in Table 1. All tests were presented under time constraints that, unless stated otherwise, were one min per item. Both accuracy (i.e., level) and speed scores were obtained for each test.

5.4.1. Acculturated knowledge or crystallized intelligence (Gc)

1. *Synonyms Vocabulary.* The task requirement was to choose from among four alternatives the one with the closest meaning to a keyword.

2. *Proverbs.* A proverb was presented and participants were required to choose, from 5 alternatives, another proverb that had the closest meaning.

3. *Esoteric Analogies.* Participants had to choose, from 4 alternatives, a word completing an analogy. For example, "Hot is to cold, as fire is to?" (Answer="ice").

5.4.2. Fluid reasoning or fluid intelligence (Gf)

4. *Swaps.* The stimuli consisted of the letters "J", "K", and "L" presented simultaneously on the monitor, with the order varying between items. Participants were instructed to mentally swap the position of two of the letters, according to a particular rule presented with the stimuli, and then choose from among six alternatives the final order of the letters. The number of swaps required ranged from two to five. One item was presented from each level, in ascending order, in each trial, with four trials at each level. A sample item is presented below.

K L J
Swap: 1 and 2
2 and 3
1 and 3
(Answer: K J L)

5. *Matrices.* This 12 item test, developed by Stankov and Roberts (2000), involved the presentation of a 3 by 3 grid, with each of these nine grid squares further subdivided into yet another 3 by 3 grid. Circles or crosses occupied a predetermined number of these smaller grid squares in each trial. The placement of the crosses and circles within each of the larger grid squares changed in every trial, but always adhered to some logical pattern across both the horizontal and vertical axes. In each trial, the bottom right-hand grid was left blank. The participants' task was to deduce the

Table 1
Descriptive statistics of the Gamma synchrony indices for Gamma 1 and Gamma 2 windows for all major EEG recording sites

	Magnitude				Latency			
	G1		G2		G1		G2	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
All	0.553	0.563	0.822	0.672	5.333	65.325	335.892	72.806
Frontal	0.534	0.461	0.719	0.640	−8.400	81.346	342.944	85.048
Centero-temporal	0.613	0.682	0.876	0.806	2.297	61.391	319.865	77.788
Parieto-occipital	0.572	0.437	0.646	0.581	−0.694	66.647	326.057	73.061
Left hemisphere	0.636	0.533	0.764	0.680	1.139	56.039	334.028	79.327
Midline	0.308	0.385	0.589	0.417	−17.216	76.774	335.351	78.320
Right hemisphere	0.597	0.576	0.740	0.605	−2.378	67.010	331.730	80.135
Left frontal	0.516	0.471	0.697	0.612	−15.054	82.697	359.800	80.695
Right frontal	0.449	0.468	0.631	0.576	−30.811	81.481	312.167	81.106
Left posterior	0.444	0.405	0.571	0.594	0.806	71.897	339.886	75.125
Right posterior	0.551	0.490	0.753	0.494	−0.838	61.974	330.147	73.833
Left temporal	0.970	0.711	0.844	0.767	−0.459	67.620	328.167	88.539
Right temporal	0.835	0.711	0.738	0.595	−10.568	68.667	328.513	86.359
Posterior	0.665	0.557	0.803	0.736	−0.005	55.748	335.514	74.261

Latencies expressed in ms. Magnitude expressed in terms of a normalized measure based on circular variance and baseline levels of activity.

correct placement of crosses and squares in this final grid square. Each item had a 90 s time limit. An example of a test item, with the correct solution, is given below:
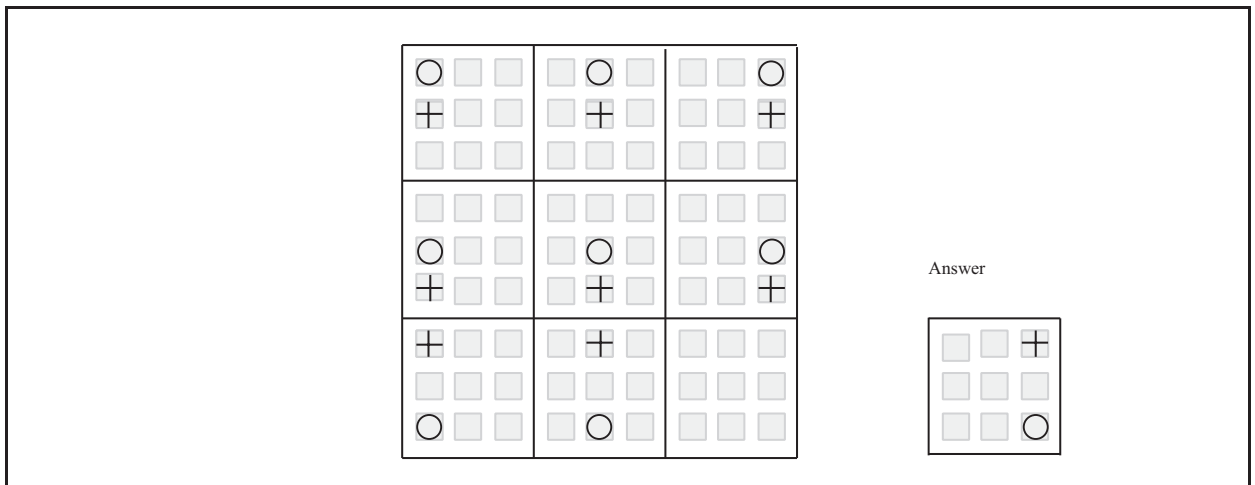
6. *Attention Switching*. This test was derived from the well known Stroop Task. A pair of words was presented, one above the other, naming, and colored in, blue, green, or orange. Participants were required to press either adjacent "Yes" or "No" response keys, according to their judgment of whether the word pair followed one of the following two rules:

Rule 1: The color *named* by the *bottom* word is the same as the color the *top* word is *printed* in.
Rule 2: The color *named* by the *top* word is the same as the color the *bottom* word is *printed* in.

Participants were to refer to Rule 1 on trials in which the stimuli appeared surrounded by a frame and Rule 2 when the stimuli appeared without a frame. During the practice session participants were required to correctly complete three consecutive items, before the start of the test proper. If during the test an incorrect response was given consecutively three times, the rules, and when they should be followed, were presented again. A time limit of 30 s per item was allowed. Whilst this task is not a traditional Gf measure, evidence suggests that it is a measure of Gf, or at least shares a strong relationship with this construct (Pallier, Roberts, Werner, & Van Dyk, 2001).

5.4.3. Broad auditory function (Ga)
7. *Tonal Memory*. Participants were presented a series of four tones, each tone one second in duration, at one second intervals. After a two second delay, the tones were presented again, with one tone different. The task was to determine which tone had changed by clicking on a button presented on the monitor representing the serial position of that tone.

5.4.4. Broad visualization (Gv)
8. *Paper Folding*. Successive drawings, illustrating two or three folds made in a square piece of paper, were presented. The final drawing showed where a hole had been punched through the folded paper. The task was to choose, from five "unfolded" drawings, where the holes would be if the paper was unfolded.
9. *Hidden Figures*. Five simple geometric shapes, labeled A through E, were presented at the top of the screen. Each test item was a rectangle, containing a number of intersecting lines, thus hiding one of the five shapes within it. The task was to determine which of the five shapes was contained within the rectangle.

5.4.5. Broad speediness (Gs)
10. *Odd-Man-Out*. This test was modeled after the odd-man-out reaction time paradigm, developed by Frearson and Eysenck (1986). A semi-circular array of eight red circles was presented to each participant, with

three of the circles becoming "illuminated" (i.e., white) after a variable fore-period. Two of the three illuminated circles were always closer together, and the task was to press the response key (either the left or right arrow button on the keypad) that corresponded to the circle that was further from the other two (i.e., the "odd-man-out"). Given that there were only two response keys and a finger was left on each response key at all times (unlike the more prototypical odd-man-out paradigm), there was no real division of RT into movement time and decision time. 18 practice items were given and up to 20 s was allowed for each item before it was judged as incorrect.

5.4.6. Competing task (Gv/Ga)

11. *Competing Task*: This test was composed of items from both the Paper Folding and Tonal Memory tasks. However, the items were different from those used in the single task condition. For each competing task item, an item from each single test was presented simultaneously, and then participants were required to answer both items. The order in which answers were given was forced, and only one set of response choices and stimuli was presented at a time (in a random fashion), and the other set appeared once the first set had been responded to. The folding of the paper in the paper folding items was animated, to make visualization easier. Each paper folding item had three elements presented (only items in which two folds were made were thus used) at two second intervals, and the five alternative answers were presented also at two second intervals. All elements remained until four seconds after the last stimuli had been presented. Consecutive with the start of the paper folding stimuli, the sequences of tones were played as described previously. The items for this tonal memory task were made easier than in the single version, to reduce the overall difficulty of the test.

5.5. Procedure

Cognitive testing time was approximately three hours, with a break of 20 min after the first hour and a quarter of testing. Participants were firstly informed of the test protocol and ethical requirements. Prior to each test, instructions for the particular task were presented, along with an example and practice items. Participants were encouraged to ask for clarification of test procedures, if required. On completion of the test battery, participants were de-briefed and thanked for their co-operation.

6. Results

6.1. Descriptive statistics: Gamma synchrony

Table 1 presents arithmetic means and standard deviations for magnitude (in standard circular variance units, corrected for baseline levels) and peak latency of synchrony, within the G1 and G2 windows, across different brain regions. These are averages over the 35 participants employed in this study.

In the absence of comparative data, it is useful to note general trends that are apparent in Table 1. First, across all sites, for both G1 and G2, and for both magnitude and latency measures of synchrony, standard deviations are large, indicating considerable variability between the participants. Second, the magnitude of the dominant peak for the G1 window is generally smaller than for the G2 window. The two exceptions to this generalization are the left- and right-temporal areas. This outcome may be interpreted to suggest that, generally, the amount of synchrony achieved for the decision process is greater than the amount present during the sensory detection stage. Third, if the amount of synchrony is defined in terms of the magnitude of the magnitude of G2, the sites with highest peaks are centero-temporal (.876) and left-temporal (.844). If short latency of the dominant peak within the G2 window is taken as the indicant of interest for synchrony, right frontal (312.167) and centero-temporal (319.865) are the most pronounced. Fourth, for G1, the highest magnitudes of the dominant peak are for left-temporal (.970) and right-temporal (.835). The shortest latencies for the G1 peak are within the right-frontal (−30.811) and midline (−17.216) regions. Clearly, for G1, within the majority of the sites, dominant peaks appear prior to the onset of the stimulus, probably indicating attention related anticipatory processes. For the majority of participants, it appears that the decision process within the oddball task leads to the most pronounced synchronous activity occurring in the centero-temporal region of the brain. Temporal regions tend to display the largest amount of synchrony for both G2 and G1 time windows. These patterns are consistent with the preferential involvement of the temporal lobe and

Table 2
Descriptive statistics for psychometric measures (Accuracy or Level) scores indicating percentage of correctly solved items

Measure	Mean	Standard deviation	Reliability (Cronbach's α)	No. of items
1. Vocabulary	82.00	15.34	.853	29
2. Proverbs	61.21	15.00	.666	20
3. Esoteric Analogies	67.76	15.42	.688	22
4. Swaps	46.88	24.65	.803	16
5. Matrices	31.62	20.90	.713	12
6. Attention Switching	69.24	14.61	.785	40
7. Tonal Memory	46.86	22.11	.737	15
8. Paper Folding	39.50	19.75	.700	17
9. Hidden Figures	31.81	15.38	.229	11
10. Odd-man-out	93.73	11.93	.942	54
11. Paper Folding — competing	27.82	16.69	.486	11
12. Tonal Memory — competing	42.42	22.46	.657	11

temporo-frontal circuits in auditory processing, contextual processing and working memory updating, and preparation of response functions associated with the oddball task.

6.2. Descriptive statistics: psychometric tests

Table 2 shows descriptive statistics and internal consistency reliability estimates (i.e., Cronbach's alpha) for number correct (level) scores from all psychometric tests employed in this study.

In order to provide information about the difficulty of each test, relative to the other tests in the battery, accuracy scores are expressed in terms of percentages of correctly solved items. All means and standard deviations for these tests are within acceptable ranges and are comparable to values obtained previously in our laboratory. Most reliability coefficients are also within acceptable limits, despite being based on a small sample size. The only exception is the Hidden Figures Test. We cannot offer a plausible explanation for its low reliability, other than to note that reliability coefficients can be unstable with such a small N. Nonetheless, this test is retained in the battery to help over-determine the Gv factor, but with a caveat that the findings with this factor may not be as replicable as might be expected for other composites.

Table 3 presents descriptive statistics and internal consistency reliability estimates (Cronbach's alpha) for speed scores from the psychometric tests.

In order to provide information about the difficulty of each test (relative to the other tests in the battery), speed scores are expressed as the averages of the number of seconds needed to solve an item in the test. All means and standard deviations for these tests are within acceptable ranges and are comparable to the values obtained previously in our laboratory (see e.g., Roberts & Stankov, 1999). Reliabilities are also within acceptable limits.

Table 3
Descriptive statistics for the speed scores from the psychometric measures indicating the average time needed (in sec) to solve an item in the test

Measure	Mean	Standard deviation	Reliability (Cronbach's α)
1. Vocabulary	7.104	3.039	.932
2. Proverbs	26.523	7.182	.889
3. Esoteric Analogies	11.537	2.812	.842
4. Swaps	33.247	11.223	.938
5. Matrices	44.831	12.009	.779
6. Attention Switching	5.044	1.794	.936
7. Tonal Memory	3.122	1.803	.818
8. Paper Folding	22.250	7.276	.905
9. Hidden Figures	30.014	12.664	.802
10. Odd-man-out	4.738	1.289	.971
11. Paper Folding — competing	3.944	2.120	.780
12. Tonal Memory — competing	3.361	1.614	.743

6.3. Correlations between Gamma synchrony and psychometric measures

In order to reduce the number of correlations to be considered, while at the same time maintaining the richness inherent in the design of the psychometric battery, z-transformed test scores for both accuracy and speed measures were added to obtain composite scores for the following:

Gf: Swaps+Matrices+Attention Switching
Gc: Vocabulary+Proverbs+Esoteric Analogies
Gv: Paper Folding+Hidden Figures
Ga: Tonal Memory
CT (Competing Task): Tonal Memory Competing+Paper Folding Competing.

In order to maintain parallelism between accuracy composites and measures of test-taking speed, speed scores for individual tests were z-transformed and added to form composites. In Tables 4 and 5, "S" as the suffix in the acronyms on the right-hand side indicates psychometric test-taking *speed* for the above accuracy composites. Furthermore, these Tables present correlations with two different reaction time measures:

Table 4
Correlations between Gamma synchrony magnitude and the composite accuracy and speed scores, and auditory oddball reaction time (ORT)

	ORT	Accuracy composites					Speed composites				
		Gf	Gc	Gv	CT	Ga	Gs	GfS	GcS	GvS	CTS
Magnitude-G1											
All											
Frontal	−.20					−.21					−.27
Centero-temporal											
Parieto-occipital		**−.31**	.23								.22
Left hemisphere		−.27							.29		
Midline				.26	.24	**.36***	**−.37***		.24		−.25
Right hemisphere				.20			**−.31**	−.26			
Left frontal	−.31			.26			−.26	−.22			**−.37***
Right frontal						−.26					
Left posterior		**.30**	.21				.21				
Right posterior											
Left temporal		−.24									
Right temporal		**−.31**						−.29			
Posterior		**−.43***					.20		−.26		
Magnitude-G2											
All											
Frontal											
Centero-temporal											
Parieto-occipital			.23				**.37***		−.28		
Left hemisphere			.21				.24				
Midline							−.20		**.40***	.22	
Right hemisphere							−.24				
Left frontal					.28			−.25		−.26	−.20
Right frontal	.21		.21	−.22							
Left posterior											
Right posterior				−.28	−.21			−.28			
Left temporal		.22				**.30**			**.31**	.21	
Right temporal	−.24					**.30**	−**.32***			−.22	
Posterior							**.44****		−**.30**		

*Correlation is significant at the .05 level (2-tailed). **Correlation is significant at the .01 level (2-tailed). All values equal to or higher than .30 are in bold type.

Table 5
Correlations between Gamma synchrony latency and the composite accuracy and speed scores, and auditory oddball reaction time (ORT)

	ORT	Accuracy composites					Speed composites					
		Gf	Gc	Gv	CT	Ga	Gs	GfS	GcS	GvS	CTS	GaS
Latency-G1												
All			−.25						**.38***			
Frontal				.21							−.21	
Centero-temporal	−.24		**−.30**	−.24					**.33***	**−.30**		
Parieto-occipital		−.23		−.23					**.32***			
Left hemisphere							−.25		.22			
Midline		−.23		.29				−.21				
Right hemisphere			**−.30**				−.23		.29		−.26	
Left frontal	**−.43***		−.20		**.33***							
Right frontal												−.20
Left posterior	.29											
Right posterior		−.26	−.23	−.23				**−.41***		**−.30**		
Left temporal	−.20											
Right temporal		−.28			**−.34***		.24		−.20		.21	
Posterior		−.24			.24	−.21						**.33***
Latency-G2												
All	**.39***		.24					−.28	−.27			
Frontal				**.35***			−.26	−.20			−.25	**−.34***
Centero-temporal				−.22					**−.39***	−.22	−.25	
Parieto-occipital	**.35**	−.22							−.20	−.24		
Left hemisphere	**.51****								−.21			
Midline		−.28				−.24			**−.35***			
Right hemisphere						−.20	−.26					
Left frontal											−.22	
Right frontal		−.25			**−.31**						−.23	−.25
Left posterior	.29	−.24										**−.40***
Right posterior	**.37***		.25	−.29				**−.38***	−.24			−.24
Left temporal	.25				.24							
Right temporal		**−.37***	−.22	−.28	**−.39***				.25			
Posterior	**.32***		.23	.26								

*Correlation is significant at the .05 level (2-tailed). **Correlation is significant at the .01 level (2-tailed). All values equal to or higher than .30 are in bold type.

Gs: Odd-Man-Out Reaction Time; and
ORT: Oddball Reaction Time, which was recorded in the process of gathering the EEG data.

Tables 4 and 5 present correlations between accuracy and speed scores listed above and measures of Gamma synchrony derived for each contiguous grouping of the EEG recording sites.

Specifically, Table 4 shows correlations with the magnitude of the dominant peak for G1 (top panel) and G2 (bottom panel) windows. Similarly, Table 5 shows correlations with the latency of the dominant peak. Only correlations above .20 are reproduced in these Tables, correlations above .30 are in bold font, and those that are significantly different from zero are marked with asterisks according to convention. In the main, to analyze and compare trends in the data, the simple "number of correlations that are above .20" (in absolute values) criterion in Tables 4 and 5 was used to make relevant assertions.[8] As mentioned earlier, general trends that can be discerned from the correlations will be focused upon rather than particular details.

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[8] Excluding the ORT column, the averages of the absolute values of the correlation coefficients for four blocks of variables (G1 — Accuracy, G1 — Speed, G2 — Accuracy, G2 — Speed) in Tables 4 and 5 range from .25 to .28. These averages, obviously do not take into account empty cells (zero correlations) and the overall average will be affected by the number of such values — large number of empty cells implies low average correlation for a given block. This is why we report only the number of correlations above .20 in the main body of the text as an estimate of the relative strength of relationship between Gamma synchrony measures and cognitive variables.

6.4. Validity of the Oddball Reaction Time Task (ORT) that generated the Gamma synchrony data

The first column in both Tables 4 and 5 presents correlations between reaction times in the oddball task, used to generate Gamma-band synchrony measures, and the synchrony measures themselves (i.e., magnitude and latency of the dominant peak). Two outcomes are worthy of consideration because they show that synchrony measures are indeed valid measures of the processes presumed to be captured by this task. First, Oddball Reaction Time (ORT) has higher correlations with the latency of the dominant peaks (11 values above .20 in Table 5) than it does with magnitude (four values above .20 in Table 4). Secondly, it is the G2 latency for the left hemisphere that shows the highest correlation (.51) with ORT. This correlation is positive, implying that faster ORTs lead to the quicker occurrence of the dominant G2 peak. Also of note is that a large number (seven) of correlations between G2 latency and ORT are above the .20 value. This is encouraging, since it suggests that there is a reasonably strong link between cognitive task performance and indices of the synchronous activity of cell populations that are activated by this performance.

6.5. Correlations between synchrony and psychometric measures

Because EEG recordings did not accompany psychometric measures, their correlations with the magnitude and latency measures of synchrony generated by the oddball task should be lower than those obtained with the ORT measures. To the extent that these correlations exist at all, they may be interpreted as indicating links between cognitive performances tapped by tests of intelligence and measures of synchrony induced by activities much less directly related to intelligence. Clearly, as can be ascertained readily from inspection of Tables 4 and 5,

a. Psychometric tests *do correlate* with both magnitude and latency measures of synchrony. In addition,
b. Correlations with *latency are more prevalent* and somewhat stronger than with magnitude measures. Thus, excluding the ORT column, there are 62 coefficients above .20 in Table 4 (magnitude) and 75 coefficients above .20 in Table 5 (latency). This may be due, in part, to greater inter-individual variation in the magnitude of Gamma synchrony.

As we move from general to specific considerations, the observations tend to become more tentative. Broad findings are as follows:

a. *Small Gamma 1 vs. Gamma 2 differences*. Horizontal divisions within Tables 4 and 5, contrary to our expectations, do not show a great difference between G1 and G2 with respect to the size of correlations. However, there is a small difference with respect to the number of noteworthy coefficients. We expected stronger correlations with synchrony measures from the G2 window, since this would implicate the tuning-in of post-sensory processes. Very slight support for this claim is present in both Tables 4 and 5, considering there are 75 correlations of .20 and above for G1 in these two Tables compared to 79 coefficients for G2.
b. *Higher Correlations with Psychometric Measures of Speed than Accuracy*. Vertical division into the Accuracy (63 coefficients above .20 in both Tables) and Speed (74 coefficients) composites indicates differences between the two, with more prevalent and very slightly higher correlations with the speed than with the accuracy measures from the psychometric domain. We suggest that this is due to speed measures capturing the efficiency of processing, indexed by Gamma synchrony, in a more robust manner.

6.6. All brain regions show correlations between psychometric and synchrony measures

Inspection of the correlations of psychometric measures with magnitude and latency measures of synchrony, across regional (horizontal in Tables 4 and 5) divisions of the brain areas, demonstrates that there are no sites showing no correlation with at least one psychometric composite. Perhaps it is worth noting, however, that measures of synchrony for the whole brain (the first row labeled "All" in Tables 4 and 5) have no noteworthy correlations with the magnitude of the dominant peaks. This finding can perhaps be interpreted to mean that no measure employed in this study (psychometric or Gamma-band EEG) captures synchronous activities from the whole brain.

6.7. All accuracy and speed composites correlate with synchrony measures

Looking down the columns in Tables 4 and 5, one finds noteworthy correlation coefficients for every column. It is difficult, in the absence of independent observations, to make specific claims that synchronous activity elicited by the oddball task at particular groupings of EEG recording sites should have significant correlation with a particular aspect of intelligence. Yet they all obviously do show some correlation, at least for one brain region. It is quite possible that neural populations activated by a particular task will be located in non-contiguous parts of the brain; however, this option has not been explored with the present data.

6.8. Positive vs. negative correlations

Finally, as can be seen from Tables 4 and 5, noteworthy correlation coefficients can be both positive and negative. While it could be assumed that high magnitude and shorter latency of the dominant peak of maximum synchrony would indicate more efficient tuning-in of cell assemblies and therefore should correlate positively (negatively for speed) with intelligence, other scenarios are equally as plausible. For instance, efficient processing of information may entail minimal synchronization in some brain regions, indicating it is not necessary to integrate those networks for the task at hand; negative correlations imply such relationships. These possibilities are in line with an EEG study finding that more able individuals not only showed a lower level of activation over the same brain regions but also deactivated particular brain regions, while undertaking a task, which the less able did not, consistent with an "efficiency" model of neural processing (see Neubauer, Freudenthaler, & Pfurtscheller, 1995). Again, we feel that it is too early to consider in any depth the meaning of the negative correlations herein; suffice to say that the relationship between the indices of Gamma synchrony and intelligence promise a rich body of interesting hypotheses.

7. Discussion

The results of this study clearly indicate that there are noteworthy and significant correlations between different measures of intelligence and two indices–magnitude and latency of the dominant peaks – of synchronous activity, or the tuning-in of brain cell populations. These correlations are marginally stronger for the later Gamma synchrony window (G2), which indicates post-sensory (mediating) processing. Psychometric test-taking speed also has somewhat higher correlations with measures of synchrony than measures of accuracy, perhaps because speed reflects more directly the efficiency of integrative processing. At this stage, detailed claims about the implications of the patterns of correlations would appear premature. However, preliminary speculations about the present findings may be put forward.

At the overall group level (i.e., in terms of arithmetic means over all participants) it is the centero-temporal region that shows the highest and fastest level of synchronous activity. However, individual differences within this region do not show patterns of correlation with measures of intelligence that set them apart from any other groupings of EEG sites employed in this study. This implies, of course, that while the centero-temporal region shows more synchrony than most other regions of the brain, those people who have higher synchrony within this region are not necessarily advantaged over those who show high synchrony at other regions of the brain.

Our findings are based on a relatively small sample of participants, especially in comparison to typical studies of intelligence, and are therefore in need of replication. Nevertheless, there is enough evidence in the present data set to suggest that synchrony measures may indeed be found to reliably correlate with intelligence. First, the number of noteworthy and significant correlation coefficients cannot be easily dismissed as merely due to random sampling effects, and our attempts to apply rather stringent criteria in the analyses by looking for outliers did not produce significant changes in the results. It is also encouraging that there were significant correlations between performance on the event-related auditory oddball task and measures of synchrony. This finding reinforces the interpretation that correlations with measures of intelligence may represent reliable findings.

There are at least three issues that should be considered in future work, which could have ramifications for the way in which cohesive activation of cell populations is conceptualized. One issue that will be necessary to examine derives from the possibility that synchrony measures from non-contiguous regions may show even greater correlations than those obtained in this study. In the absence of sufficient leads regarding the possible localization of cell populations that need to be tuned-in in order to perceive an object or to carry out information processing activities, the number of possible

sites that may function synchronously is rather large. It would therefore be useful to develop a rational approach to a plausible choice of options for examination. For instance, one might choose to investigate synchronous activity between brain regions that have been shown to be active during a particular task, using neuroimaging methods. Another issue is the possibility that intelligence may show more robust correlations when synchrony across frequency bands other than 40 Hz Gamma may be considered, given that cognitive function has been associated with more complex synchronization of large-scale networks across a range of high frequencies (Bressler, Coppola, & Nakamura, 1993). Finally, it may be useful to replace the oddball task with other cognitive tasks, particularly those typically employed in tests of intelligence. It seems logical that more complex tasks would engage cell populations whose synchronous activity would be even more closely related to intelligence than the rather simple oddball task. It has been important to establish the functional significance of task-related EEG activity initially in tasks tapping fundamental cognitive processes. However, the use of EEG with more complex tasks is now being developed (Connolly & D'Arcy, 2000).

There are also theoretical implications of the work presented here. First of all, given that there are relatively small differences in the size (but not in the number) of correlations between the G1 and G2 latency windows (as shown in Tables 4 and 5), it is possible to claim that Hebb's distinction between sense-motivated and mediating (thinking) process is not justified and should be abandoned. This is certainly supported by the difficulties psychologists generally experience in distinguishing between "lower-order" and "higher-order" cognitive processes. Another issue is the role of "speed vs. power" in the activation of cell populations. The question arises is there an analogue of the speed-accuracy trade-off such that different cell populations may be activated under different instructions (i.e., between those emphasizing speed and those emphasizing accuracy)? What is the relationship, if any, between the magnitude and the latency of the dominant peak of synchronization?

The present results are clearly encouraging and hold promise as a potential means for an improved understanding of neural plasticity, as well as the relationship between environment and heredity in the development of individual differences in cognitive abilities. Although it would be interesting to attempt to identify localization of the active populations, and link them to anatomical features of the brain, this task appears too difficult to tackle at present. However, synchronous activity goes further and in fact provides a plausible physiological mechanism, which may account for the quality of cognitive processing and individual differences therein, since it points to the source of errors in the binding of neural activity underlying cognition.

Acknowledgements

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