Gamma Synchrony in Conscious Visual Processing

A Thesis
Presented to
The Division of Philosophy, Religion, Psychology and Linguistics
Reed College

In Partial Fulfillment
of the Requirements for the Degree
Bachelor of Arts

Tristan Eric Ryan Roberts

May 2012

Approved for the Division
(Psychology)

Michael Pitts

Table of Contents

Abstract

Consciousness and attention are two of the most commonly studied topics in the cognitive sciences, yet their dynamics remain poorly understood. The relationship between these two processes is a topic of recent debate: is attending to something the same as being conscious of it, or does attention's mechanisms independetly precede consciousness to select what actually does enter into awareness? This study attempts to address this question by analyzing data in which consciousness and goal-oriented attention vary while the actual physical stimulus remains the same. To do so, measures of phase relationship (alternatively known as synchrony) in the gamma frequency range were computed and then compared between the conditions and stimuli of a vision based procedure. In addition to potentially extricating differences between these two complex processes, the analysis of this information provides an intimate view into the inner workings of the cognitive system.

Dedication

For my fellow adventurer of the mind and multiverse, Adam

Introduction

Neural oscillations, or brainwaves, are at the very least a temporally sensitive index of brain dynamics and at the most a necessary condition for consciousness[11][26]. In order to ellucidate their role in cognitive function, this paper explores the flow of visual information starting with the retina and ending with conscious awareness.

0.1 Visual Processing

When light strikes the retina, one of the most complex processes known to man begins. Some preliminary processing is done locally in the retina, converting photons into neuronal impulses that are transmitted along the optic nerve and tract before reaching the midbrain structures known as the superior colliculus and lateral geniculate nucleus (LGN). Information is both consolidated and divided during this feed-forward process. The superior colliculus relays its processed information to the frontal eye fields while the LGN forwards signals to the occipital cortex, where the majority of visual processing is carried out.

The spatial relationships between patterns of light that struck the retina are fairly well correlated with fields in the first layers of the occipital cortex[17]. This direct correlation between cortex and retina location begins to fade as the visual information ascends the processing hierarchy. Higher increasingly focused on the relation of features into objects and their abstract qualities, although the spatial relations are preserved through some other mechanism in other areas such as the posterior parietal cortices. The first field of visual processing in the occipital cortex, V1, is devoted to simple features such as borders and lines. As representations move up the visual hierarchy the spatial correlation begins to fade as features congeal into objects. The values of these proto-percepts is sent to the temporal cortex via the ventral stream. Here, objects are assigned meaning by sets of neurons that fire only in the presence of a particular object, such as Jennifer Anniston[33].

While this feed-forward hierarchy of increasing complexity is the dominant model used to explain how the brain transforms light into objects and objects into concepts, it doesn't reveal how this process simultaneously preserves information about the features that led to that activation. The semantic value of an object doesn't occur in absence of the percept's features. Thus, maintenance and integration of the initial information must occur by some method.

0.2 Oscillations

Neural oscillations were first observed by the inventor of the electroencephalography device (EEG), Hans Berger, in 1929. He noted dramatic shifts in the electrical signals being read on the scalp of human subjects accompanying their gradual loss of consciousness as they drifted to sleep[6]. Jagged waves in the beta-range (12-30Hz) give way to more regularly formed alpha waves (8-12Hz), then theta waves (4-8Hz)[39]. The deeper levels of sleep alternate between high amplitude, low-frequency patterns called delta waves as well as rapid-eye movement (REM) sleep, which exhibits a chaotic mix of alpha and beta activity similar to wakefulness[24].

Higher frequency oscillations, referred to as gamma waves (>30Hz), were undetectable with early techniques. These patterns were first recorded using intracortical electrodes implanted in rats and primates. This method circumvented one of the primary factors that obscured the detection of gamma activity with EEG: the intermediary matter between the cortex and scalp which diffuses the relatively low-power signal. The other difficulty to their detection is the interference from the higher amplitude, lower frequency oscillations, which necessitate signal analysis in order to extricate the gamma waves from their context.

0.2.1 Early Correlates

Inquiries into the functional significance of neural oscillations were first conducted with rodent subjects. The EEG signal of the rat predominantly exhibits theta-range activity during locomotion, orienting, and other voluntary behaviors, and is strongest when drawing from spatial memory such as with a maze task [12]. In both humans and other mammals, this pattern has been found to originate in the primary memory center, the hippocampus, although frontal regions of the cortex have also been implicated in generating these oscillatory patterns in primates[18]. Early behavioral paradigms noted an increased amount of theta activity during trials in which memory was successfully encoded during the navigation of mazes. By generating its own consistent rhythm, the hippocampus is believed to be able to utilize the remainder of the brain as a spatial map without significantly interfering with the other structures′ functionality[21].

In the late 1980s, gamma waves were experimentally associated with perceptual binding – the process by which features are united into a cohesive object. In the occipital cortex of cats, cytoarchitectural columns represent distinct portions of the receptive field, i.e., portions of the retina. Using electrodes implanted in proximate but distinct columns, Gray et al. (1989) found synchrony between sites in the gamma range when a visual stimulus spanned across the receptive field, as well as when two bars in each respective receptive field moved in the same direction [15]. This finding generated the hypothesis that conceptually related but spatially disparate neuronal information is integrated using frequency as reference point. The implications of this seminal paper are debated to the current day, with a multitude of subsequent papers supporting, extending, or contesting their bold conclusion[40][37][26] .

0.2.2 Function

Since Gray et al., a plethora of functions besides feature binding have been correlated with gamma synchrony: fusing spatially-distributed neuronal assemblies, attentional modulation of sensory signals, sensorimotor integration, working memory, and conscious perception[37]. This versatility suggests that oscillatory activity reflects a general computational process rather than a specific function. Integration and differentiation are perhaps the most general terms that characterize oscillations' function, as they can both bind elements and differentiate sets of elements (objects) utilizing the temporal axis. Of central importance to understanding neuronal processing is the modulation of the signal-to-noise ratio, by which relevant information is selected. Classically, feature intensity was believed to be solely encoded by the firing rate of a neuron: faster firing, sharper feature. However, the cognitive system has other means of amplifying signals above the din of stochastic firing. Gamma-band activity in the occipital cortex was found to be modulated by the speed of a stimulus's movement in a magnetoencephalography study by Siegal et al[36]. Using a distributed source reconstruction technique, they found that this variable-dependent increase in gamma power most likely came from occipital area V5, which was already well-documented in having a role in the perception of movement. Oscillatory activity has long been theorized to play a role in modulating gain for percepts, either by amplifying the signal or reducing proximate noise to facilitate the perception of salient features[25].

While Siegal et al. concluded that their findings were evidence of gamma being a marker of feature intensity, they neglected to expand on one of the more interesting corollaries of their data: their source reconstruction indicated that the majority of variable-independent gamma activity originated from the pericalcarine cortex[36]. In primates, the upper bank of calcarine fissure responds strongly to the lower half of the visual field, while the lower bank processes the upper visual field[10]. Despite this anatomical divide, our visual field is perceived as a cohesive whole. Binding across space seems to be a critical function of oscillatory activity.

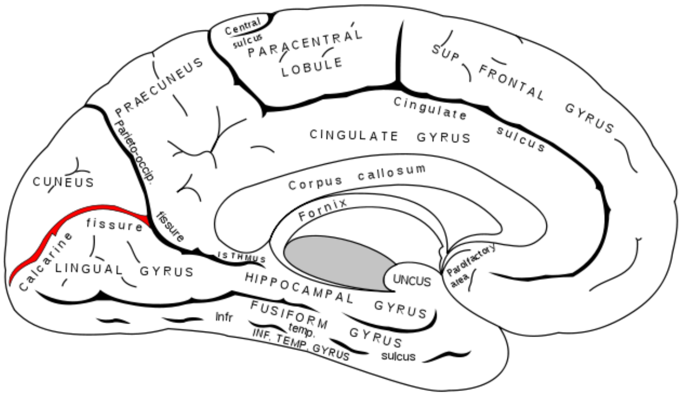

Figure 1: The calcarine fissure, located in the occipital cortex.

0.2.3 Interactional Effects

While gamma waves have been tied to a number of functions, much less has been definitively said about the slower frequency bands. These oscillations have been theorized to synchronize information over greater distances[19], but this conflicts with evidence suggesting that gamma coherence can occur between spatially distant structures[16]. However, the long range coordination of gamma may be mediated by the slower rhythms. Historically, alpha activity was believed to indicate idling or inhibition, but recent studies have found interactions between the phase lengths of different spectral patterns, suggesting that certain ratios such as three gamma waves for each alpha wave are maintained during certain mental tasks[29]. Visual processing of percepts increases gamma power while decreasing the slower alpha and beta frequency power[7]. Whether this represents a temporal-axis processing bottleneck, reduced inhibition, or some other function has yet to be uncovered. Similarly, phase and power mesh in ways not yet fully understood. Canolty et al. analyzed recordings from intracortical electrodes in humans during a variety of cognitive tasks. They found that the phase of theta modulated the amplitude of gamma[9]. Both of these bands had previously been implicated in the maintenance of items in short-term memory, and this interaction offers a tantalizingly simple albeit untested explanation as to why humans can hold 7 ± 2 items in mind at once: each instance of a theta wave($\backsim$140ms) contains enough space for around seven gamma waves($\backsim$20ms), permitting a means of both differentiating and integrating conceptual representations. Just as information flows between the spaces of anatomical structures, oscillatory patterns seem to interact in all possible manners during the course of neuronal processing. A taxonomy of these interactions has yet to be plotted, but the specific interactions are likely distinct for different cognitive tasks and perhaps even between individuals.

0.3 Consciousness

The transition from sleep to consciousness gives us some clues as to what systems are central to consciousness. fMRI data from waking subjects show an increase in blood flow in the brainstem and thalamus, followed by the cortex, especially in the prefrontal and cingulate regions[31]. Recurrent connections between the thalamus and cortex are believed to be necessary for the maintenance of consciousness, as any damage or disruption to the thalamus obliterates consciousness[1]. During the transition to wakefulness, there is a marked increase in the release of acetylcholine. Spontaneous, seemingly chaotic firing increases until high-frequency oscillations start to occur in the gamma band[20]. This increase in synchronized activity brings sensory input closer to the threshold necessary for it to propagate to the rest of the system[13].

0.3.1 Experimental Definition of Conscious Perception

Besides monitoring the global shifts in and out of sleep, consciousness has long been considered outside of the domain of empirical research. Subjective reports are notably unreliable and their corresponding perceptual content is inherently unobservable. Despite this technical hurdle, recent experimental protocols have managed to vary whether a stimulus is conscious perceived by keeping the stimulus near the threshold of detectability through a variety of methods. Crucial to this approach is that the stimuli presented remain identical throughout the experiment while the subjects' responses vary. By keeping the definition of consciousness to what is accessible by verbal report, the neural correlates of consciousness can be extricated by comparing behavioral outcomes: when a participant accurately reports their perception of a stimulus to when it fails to reach the necessary threshold.

0.3.2 Subtraction Experiments

By masking a stimulus i.e., obscuring it to the point where it is only occasionally detected researchers have been able to produce data that show a contrast between conscious and non-conscious processing. Utilizing the subtraction method outlined above, Melloni et al. investigated phase relationships based on prior evidence suggesting a correlation between consciousness and oscillatory activity. They found a significant increase in both the power and coherence of gamma oscillations before the anticipated presentation of the test word, and an increase in theta power over frontal regions while maintaining memory of the target[26]. As consciously-reportable stimuli differed in the amount of phase synchronization between spatially-disparate electrodes, they hypothesized that widely-distributed gamma synchrony is a necessary condition for consciousness. While this experiment provides compelling research for the above conceptualization of consciousness, it does have two criticall flaws. Controlling for attention is crucial to properly delineate conscious processing. This is a particularly difficult task because attention and consciousness are heavily entwined. Without controlling for this confound, it is impossible to be certain that they were not just detecting gamma synchrony related to the top-down attentional expectation of the stimulus. Additionally, as their measure of spatially-disparate electrodes was simply an aggregate of all electrode pairs, they may have mistaken a surge in local coherence as an increase in global synchrony.

0.3.3 Current Models

By evaluating the difference between when a stimulus is consciously perceived and when it is not, a number of neural correlates of consciousness (NCCs) have been uncovered. In additional to an increase in thalamocortical activity, the prefrontal and parietal association areas show an increase in their BOLD response[27]. Meanwhile, substantial occipital and temporal processing of visual and auditory stimuli can occur without the contents entering conscious awareness[14]. These results suggest that information must pass a threshold in order to reach the global level of processing, at which point one becomes consciously aware of it[13]. These findings led to the creation of the global neuronal workspace (GNW) theory, which states that if information passes a certain threshold, it is distributed to most, if not all, of the brain. When a percept or concept enters the GNW, a certain level of abstraction occurs. For instance, when commenting on the beauty of a particular object, the original visual information is processed into semantic concepts and then muscle movements. However, when uttering these words there is no loss of the original sensation.

0.4 Attention

[Section still in progress - make less pessimistic] Attention is one of the most thoroughly studied concepts in the cognitive sciences. Despite this, our knowledge of phenomena deemed attentional has increased little since ancient times. While attention is frequently attributed as the cause of experimental effects this is often in absence of a thorough definition. Anderson contends that the reliance on this concept as an explanation has resulted in a terminological oversimplification that occludes the underlying forces responsible[2]. No single structure, neurotransmitter or network has been determined to cause attentional effects. Because of this, Anderson contends that attention should not be cited as the cause of effects, as it is not a thing itself. Instead, attentional phenomena are an observable byproduct of the cognitive system in action. In light of these concerns, this paper will use a conservative definition of attention: "a basic cognitive faculty that allows us to filter out irrelevant sensory information in favor of the relevant." [28] Attention has traditionally been dichotomized into two flavors: top-down and bottom-up. Top-down attention refers to goal-orientated behavior, while bottom-up attention refers to the intrinsic properties of a stimulus. The former type will be addressed in this study.

0.4.1 Critical Component or Confound of Consciousness?

One of the most frequently addressed questions in consciousness studies is whether or not attentional effects can be dissociated from conscious awareness. Are they both facets of the same process, or does attention determine the contents of consciousness? Intuitively, what we attend to, whether it be external sensations or internal conceptions, seems to be what is consciously experienced. Research by Ansorge et al. has shown that goal-directed attentional effects can manifest in behavioral outcomes outside of conscious awareness, suggesting some dissociation between these phenomenons[3].

By some means the cognitive system is able to dynamically alter the gain of signals according to both stimulus driven salience (bottom-up) and behavioral goals (top-down). Attention has been demonstrated to increase gamma power during the expectation of a stimulus in primates[38]. Thus, neural oscillations may provide an means of interfacing the top-down and bottom-up drivers with incoming stimuli[28].

0.5 Experimental Aims

In order to dissociate attention from consciousness, an experiment must somehow present the same visual information, alternating between both conscious or unconscious processing, with or without attention. Finding a global increase in phase synchrony of gamma oscillations (i.e. consistent phase relationships between signals recorded at from spatially distant scalp electrodes) during conscious, relative to unconscious processing, would confirm Melloni et al.'s hypothesis that distributed synchrony is a necessary condition for consciousness, while finding an increase in intra-area phase relationships only during goal-orientated behavior would suggest such that increases in gamma synchrony are a marker of attention.

The following analysis will utilize data from a previously performed experiment that used inattentional blindness to obscure a visual pattern in the first condition. Inattentional blindness is the amply demonstrated phenomena in which a resource-demanding task prevents subjects from noticing otherwise obvious stimuli[23]. In the first condition, the detection of square and diamond-shaped patterns forming in the center of fixation was prevented by the attentional demands of a distracting task. Following the first condition, subjects were queried about whether they noticed patterns forming from the lines. Half of the subjects reported not seeing the square and diamond-shaped patterns forming, and it is their data that will be analyzed here. In the second condition, participants were given the same task but all reported seeing the shapes when queried afterwards, despite that they were not the the target of their task, and thus their goal-orientated attention. In the final condition, participants were both aware and explicitly attending to these shapes, as the task was to respond only when the diamond-shaped pattern was presented. In both the second and third condition, the square and diamond shapes were attended to, but only in the later condition was this mediated by an explicit task. By separating whether or not the participant consciously saw the stimulus, and whether or not their task was to respond upon seeing the stimulus, this experiment aims to extricate attention from consciousness.

Chapter 1

Method

1.1 Experimental Protocol

Participants

Thirty-eight adult volunteers participated in the experiment, but the data from only thirty-two was used in the analysis due to excessive artifacts in the EEG recording.

1.1.1 Stimuli

A large, red disc with eight nodules surrounded a 20x20 grid of small white line segments. These lines maintained a random configuration for 600-800ms before shifting into one of three possibilities: an array with an embedded diamond (10% likelihood), or square (40%), or another chaotic jumble (50%) for 300ms before returning to a baseline, chaotic configuration. A video of the stimulus can be found at: `http://www.youtube.com/watch?v=8-9NAFUn_CI`

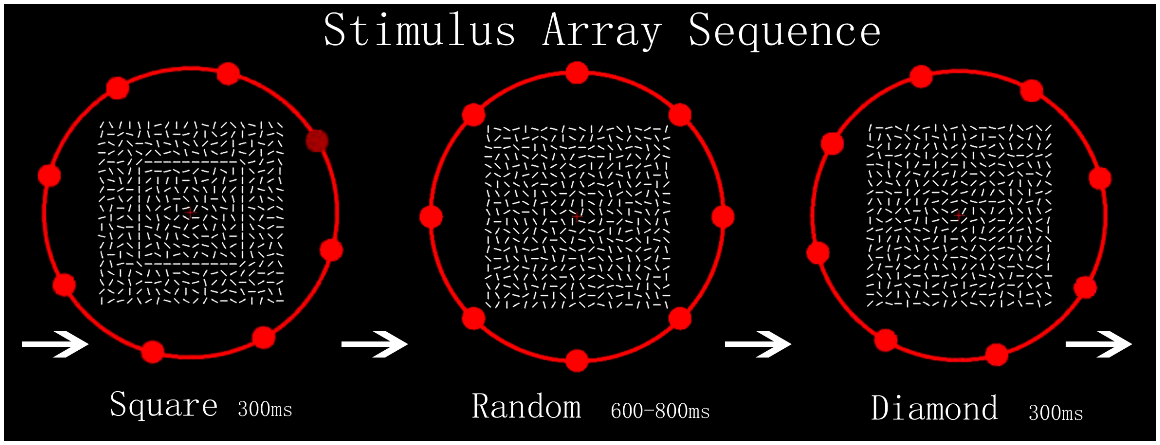

Figure 1.1: Figure 2: An example of the sequence of the stimulus array

1.1.2 Conditions

The same stimulus array and sequence was used for each of the three conditions. In the first condition, participants were instructed to respond when they detected a decrement in luminance in one of the red orbs after undergoing some practice rounds. Following 240 presentations of the square pattern, the first condition ended. Participants were asked to rate their confidence from 1 to 5 in noticing the square and diamond patterns, as well as for four distractors. Only data from the participants marked their confidence in seeing the actual patterns as 3 or below was used in the analysis. In the second phase, the task and stimulus remained the same, but afterwards all participants rated their confidence in detecting the square and diamond as 4 or 5. In the third phase, the stimulus remained the same, but participants were tasked with responding upon detection of the diamond pattern. These conditions will be referred to as 1) unconscious, task irrelevant 2) conscious, task irrelevant and 3) conscious, task-relevant.

1.2 EEG Processing

Analog signal from 64 electrodes was digitized at 500 Hz. A right mastoid was used for reference, and two vertical EOGs were used for detecting eye movements. The data was re-referenced to an average of all electrodes. Muscle and eye-movement related artifacts were removed. The data was time-locked to transitions away from the base stimulus, and -1000ms to +1000ms segmentation was applied, leaving slices of electrical data surrounding the presentation of the different stimuli arrays.

1.3 Spectral Analysis

Fast fourier transforms were applied to the processed EEG data to obtain spectral information. 32 frequency steps were applied to the 20 to 80 Hz range. Lachaux et al.'s phase-locking statistics method was used to acquire a measure of phase relationship between electrodes that is independent of amplitude for each electrode pair[22]. Groups of electrode pairs were then established. The first group was selected from the primary visual processing areas. This intra-occipital group contained the 31 electrode pairs between P3, P4, P7, P8, O1, O2, P04, P07, P08, and P09, and will be referred to the "local" group of electrodes. In order to measure communication across the cortex, a second group of electrode pairs was also selected. These 389 pairs were between occipital and non-occipital electrodes, and will be referred to as the "global" group.

1.4 Statistical Analysis

The main comparisons of this study are between the square and random array values for each condition. Additionally, the differences between conditions from the square stimulus was also be analyzed.

For both the local and global grouping of electrodes, t-tests were performed on the 50 to 700ms time window for every frequency and time point therein, using the false discovery rate (FDR) correction to balance for the number of tests.

Additionally, regions of interest (ROIs) were selected based upon groupings consisting of at least 15 contiguous positive t-tests (p value $= <.03$). These regions were selected from 28 to 72hz, to avoid contamination from other frequency bands. T-tests were then performed for the average value of each ROI relative to the same window in the random array data, as well between the values of the square responses of the other conditions.

Chapter 2

Results

Using the false discovery rate method of correction, no differences between individual frequency/time locations was deemed statistically significant. However, four regions of interest were selected.

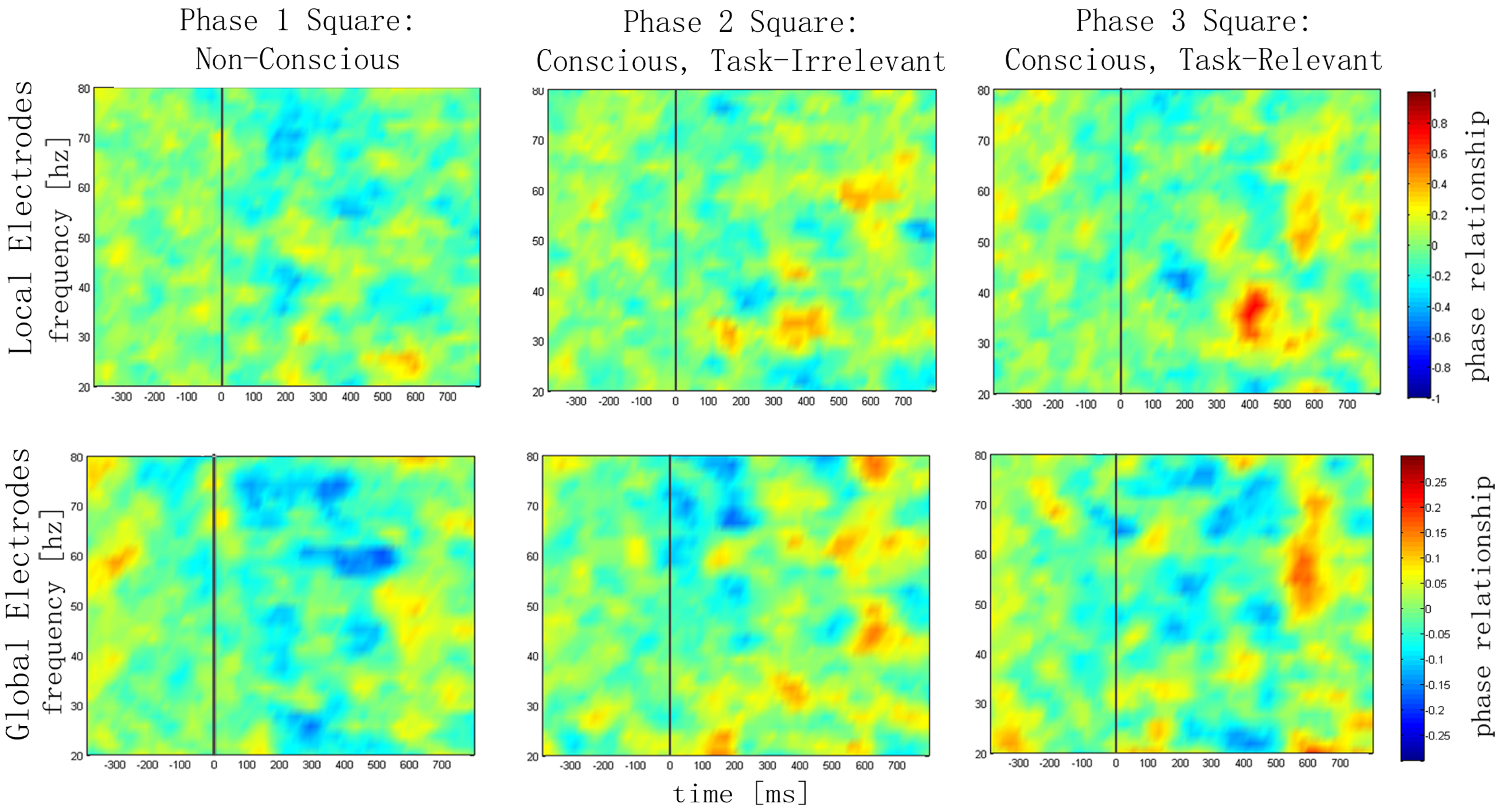

Figure 2.1: Phase relationships of intraoccipital/local electrode pairs (on top) and interoccipital/global electrode pairs (on bottom) resulting from the presentation of the square stimulus at time 0. Average strength of gamma synchrony (phase relationship) between selected electrodes is indicated by color. (Please note difference in power bar between local and global)

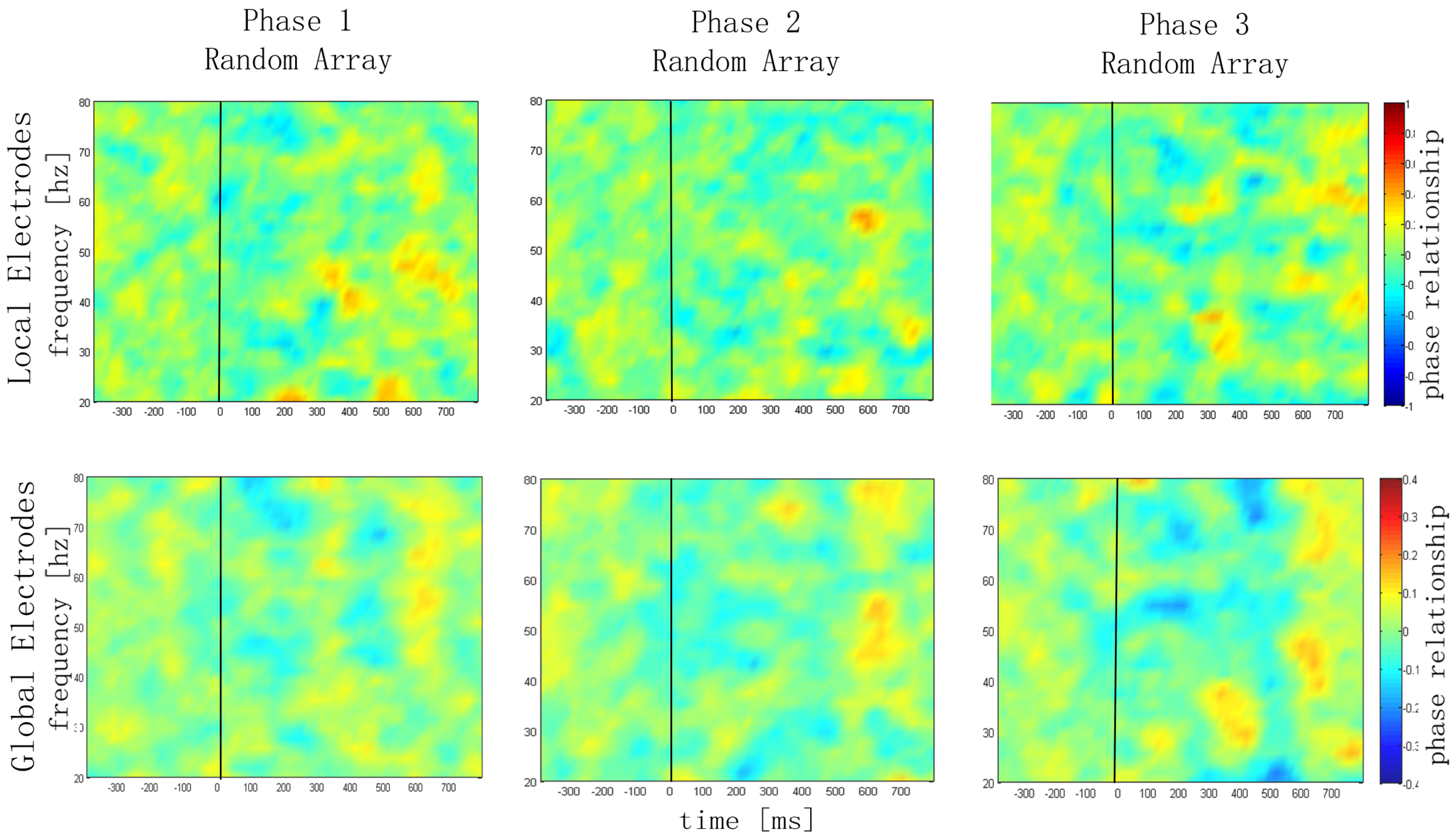

Figure 2.2: Phase relationships of intraoccipital/local electrode pairs (on top) and interoccipital/global electrode pairs (on bottom) resulting from the presentation of the random stimulus at time 0. Average strength of gamma synchrony (phase relationship) between selected electrodes is indicated by color. (Please note difference in power bar between local and global)

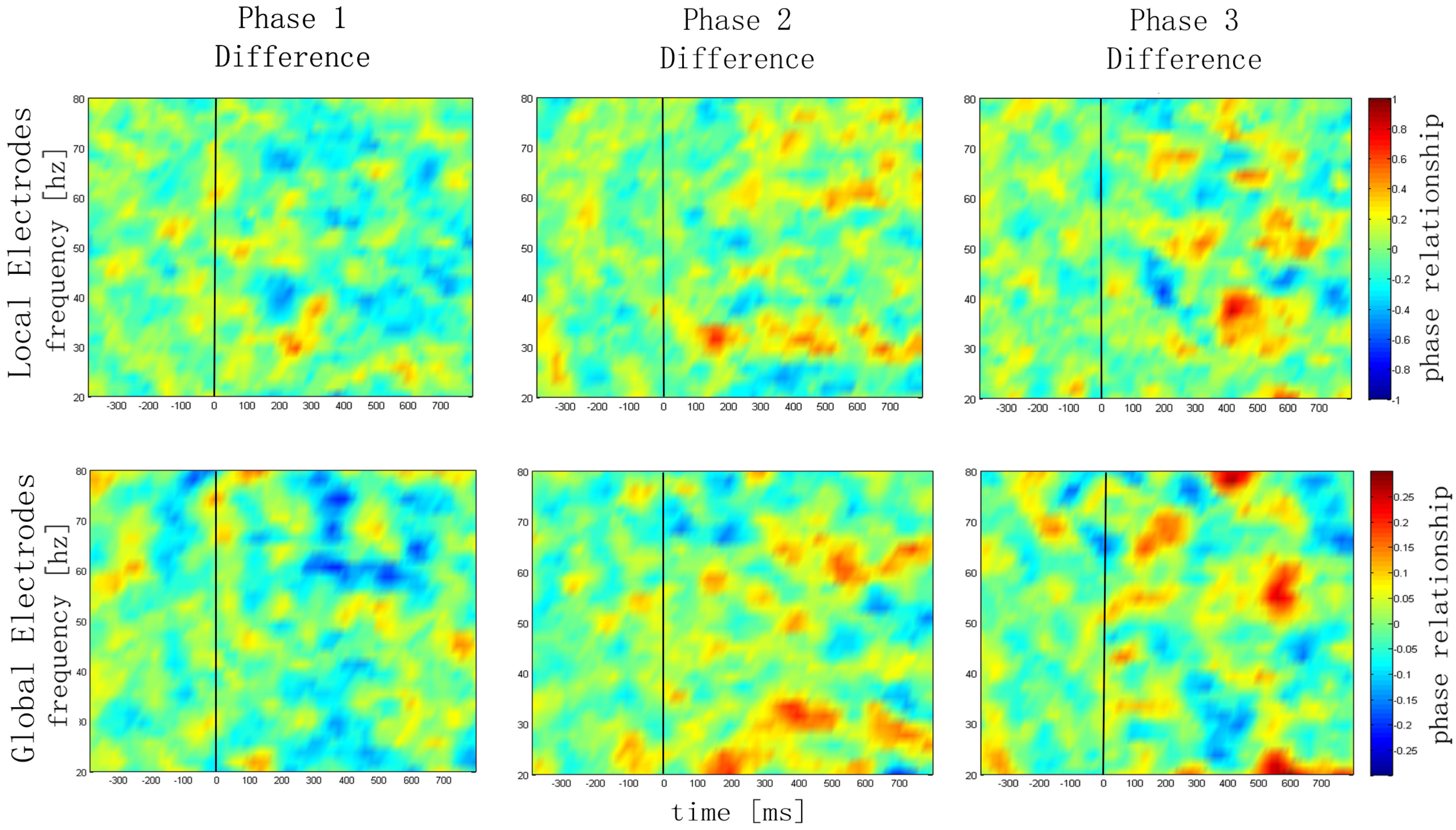

Figure 2.3: Phase relationships of intraoccipital/local electrode pairs (on top) and interoccipital/global electrode pairs (on bottom) resulting from the presentation of the random stimulus at time 0. Average strength of gamma synchrony (phase relationship) between selected electrodes is indicated by color. (Please note difference in power bar between local and global)

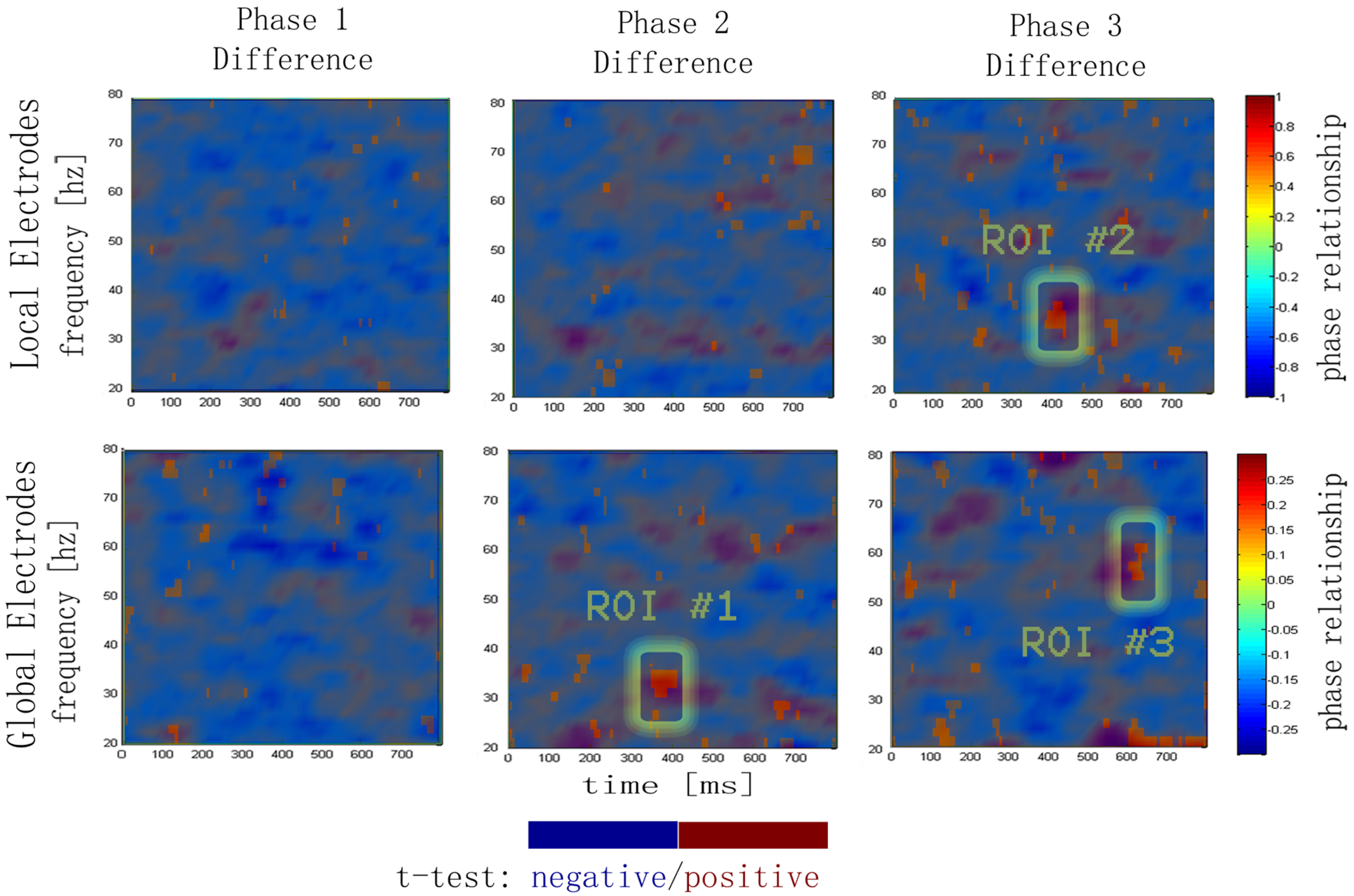

Figure 2.4: A composite of both the synchrony plot for the difference in synchrony between square and random responses and a plot of t-tests for each respective individual time/frequency point. Regions of interest were selected based upon number of contiguous positive t-tests.

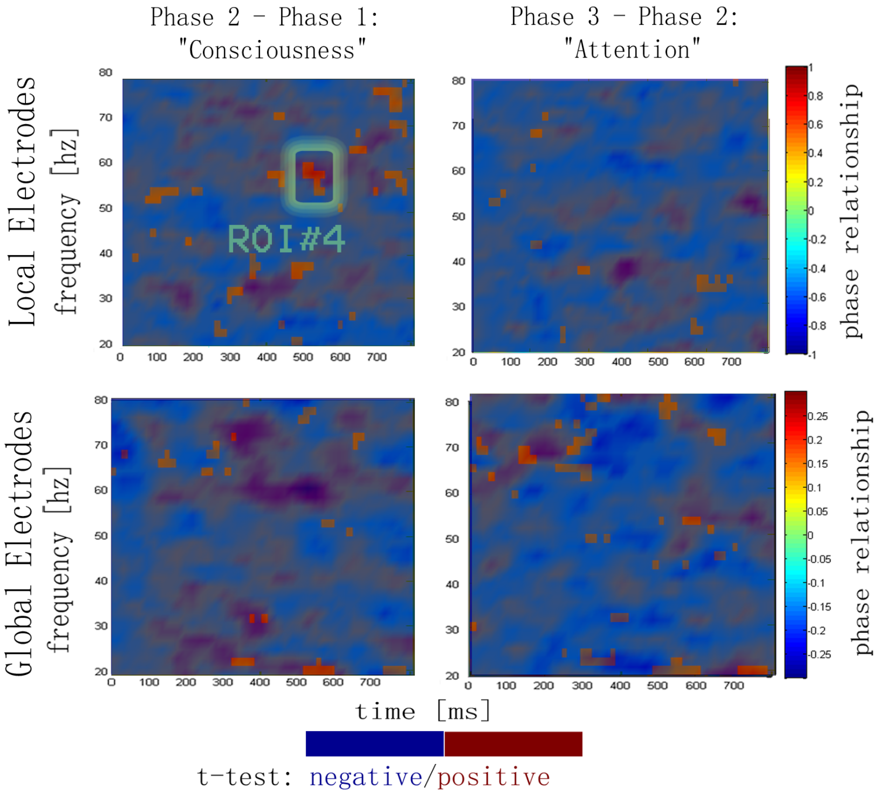

Figure 2.5: A composite of both the synchrony plot for the difference in synchrony between square responses from different conditions and a plot of t-tests for each respective individual time/frequency point. Region of interest was selected based upon number of contiguous positive t-tests.

Table 2.1: Regions of Interest Statistics

ROI#	Freq/Time Range	vs.	p value <...
1	28-33Hz/340-400ms	Ph2-Square vs. Ph2-Random (Global)	.03
2	31-41Hz/380-520ms	Ph3-Square vs. Ph3-Random (Local)	0̇5
3	54-62Hz/580-640ms	Ph3-Square vs. Ph3-Random (Global)	.05
4	52-60Hz/520-560ms	Ph2-Square vs Ph1-Square (Local)	.05

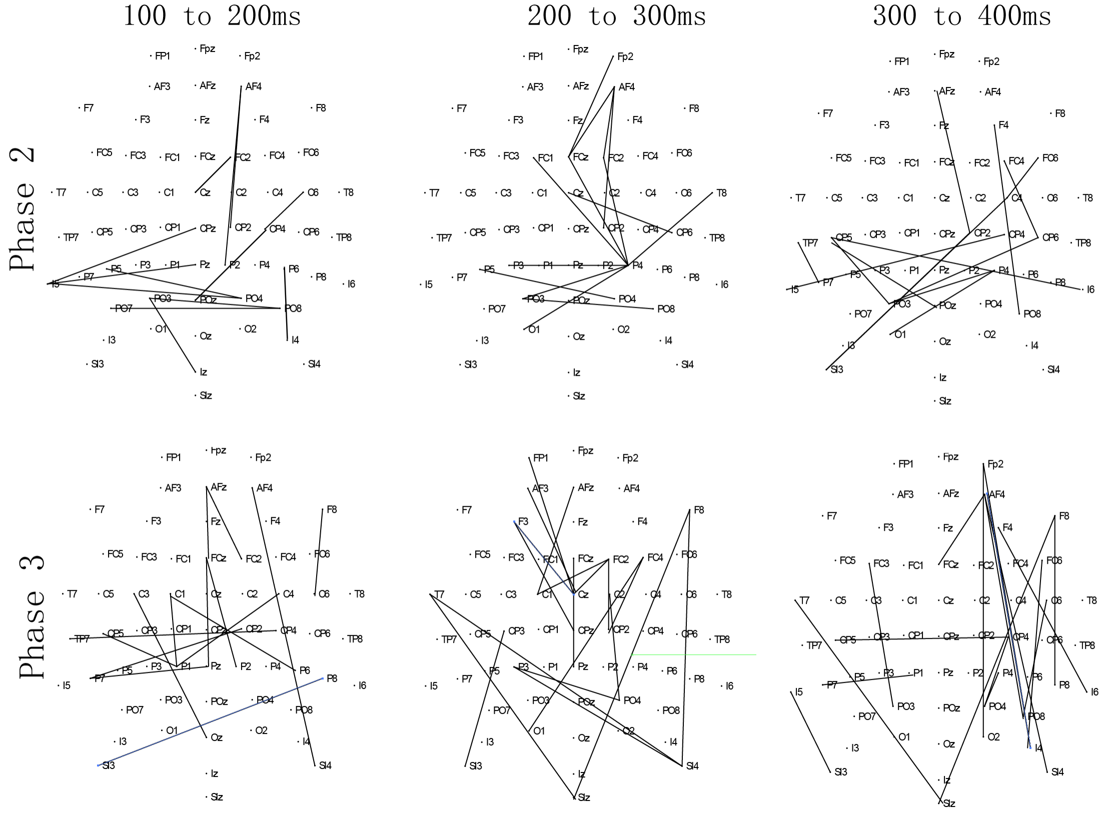

Figure 2.6: A plot showing the 15 most synchronous electrode pairs for the given time windows, taken from the square stimulus.

Chapter 3

Discussion

3.0.1 Summary of Results

Utilizing the gamma frequency to inspect the present data, one clear difference between the square and random stimuli emerges: both conscious conditions feature a substantial increase in the amount of gamma synchrony following the ∽100ms it takes information to reach the occipital cortex[41]. As an increase in global synchrony was found in the conscious, task-irrelevant condition, this data is taken as supporting Melloni et al.s hypothesis that long-range synchrony is a necessary condition for consciousness. Before an interpretation of the four regions of interests (ROIs) can be performed, a brief account of how the cortex processes visual information is necessary.

3.1 A Model of Information Flowing between Cortical Processing Modules

In the first condition, the salient shape of the square array was consistently ignored due to the subjects attention being placed elsewhere. Only a fraction of the information from the retina that the occipital cortex processes rises above the competing signals in order to be forwarded to other cortical structures. The subconscious processing of visual stimuli is detectable utilizing objective measures, but since the signal from undetected stimuli does not propagate to other cortical structures it never becomes verbally reportable by the subject[13][32]. When a particular percept does rise above the din of its competitors, the signal is not just forwarded to other cortical regions. If these other regions evaluate the percept as salient, it enters the global neuronal workspace: the signal is distributed to the entirety of the cortex, making it interpretable by a wide range of processing centers. In the case of this experiment, this event is demonstrable by the square and diamond arrays becoming verbally reportable: the processing of the visual cortex has spread to, at the very least, both the linguistic and motor areas (temporal and parietal cortices, respectively). Additionally, the signal may be fed back to its origin as the cortices feature multiple pathways for recursion[8]. In the present study, this feedback is evidenced by an observable event-related potential (ERP) commonly found with task-related discrimination. This event-related potential is a tendency towards positive voltage 340ms following stimulus onset over both occipital and parietal regions. Presumably, the frontal regions of the cortex are the origin of this signal, as they are thoroughly implicated in task-relevant discrimination[34]. Although the preceding account of how visual information flows is well documented through event-related potential research, the present data can illuminate crucial details of this process. We can conceptualize a particular neuroanatomical structure as being a cognitive module. A cognitive module receives information from elsewhere, processes it in a feed-forward manner, and then transmits it to other regions. As noted earlier, underlying this process is some level of conservation of initial information. For instance, the visual information of the letters of this sentence as retained even after being transmitted to regions that interpret their meaning. In order for these initial details to be maintained, the cognitive system must be able to bind the initial information to the output of subsequent cognitive modules. One possible way by which this binding of information is managed is through gamma synchrony.

3.2 Regions of Interest

The first region of interest occurs between 300 and 400ms in the lower gamma range (∽30hz), in the conscious condition without attention. This region is derived from the global electrode pairs, which in the case of the present study means pairs that consist of one occipital and one non-occipital electrode. This ROI indicates the very sort reference outlined above, in that the synchronization to a particular frequency may be used as a stable referent to the initial information, no matter how many cognitive modules the information is fed through. Furthermore, this burst in synchronous activity may signal the initial percept entering the global neuronal workspace, which has been suggested by previous researchers to occur within this time frame[35]. Soon after the first ROI there is a consistent pattern of synchronous activity within the occipital electrode pairs in the conscious, attentive condition. This second ROI is localized to 400ms post-stimulus, and may be an observable manifestation of visual information returning to the occipital cortex following processing by other areas. The third ROI occurs nearly 600ms following the stimulus onset in the conscious, attentive condition, between the global electrode pairs. This corresponds to the average response time it took subjects to respond to their discrimination task in the third condition, and thus may represent the decision to not respond. A second possible interpretation of this burst of synchrony is the occipital cortex forward feeding the visual information to other cortical areas for a second time. This ROI is of a significantly higher frequency than the first two, and this may be the natural degradation of a percept that is not actively maintained by memory, permitting the lower gamma range to be occupied with newer visual information. The final ROI was derived from subtracting the response to the square stimulus in phase 1 from the response to the same stimulus in phase 2. Theoretically, this difference eliminates sub-conscious processing while leaving behind an electrophysiological correlate of consciousness. Found amongst the occipital electrode pairs, the meaning of this ROI is indeterminable under the current frameworks that suggest that consciousness occurs approximately 300ms after stimulus onset as this region occurs after 500ms. If this ROI is a legitimate pattern of synchrony, it is almost certainly induced by feedback from the rest of the cortex. As postulated above, there may be a transition to higher frequencies following the first cycle through the recursive cortical loop, so that the lower gamma frequencies could be binding the elements of the ring stimulus that was the focus of attention in the second condition.

3.3 Implications

3.3.1 Attention

While there is a visible increase in synchrony following the presentation of the square stimulus in condition 2 within the occipital region, there is no discernible localization to a specific time/frequency region. In contrast, the third condition features definite islands of synchronicity. Thus, attention may modulate the strength of signals through focusing oscillatory patterns. Since visual attention was focused elsewhere, the presence of the square stimulus was minimally processed but not selected for further analysis. Despite this, it seems that the bottom-up salience of the stimulus evoked a global response, as evidenced by the first ROI . The results of the current analysis additionally suggest that although goal-orientated attention can modulate gamma rhythms, synchrony also occurs in absence of attention. The comparison between phase 2 and phase 3, which should contrast the effect of attention, is surprisingly bereft of any notable differences. As attention is the process of determining the value of neuronal information, and the contents of consciousness have by definition been evaluated as more salient than the competing information, it is entirely possible that attention and consciousness are different sides of the same coin.

3.3.2 Consciousness

In their 2007 study, Melloni et al. postulated that distributed (global) oscillatory synchrony is a necessary condition of consciousness. The present study extends and confirms their conclusion. One of the greatest shortcomings in their method was pooling together all electrode pairs in order to assess the global level of synchrony. Because of this, a substantial increase in synchrony within the occipital region could have led to the confirmation of their hypothesis. The first region of interest of this study provides evidence that inter-area synchrony is a correlate of, if not a fundamental aspect of, conscious awareness. The lack of any significant difference between the square and random stimulus in the second phase within the occipital electrode pairs confirms a common thread amongst consciousness theories: whatever consciousness is, it is not localized to any particular structure.

3.4 Methodological Shortcomings

EEG data has been collected for nearly a century, but the method of analysis employed by this study has hardly been around for a decade. The cognitive system is so densely packed with information that any method of observing its information and then analyzing it is equivalent to removing a single slice from a ∞-dimensional pie. While the present analysis was not able to arrive at a conclusion that satisfied the stringent requirements of the FDR correction, this shortcoming could be easily circumvented by selecting the "right" electrodes pairs and concatenating time and frequency windows so that only dozens of t-tests were performed instead of hundreds. However, a handful of significant p-values do very little to illuminate a system as complex as the human brain; hopefully the figures and analysis presented here provide a substantial flicker of elucidation. Theoretically, the experimental procedure that underwent analysis here provides an unrivaled means of accessing both attention and consciousness. In practice, however, the demands of a distracting task diminished the signals of interest, precluding any definitive conclusion from being reached about the relationship between these two enigmatic processes. Without standard definitions of attention and consciousness, any attempts to ensnare these complicated forces will, by definition, fail to adequately illuminate the actual reality anyways.

3.5 Conclusion

Consciousness, as well as other higher level cognitive processes, requires a precarious balance of integration and differentiation of information. Processing by definition entails change over time, but in order for the results to be meaningful some bits of the original elements must be preserved. While the firing rates of neurons provide an essential method of differentiation, oscillatory synchrony seems to provide the fundamental means of integrating information into coherent bundles.

References

[1] M.T. Alkire, A.G. Hudetz, and G. Tononi. Consciousness and anesthesia. *Science*, 322(5903):876–880, 2008.

[2] B. Anderson. There is no such thing as attention. *Frontiers in Psychology*, 2, 2011.

[3] U. Ansorge, M. Kiss, and M. Eimer. Goal-driven attentional capture by invisible colors: Evidence from event-related potentials. *Psychonomic bulletin & review*, 16(4):648–653, 2009.

[4] B.J. Baars. Global workspace theory of consciousness: toward a cognitive neuroscience of human experience. *Progress in brain research*, 150:45–53, 2005.

[5] T.J. Balkin, A.R. Braun, N.J. Wesensten, K. Jeffries, M. Varga, P. Baldwin, G. Belenky, and P. Herscovitch. The process of awakening: a pet study of regional brain activity patterns mediating the re-establishment of alertness and consciousness. *Brain*, 125(10):2308–2319, 2002.

[6] H. Berger. Über das elektrenkephalogramm des menschen. *European Archives of Psychiatry and Clinical Neuroscience*, 87(1):527–570, 1929.

[7] A. Bruns and R. Eckhorn. Task-related coupling from high-to low-frequency signals among visual cortical areas in human subdural recordings. *International journal of psychophysiology*, 51(2):97–116, 2004.

[8] M. Camperi and X.J. Wang. A model of visuospatial working memory in prefrontal cortex: recurrent network and cellular bistability. *Journal of Computational Neuroscience*, 5(4):383–405, 1998.

[9] R.T. Canolty, E. Edwards, S.S. Dalal, M. Soltani, S.S. Nagarajan, H.E. Kirsch, M.S. Berger, N.M. Barbaro, and R.T. Knight. High gamma power is phase-locked to theta oscillations in human neocortex. *science*, 313(5793):1626–1628, 2006.

[10] PM Daniel and D. Whitteridge. The representation of the visual field on the cerebral cortex in monkeys. *The Journal of Physiology*, 159(2):203–221, 1961.

[11] F.P. De Lange, O. Jensen, M. Bauer, and I. Toni. Interactions between posterior gamma and frontal alpha/beta oscillations during imagined actions. *Frontiers in human neuroscience*, 2, 2008.

[12] W.E. DeCoteau, C. Thorn, D.J. Gibson, R. Courtemanche, P. Mitra, Y. Kubota, and A.M. Graybiel. Learning-related coordination of striatal and hippocampal theta rhythms during acquisition of a procedural maze task. *Proceedings of the National Academy of Sciences*, 104(13):5644, 2007.

[13] S. Dehaene, J.P. Changeux, L. Naccache, J. Sackur, and C. Sergent. Conscious, preconscious, and subliminal processing: a testable taxonomy. *Trends in cognitive sciences*, 10(5):204–211, 2006.

[14] R. Goebel, L. Muckli, F.E. Zanella, W. Singer, and P. Stoerig. Sustained extrastriate cortical activation without visual awareness revealed by fmri studies of hemianopic patients. *Vision Research*, 41(10-11):1459–1474, 2001.

[15] C.M. Gray, P. König, A.K. Engel, W. Singer, et al. Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties. *Nature*, 338(6213):334–337, 1989.

[16] G.G. Gregoriou, S.J. Gotts, H. Zhou, and R. Desimone. High-frequency, long-range coupling between prefrontal and visual cortex during attention. *science*, 324(5931):1207–1210, 2009.

[17] D.H. Hubel and T.N. Wiesel. Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *The Journal of physiology*, 160(1):106–154, 1962.

[18] R. Ishii, K. Shinosaki, S. Ukai, T. Inouye, T. Ishihara, T. Yoshimine, N. Hirabuki, H. Asada, T. Kihara, S.E. Robinson, et al. Medial prefrontal cortex generates frontal midline theta rhythm. *Neuroreport*, 10(4):675, 1999.

[19] O. Jensen, J. Kaiser, and J.P. Lachaux. Human gamma-frequency oscillations associated with attention and memory. *Trends in neurosciences*, 30(7):317–324, 2007.

[20] B.E. Jones. From waking to sleeping: neuronal and chemical substrates. *Trends in pharmacological sciences*, 26(11):578–586, 2005.

[21] M.J. Kahana, R. Sekuler, J.B. Caplan, M. Kirschen, and J.R. Madsen. Human theta oscillations exhibit task dependence during virtual maze navigation. *Nature*, 399(6738):781–784, 1999.

[22] J.P. Lachaux, E. Rodriguez, J. Martinerie, F.J. Varela, et al. Measuring phase synchrony in brain signals. *Human brain mapping*, 8(4):194–208, 1999.

[23] A. Mack, I. Rock, and MITCogNet. *Inattentional blindness.* MIT press Cambridge, MA, 1998.

[24] M. Massimini, F. Ferrarelli, MJ Murphy, R. Huber, BA Riedner, S. Casarotto, and G. Tononi. Cortical reactivity and effective connectivity during rem sleep in humans. *Cognitive neuroscience*, 1(3):176–183, 2010.

[25] A. Mazaheri, I.L.C. Nieuwenhuis, H. van Dijk, and O. Jensen. Prestimulus alpha and mu activity predicts failure to inhibit motor responses. *Human brain mapping*, 30(6):1791–1800, 2009.

[26] L. Melloni, C. Molina, M. Pena, D. Torres, W. Singer, and E. Rodriguez. Synchronization of neural activity across cortical areas correlates with conscious perception. *The Journal of Neuroscience*, 27(11):2858–2865, 2007.

[27] H.R. Naghavi and L. Nyberg. Common fronto-parietal activity in attention, memory, and consciousness: Shared demands on integration? *Consciousness and cognition*, 14(2):390–425, 2005.

[28] B. Noudoost, M.H. Chang, N.A. Steinmetz, and T. Moore. Top-down control of visual attention. *Current opinion in neurobiology*, 20(2):183–190, 2010.

[29] S. Palva and J.M. Palva. New vistas for α-frequency band oscillations. *Trends in neurosciences*, 30(4):150–158, 2007.

[30] S. Palva and J.M. Palva. Discovering oscillatory interaction networks with m/eeg: challenges and breakthroughs. *Trends in Cognitive Sciences*, 2012.

[31] D. Picchioni, S.G. Horovitz, M. Fukunaga, W.S. Carr, J.A. Meltzer, T.J. Balkin, J.H. Duyn, and A.R. Braun. Infraslow eeg oscillations organize large-scale cortical–subcortical interactions during sleep: A combined eeg/fmri study. *Brain research*, 1374:63–72, 2011.

[32] M.A. Pitts, A. Martínez, and S.A. Hillyard. Visual processing of contour patterns under conditions of inattentional blindness. *Journal of Cognitive Neuroscience*, 24(2):287–303, 2012.

[33] R.Q. Quiroga, L. Reddy, G. Kreiman, C. Koch, and I. Fried. Invariant visual representation by single neurons in the human brain. *Nature*, 435(7045):1102–1107, 2005.

[34] K. Sasaki and H. Gemba. Electrical activity in the prefrontal cortex specific to no-go reaction of conditioned hand movement with colour discrimination in the monkey. *Experimental Brain Research*, 64(3):603–606, 1986.

[35] C. Sergent and S. Dehaene. Neural processes underlying conscious perception: Experimental findings and a global neuronal workspace framework. *Journal of Physiology-Paris*, 98(4-6):374–384, 2004.

[36] M. Siegel, T.H. Donner, R. Oostenveld, P. Fries, and A.K. Engel. High-frequency activity in human visual cortex is modulated by visual motion strength. *Cerebral Cortex*, 17(3):732–741, 2007.

[37] C. Tallon-Baudry. The roles of gamma-band oscillatory synchrony in human visual cognition. *Frontiers in bioscience: a journal and virtual library*, 14:321, 2009.

[38] P.J. Uhlhaas and W. Singer. Neural synchrony in brain disorders: relevance for cognitive dysfunctions and pathophysiology. *Neuron*, 52(1):155–168, 2006.

[39] E. Werth, P. Achermann, and A. BORBÉLY. Fronto-occipital eeg power gradients in human sleep. *Journal of sleep research*, 6(2):102–112, 1997.

[40] S. Yuval-Greenberg, O. Tomer, A.S. Keren, I. Nelken, and L.Y. Deouell. Transient induced gamma-band response in eeg as a manifestation of miniature saccades. *Neuron*, 58(3):429–441, 2008.

[41] W. Zhang and S.J. Luck. Feature-based attention modulates feedforward visual processing. *Nature neuroscience*, 12(1):24–25, 2008.