Rhythms in Perception: oscillatory patterns of colour-to-form filling-in

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ABSTRACT

Neuronal oscillations are now generally believed to underlie variations in perception, particularly under constant environmental input. In recent years there has been an increase in interest into the influence of the alpha frequency band on visual perception. Alpha has been found to strongly correlate with basic aspects of visual perception. The current study aims to investigate if alpha also has a role in the underlying processing of more complex visual processing through examining patterns of the filling-in effect over different stimulus onset delays. It was found that colour-to-form filling-in occurred in a cyclic pattern at a frequency of 27Hz, corresponding with high beta/low gamma. Such higher frequencies therefore appear to have more importance for complex featural integration. Activity at this frequency may mediate communication between distributed neuronal assemblies leading to integrated perception.

Keywords:	Vision	Perception	Integration	Oscillations	Filling-in

Introduction

Oscillations in neuronal activity are ubiquitous throughout the central nervous system. How this oscillatory activity relates to behaviour has been the subject of intense interest from behavioural neurophysiologists for many years. Oscillations highlight rhythmic fluctuations of local field potentials most commonly recorded using electroencephalography (EEG) or magnetoencephalography (MEG). These fluctuations are thought to have a variety of functions throughout the brain such as influencing cognitive functions for instance memory (Gruber et al, 2004) and attention (Womelsdorf et al, 2006), enabling communication between neuronal populations (Jensen and Mazaheri, 2010), facilitating synaptic plasticity (Buzsaki and Draguhn, 2004), and importantly they are believed to have an extensive role in perception (e.g. Mathewson et al , 2009; Romei et al, 2010; Ergenoglu, 2004; VanRullen et al, 2005) as well as many other functions.

Neuronal oscillations can vary across a multitude of properties including power and frequency as well as phase. These properties of rhythmic changes are believed to result from a variety of biological processes. For example, frequency of oscillation may be altered by processes such as conduction speed, excitation refractory periods, calcium channel properties and receptor saturation (Wang 2010). The frequency of brain oscillations ranges from 0.05Hz-600Hz (Buzsaki and Draughn, 2004). However this extensive range is typically divided into specific frequency bands generally defined as: delta (<4Hz), theta (4-8Hz), alpha (8-14Hz), beta (13-20Hz) and gamma (30-100Hz). Further, the division of these frequency bands can be related to distinct functions, low frequencies are typically associated with sleep rhythms while faster oscillations correlate with a waking state including active cognitive processing.

While a great deal of research has been conducted into the functional significance of on-going brain oscillations on behaviour, a vast amount is still unknown about how these underlying processes effect human performance. Currently, there is a body of renewed interest in the functional importance of neuronal oscillations in visual perception. Specifically, interest is developing to examine variations in visual perception when sensory input and environmental conditions remain constant. It has therefore been proposed that any variation in perception under constant conditions may be due to changes in internal brain state, possibly related to fluctuations in on-going brain oscillations (e.g. Varela et al, 1981; Mathewson et al, 2009; Busch et al, 2009; Dugue et al, 2011) from which it follows that perception is not solely stimulus driven.

Historically, focus has centered on the influence of gamma frequency due to its apparent association with higher cognitive function. Indeed gamma activity has been found to be most representative of actively functioning neocortex (Buzsaki and Draughn, 2004) and therefore is believed to play a central part in underlying visual perception processes. This proposal is supported by numerous studies examining a multitude of visual functions using a variety of paradigms: Gamma activity has been found to correlate with fMRI BOLD signals (Logothetis et al, 2001), perception of familiar/coherent stimuli (Lutzenberger et al, 1995) and object recognition (Singer et al, 1997) to name only a few. However more recently, interest has moved to investigate the role of oscillations in the alpha frequency band in visual perception.

Originally alpha activity was believed to solely reflect “cortical idling” (Pfurtscheller et al, 1996), inferred from the observation that the increases in alpha activity arose during an awake but unengaged state. Yet evidence is now accumulating to suggest that alpha may have a more active role in visual perception.

With research beginning to focus on alpha, it has been suggested that oscillatory activity operates in a phasic manner. This contrasts with some studies on EEG activity in which most emphasis was placed on the importance of amplitude on resulting behavioural output (eg Berger, 1929; Basar et al, 1998; Worden et al, 2000). The proposal of a phasic contribution of oscillations to perception originated from an early study conducted by Varela et al (1981) in which a critical time period of 0.1s (one alpha cycle) between stimuli appeared necessary for variation in perception of these stimuli (as being one or separate). Following this finding Varela et al proposed that perception may arise through recurrent discrete phases or “perceptual frames”. Furthermore, the time period noted in this study would suggest that these discrete phases occurred within the frequency range of alpha (8-14Hz). This concept of a “perceptual frame” was later supported by VanRullen et al (2006), following up on Purves et al’s (1996) “Wagon-wheel” illusion, where the subjectively perceived direction of movement of a wheel appears to reverse regardless of the veridical movement, but depending on the presentation frequency. This subjective perception was highest when the stimulus frequency was manipulated to cycle at alpha. It was consequently proposed that endogenous oscillations interact with stimulus presentation frequency (aliasing effect) to lead to this variation in perception (i.e. the Wagon-wheel illusion). From these results, VanRullen et al (2006) suggested that perception occurs in discrete “snapshots”, a concept very similar to Varela’s “perceptual frame”. Accordingly, VanRullen and Koch (2003) argue that in order to fully evaluate the role of oscillations in perception it is necessary to examine perception across a fine grained temporal scale, corresponding to the temporal resolution of brain oscillations and ultimately our perceptual experience. It is through the examination of oscillatory phase that the investigation of such temporal dynamic may be accomplished. Therefore while a great deal of early research took a preferential approach to examining oscillatory power, current literature now turns to focus more on the roles of frequency and phase in influencing perception.

Further converging evidence that perception depends on on-going brain waves came from EEG studies focusing on how oscillatory activity prior to stimulus onset (i.e. a prestimulus brain state) may relate to subsequent stimulus processing (Ergenoglu et al, 2004; Thut et al, 2006; Mathewson et al, 2009; Busch et al, 2009). This contrasts with the traditional approach generally focusing on brain activity following an experimental event (Varela et al., 1981; Jansen and Brandt, 1991; Haig and Gordon, 1998; Makeig et al., 2002). The above studies consistently noted that prestimulus activity did appear to operate substantial influence over forthcoming perception in both humans (Ergenoglu et al, 2004; Thut et al, 2006; Busch et al, 2009) and monkeys (Fries et al, 2001). Importantly, the particular study conducted by Busch et al (2009) not only noted that prestimulus activity influenced subsequent perception but also that the momentary phase of this activity had a substantial influence. Thus these findings added credence to the conclusions of VanRullen et al (2006) and Varela et al (1981) that perception occurs through cyclic periods of waxing and waning neuronal activity.

Interest also advanced on the exact frequency at which the phasic EEG changes modulate perceptual fate. Using EEG, Mathewson et al (2009) investigated whether variability in perception co-varies with momentary phase of alpha oscillations. Consistent with VanRullen et al's (2006) findings, Mathewson noted a relationship between perception and alpha-phase, in addition to an inverse relationship between perception and alpha-power. Support of this latter, inverse relationship also came from studies into attention in which suppression of alpha power appeared to operate as a mechanism of controlled attention enhancement (Worden et al, 2000; Fries et al, 2001). Following on from the finding of phasic activity and discrete perceptual framing, Mathewson et al (2009) therefore suggested that this cyclic pattern occurs in states of high alpha-activity (power) in the form of "pulsed inhibition". Today, it is widely accepted that perception is organised into cyclic patterns at temporal dynamics of neuronal oscillatory activity in the alpha band (Mathewson, 2009; Romei and et al, 2012; VanRullen and Dubois, 2011).

With these general properties of oscillatory alpha activity established, more recent work in this field progressed to investigate whether it was possible to directly induce entrainment of alpha phase preceding stimulus presentation and hence measure effects of entrained phase on visual perception. Mathewson et al (2010) investigated the modulation of awareness of a near-threshold stimulus as a function of pre-stimulus alpha-entrainers in the visual modality (i.e. rhythmic visual events presented at alpha-frequency). He found that detection of visual stimuli presented in-phase with preceding entrainers was improved, while stimuli presented out-of-phase were less likely to be detected. This was therefore the first study to illustrate the possibility of entraining visual sensitivity to precise cycles of pre-stimulus rhythmic events. Further research into entrainment progressed to directly stimulating the cortex via non-invasive, transcranial brain stimulation techniques. Romei et al (2010) were able to show for the first time that rhythmic transcranial magnetic stimulation (TMS) could be used to directly induce alpha oscillations, leading to transient perceptual suppression. These findings are supported by similar studies using TMS (Sauseng et al, 2009; Rosanova et al, 2009) as well as transcranial alternating current stimulation (tACs; Kanai et al, 2008). In addition, another approach was used, to present stimuli in one modality entraining oscillations in sensory areas of another modality. This approach was utilised in pioneering animal studies to examine cross-modal effects, finding that visual stimuli can modulate phase and power of auditory core activity (Kayser et al, 2008). Further animal research on the efficacy of cross-modal entrainment showed that V1 was achieved by both auditory and visual cues alike (Lakatos et al, 2008). Yet strong causal evidence of cross modal entrainment was only presented very recently (Romei et al, 2012) in a combined TMS-EEG study into phosphene perception. Romei et al found direct causal evidence that sound can phase lock alpha oscillations in the human visual cortex with resulting consequences on perception. Thus it is now possible to use a pure psychophysical approach as a minimally invasive and ecologically valid method for examining the influence of ongoing endogenous oscillations on perception. It is this approach that is used in the current study.

While the combined findings of these previously discussed studies are substantial it can be noted that the investigations have typically focused on the influence of alpha activity on fairly basic aspects of visual perception such as perception of simultaneity (Varela et al, 1981), phosphene perception (Romei et al 2012; Kanai et al, 2008) and detection of stimuli at awareness threshold (Mathewson et al, 2009). In contrast, the current study aims to investigate the possible nature of perceptual modulation by neuronal oscillations in more complex perceptual phenomena. Here, we examine cyclic patterns in the perceptual “filling-in” effect. The filling-in effect, a form of perceptual integration, arises when the visual features of one location spread to fill surrounding areas where the feature is not truly present. It is the visual system’s attempt to extrapolate visual information from what is known of the surrounding area. This definition is generally taken as standard throughout the literature into filling-in, however this type of visual binding can take many forms. Komatsu (2006) attempts to addresses each of the different filling-in phenomena as three groups, the first detailing the filling-in of blind-spots or scotomas, the second being peripheral vision filling-in during stable fixation as in Troxler’s (1804) illusion. The paradigm investigated in the current study, however, falls into Komatsu’s final category of neon colour spreading, the illusion of a bright colour spreading to fill an achromatic area. The colour spreading here examined neon colour spreading to an illusory contour of a Kanizsa square (Kanizsa, 1979), enabling the examination of integration of colour to form. Furthermore, these stimuli can be considered to fall into the category of instantaneous filling-in, dependent upon stimulus configuration, in accordance with Weil and Rees’s (2011) taxonomy of filling-in.

The majority of literature on filling-in has tended to focus on blind-spot and scotoma research (Greenlee et al 2012; Komatsu et al, 2000; Alvarenga et al, 2008) with few attempts to generalise across the different forms filling in may take and even fewer studies examining EEG or MEG correlates (Weil et al 2007) of these phenomena. Thus a systematic approach to study filling-in has been somewhat neglected and research approaches generally lack coherence, such that findings across the different forms of filling-in are inconsistent (e.g. Meng et al, 2005; von der Heyt et al, 2003; Kanai et al, 2006). Indeed, it is entirely plausible that these phenomena arise through a large variety of underlying mechanisms (Komatsu, 2006). As to the filling-in phenomena studied here (colour spreading to form), we hypothesized that this form of colour-to-form integration may also depend on internal oscillations, much as more simplistic aspects of visual perception do (Romei et al, 2010; Mathewson et al, 2009; Busch et al, 2009) but possibly at distinct frequencies. Some arguments do exist that gamma band activity may be related to visual feature integration and object representation (Crick & Koch, 1990; Eckhorn et al, 1988; Engel et al, 1997; Gray and Singer, 1989). However, due to the belief that alpha activity reflects cortical idling (Pfurtscheller et al, 1996), many of these early studies filtered out spectral components in the alpha range. Here, we aim to continue the developing trends in research, to investigate whether gamma versus alpha activity may also be revealed in complex aspects of visual processing using cross-modal entrainment as a paradigm.

The stimuli utilised in the current investigation are largely based on those used in a recent study by Feitosa-Santana et al (2011). The authors investigated the necessity of an edge in bounding colour filling-in, finding that colour filling-in is bound not only by real luminance edges but also illusory contours. With the support of this finding, the current study therefore utilises illusory contours in the investigation of colour filling-in, with a Kanizsa square (Kanizsa, 1979; induced by grey solid “pacmen”) forming the basic stimulus of our paradigm. To examine colour filling-in to form, the centre of the Kanizsa square was varied across conditions, containing either a yellow circle or yellow square. The filling-in effect was noted upon perception of a yellow square when stimuli actually contained a circle. We presented these Kanizsa stimuli and studied filling-in as a function of different delays from sound onset (cross modal entrainment, analogous to Romei et al, 2012) to examine the presence of a cyclic pattern in filling-in and to study its frequency through a minimally invasive approach.

It was expected that trends of filling-in would occur in a cyclic pattern similar to previous studies, with fluctuations of increased and decreased occurrence of filling-in corresponding with the frequency of known brain oscillations. Furthermore, it was predicted that this cyclic pattern of perceptual advantage may occur within the alpha frequency range (8-14Hz) or gamma frequency range (30-100Hz), the most predominant oscillations of the visual system.

Methods

Participants

20 healthy volunteers (14 female and 6 male) participated in this study. The mean age of the participants was 21.4 (ranging between 18-38). All participants were right-handed according to the Edinburgh Oldfield Handedness Inventory (Oldfield, 1971). All participants had normal or corrected-to-normal vision and normal hearing. One participant was a professional from the Glasgow area and the remaining 19 were undergraduates attending the University of Glasgow, 10 of which were studying psychology. All participants gave written informed consent to the study which was approved by the local Ethical Committee.

Stimuli and Apparatus

Participants were seated comfortably with their in chin in a chin rest at a distance of 1m from a 21 inch SONY CRT monitor with refresh rate of 85Hz. The chair and the chin-rest were adjusted vertically for each participant to ensure the monitor was at eye level. The room was in darkness with all extraneous light sources blocked as much as possible. Participants were darkness adapted for several minutes before beginning the experiment.

Our paradigm aimed to examine featural integration using the “filling-in” effect. To this end, 1 of 4 images was flashed per trial in the centre of the screen for a duration of 11.8ms. Each image consisted of a Kanisza square outlined by solid grey “pac-men” stimuli. The Kanizsa squares measured 2.5cm (1.4 visual degrees) and were displayed against a white background. This Kanizsa square was either displayed (1) alone (stimulus 1), with (2) a small or (3) a large, filled, yellow, central circle that did not reach the contours of the Kanisza square (stimuli 2 and 3; measuring 1.3cm (0.75 visual degrees) and 1.7cm (1 visual degree) in diameter respectively); and (4) with a yellow centre reaching the contours of the illusory square (stimulus 4). Yellow colour was of low (near-equiluminance) contrast to the white background. Each stimulus is illustrated in figure 1.

The auditory stimulus (sound condition) was a 14ms-duration, 900Hz pure tone [75 dB sound pressure level at the ear; 44199 kHz sampling rate], presented through two loudspeakers located on each side of the computer monitor.

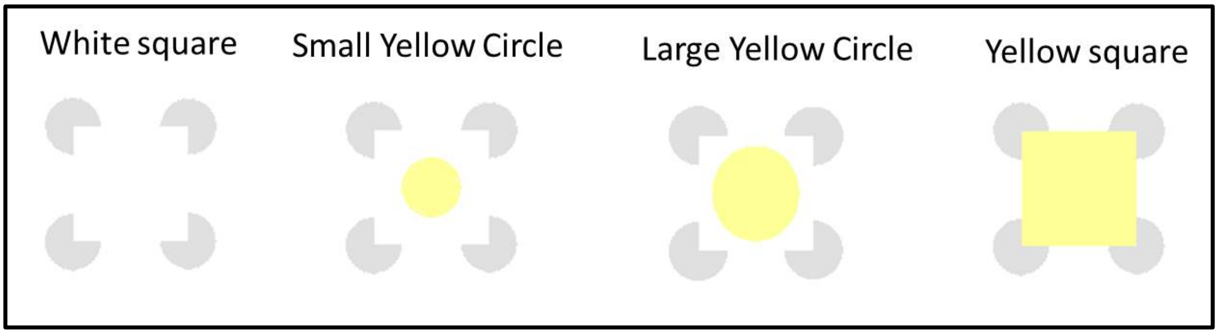

Figure 1: Kanizsa square stimuli outlined by grey "pac-men". Basic Kanizsa square with white centre; small yellow circle in centre (YC); large yellow circle in centre (YC); full square yellow centre (YR).

Experimental Design and Procedure

In the sound condition, visual stimuli were displayed after the sounds with delays between sound- and visual stimulus-onset varying between 11.8 and 294.2 ms in steps of 11.8 ms (increments dictated by the refresh rate of the monitor). In total, there were 25 time delays from the onset of the auditory stimuli, covering approximately 3 alpha cycles (300 ms). No sound trials were randomly intermixed with sound trials. The inter-trial interval was varied pseudo randomly from 1000 to 2000ms in steps of 500 ms. The experimental design is illustrated in Figure 2.

Each block of 312 trials was initiated by the experimenter once the participant signalled they were ready. Participants were instructed to indicate the perception of a Kanizsa square (white centre) by pressing key 1 on a key pad with their right index finger, to indicate perception of a Kanizsa square containing a yellow circle by pressing key 2 with their right middle finger, and to indicate perception of a Kanizsa square with a yellow square centre by pressing key 3 with their right ring finger. Participants were told that the auditory stimulus was not relevant to the task and to respond as quickly and accurately as possible.

Eighteen trials were assessed per participant, condition and visual delay, the latter randomized in order within blocks. Each participant completed 6 blocks of 312 trials, giving rise to a total of 1872 trials. Each block lasted approximately 13 minutes and breaks were encouraged between blocks. The duration of the experiment varied between around 90 to 120 minutes.

Before running the full experiment, each participant completed a titration block (312 trials). The aim was to make experimenters aware of participants performing at either ceiling or chance level performance, thus ensuring that there was scope for the sound to modulate visual perception by either increasing or decreasing the proportion of visual stimuli perceived as having featural integration (filling in when yellow circles are presented). The conditions in the titration block were identical to those in the experimental blocks, excepting the absence of the sound stimulus. The participant’s performance in identifying each stimulus correctly was assessed immediately after the titration block. This assessment was purely for the experimenter’s awareness and no participants were excluded at this stage.

This led to a full within subjects design, with all conditions (25 time delays + 1 no-sound condition x 4 visual stimuli) measured in each subjects. There were two dependent variables: the hit/error rate (in perceiving the white or yellow Kanizsa square or one containing a circle) and reaction time.

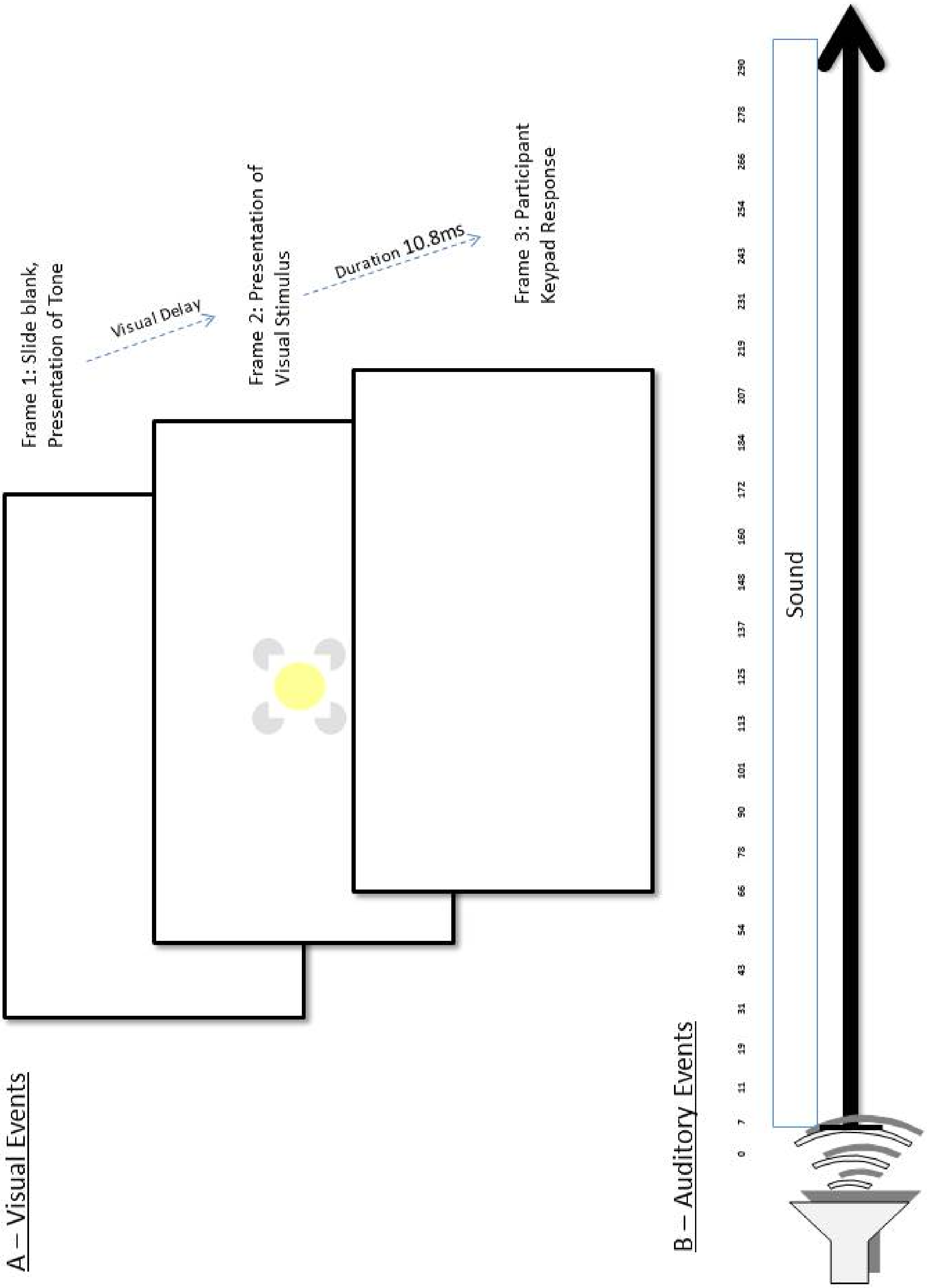

Figure 2: Experimental Design set-up of presented visual stimulus sequence (A), auditory stimulus and visual delay (B)

Data Analysis

Pre-processing

To control for effect of colour presence, analysis was only carried out on conditions containing the yellow circle or the yellow square, i.e. (i) when a yellow circle was perceived correctly (YC_YC), (ii) when a yellow circle was perceived as a yellow square (YC_YR, filling in); and (iii) when a yellow square was perceived correctly (YR_YR). This analysis ensured that only form was investigated in this study with the presence of colour remaining constant. Thus, the white square condition was discarded from analysis but was important as a control to ensure that participants did see colour, i.e. responded in all categories, not only (i).

Trials with reaction times shorter or longer than the mean average reaction time ± 3 SD were also discarded to eliminate outliers. This led to an exclusion of an average of 1.26% of trials per subject. For each participant, trials were split into fast and slow responses using the median reaction time as a cut-off value for each stimulus condition and at each sound-visual delay. Only fast reactions times were included in the final analysis based on the rationale that these were representative of high confidence responses. This approach has been validated by previous maxi project work, and another work within the lab which is yet to be published, which found that only fast reaction times yielded a significant time-modulated (oscillatory response) in perception from sound-onset across tested time delays

Average hit rates for each condition and visual delay were then calculated across fast-response trials per subject. These data are represented in Figure 3 averaged across participants. A linear drift is apparent, with improved performance due to enhanced readiness/expectancy with increasing delay from sound onset (Fig 3, Graph A). In a first pass through the data, this linear drift was eliminated in individual data by linear detrending of the individual dataset (average hit rates over visual delays per condition and subject). Linear drift was removed by fitting a regression line to the results and then retaining the residuals. These residuals are shown in Figure 3 (Graph B) over delays. Linear detrending was thus utilised to eliminate time-modulated changes in perception which were unlikely related to oscillations (at frequencies of brain oscillations). Following this initial detrending, a remaining, very low frequency (3-5Hz, inverted U-shape function) was apparent in the residuals (Fig 3, Graph B). In a second, final pass through the data, this low frequency modulation of perception was eliminated by fitting a cosine function at 3-5Hz, and retaining the residuals, the latter shown in Figure 3 (Graph C). These data were then analysed for the presence of high-frequency oscillatory patterns (see below).

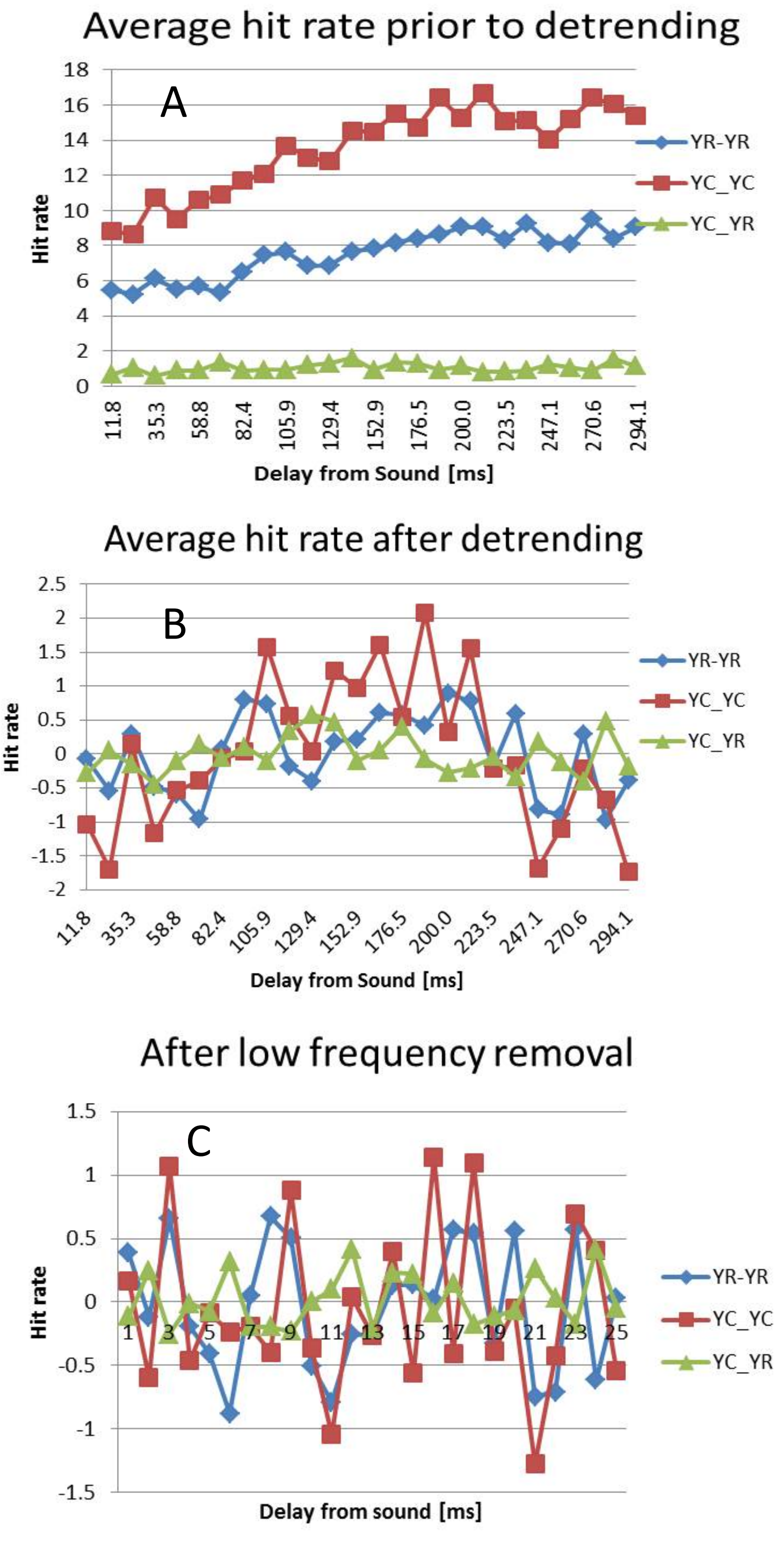

Figure 3: Average hit rates per condition prior to detrending (A), following detrending (B) and after removal of a low frequency (C)

Spectral Analysis through Cosine Fitting and Bootstrapping

In order to determine if there was a presence of a cyclic pattern in task performance, curve-fitting procedures were applied using robust non-linear least-squares fitting in Matlab software. Group-averaged hit rate were fitted with a cosine function (see formula below) across a 1-35Hz frequency range (in steps of 1Hz step) for each of the three conditions: yellow circle seen as yellow circle; yellow square seen as yellow square; yellow circle seen as yellow square (filling-in).

To examine the presence of significant frequency trends within the data, R-squared values of group mean fitted data across all three conditions were evaluated statistically using bootstrapping per fitted frequency. For bootstrapping, labels of the 25 visual delays were randomly rearranged over 200 resamples with a cosine model fitted to each resulting behavioural pattern, thus creating a null-distribution of all the resampled R-squared values per frequency (1-35Hz). This null-distribution was used to investigate whether the R-squared values from the actual data fell above the 95th percentile, suggesting that variance within the group was significantly accounted for by the cosine model.

Formula:
The fitted cosine function was defined as:

$$y = a * \cos(b*2\pi *x + c)$$

where y represents the average hit rates (for fast reaction time trials), x is the time delay between the sound onset and visual stimuli onset and a, b, and c are constants (a is the amplitude, b the frequency, c the phase lag).

Results

Overall Hit Rates

Mean hit rates for each of the three stimulus response pairs were calculated (Table 1). Filling-in (YC reported as YR) was noted to occur infrequently (6.31%) with the majority of responses being correct upon presentation of the yellow circle (YC reported as YC: 73.95%) or yellow rectangle (YS reported as YS: 83.11%).

Table 1: Mean hit rate per stimulus-response pair

Stimulus	Response	Hit Rate (%)
YC	YC	73.95
YR	YR	83.11
YC	YR	6.31

Time Course of Hit Rate Across Visual Delays

Following data pre-processing fluctuations of hit rate across different visual delays from the entraining sound stimulus were plotted for each stimulus-response pair of interest (Fig 4, graphs A-C). Initial inspection of these waveforms suggests a clear cyclic pattern in the filling in condition (yellow circle seen as yellow rectangle, graph A). However, cyclic patterns of correct responses on yellow circles and yellow squares are less clear with greater amount of noise apparent in both graphs B and C in comparison to A.

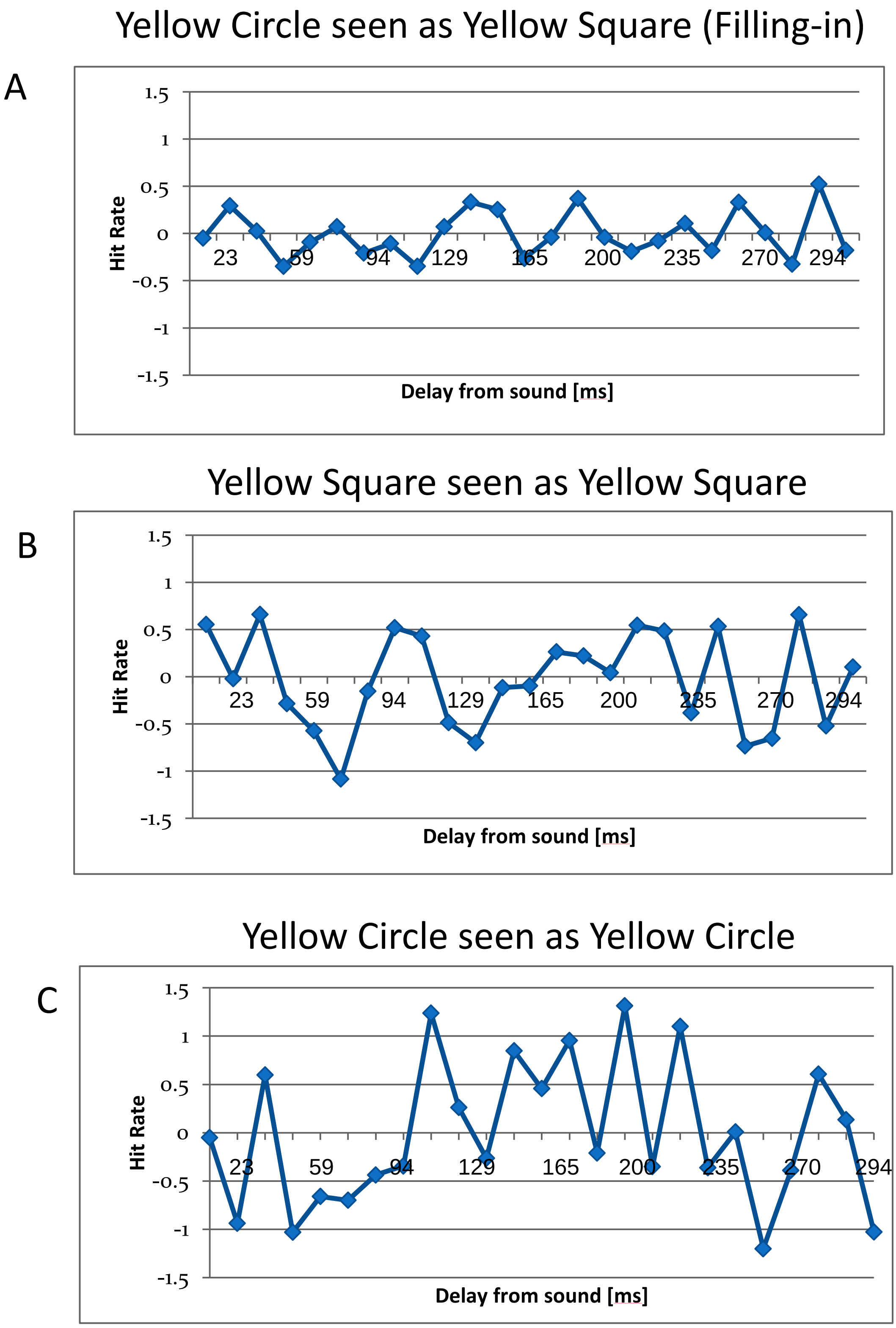

Figure 4: Average hit rates across visual delays. Clear cyclic pattern are seen for filling in condition (A), but not for correct square (B) or circle (C). We can count 8 peaks in the 300ms interval, which suggests a frequency of 8/300*1000=26.6.

Spectral Analysis Data Analysis

Figure 5 illustrates the R-squares of the cosine functions which best fitted the report-curves over time per stimulus-response pair (fitting from 1-35Hz). Bootstrapping analysis identified only one frequency (of 27Hz) that was above the threshold of significance (r-squared = 0.199) and this for the filling in condition (YC_YS). Other obvious peaks can be noted at around 10Hz (alpha) and 16Hz (beta), which however were not significantly different from noise.

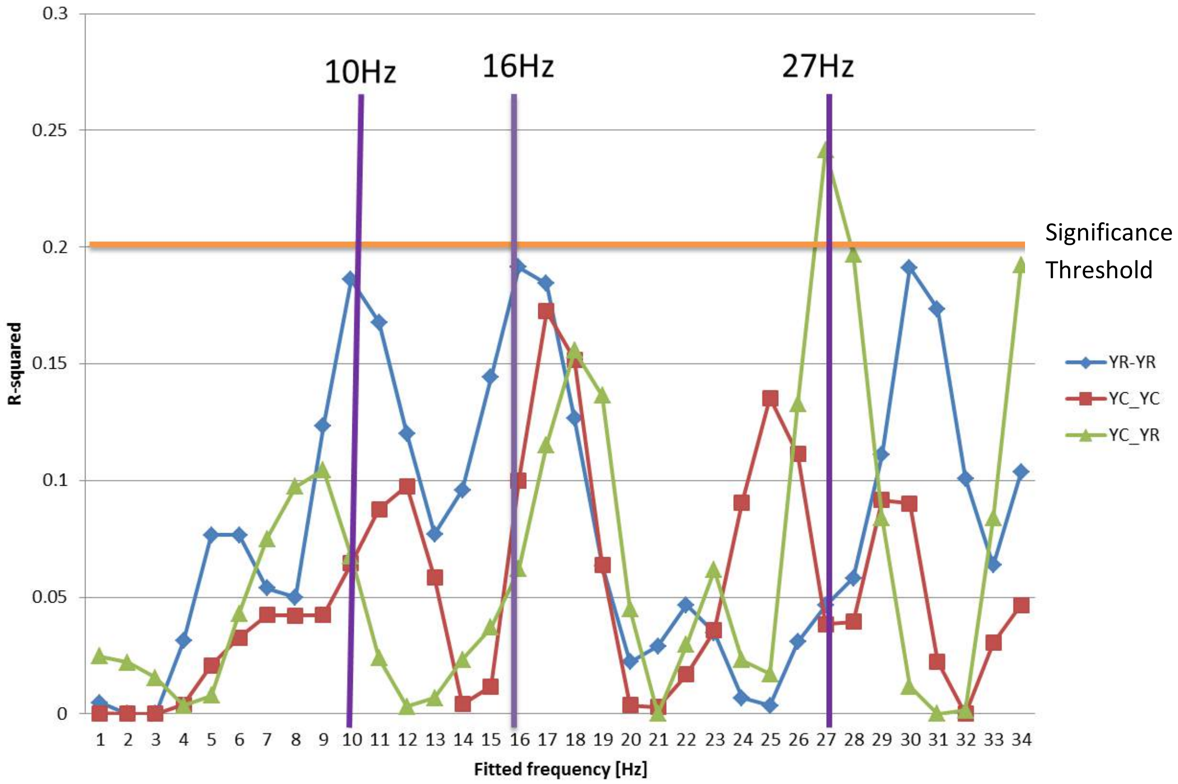

Figure 5: Bootstrapping results, significance of fitted frequencies. 27Hz is above significance threshold (orange line), peaks also at 10Hz and 16Hz below threshold.

To further test for a cyclic pattern within the data of each condition, a cosine function with a frequency of 27Hz was fitted to the average data of each condition, illustrated in Figure 6. This cosine function significantly fitted the mean response curves (associated with fast reaction times) of the filling-in condition (F = 3.75, p= .026). The best fitting curve was characterized by significant estimates on all parameters, with an amplitude equal to 0.19 (p= .003), a frequency of 27.07 Hz (p<.001) and a phase of 1.78 (p=.001). Note that this frequency corresponds to a high beta/low gamma rang, not alpha.

In contrast, the cosine function did not significantly fit the mean responses curves neither of the yellow circle seen as yellow circles nor the yellow square seen as yellow square conditions (F=0.67, p = 0.52, and F = 0.37, p=0.67 respectively).

See figure 6 for an illustration of the time course of task performance across all visual delays superimposed with the 27Hz best-fitted cosine function.

Therefore these results provide some support for the hypothesis of a cyclic pattern in perception however with a significant cyclic pattern only occurring for the filling in phenomenon, and not with any other condition. Finally, as to the second hypothesis, these data suggest that these cyclic patterns do occur at 27Hz, a frequency considered to be high beta/low gamma, at least for filing in, and not at alpha frequency as reported in several previous studies (which however used other paradigms).

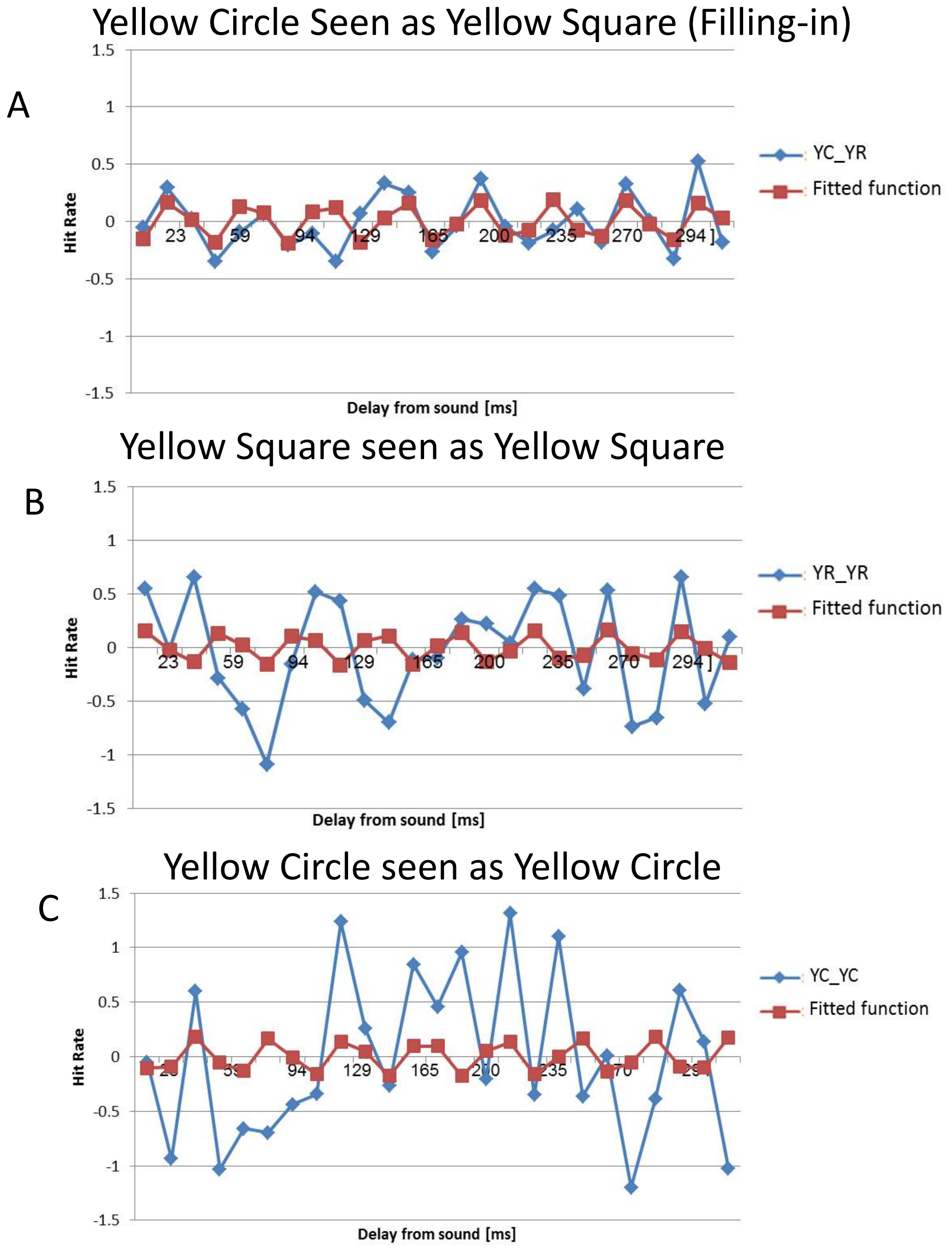

Figure 6: Fitted frequency of 27Hz superimposed with task performance of filling-in (A), correct square (B), correct circle (C).

Discussion

We present an investigation into the oscillatory nature of complex visual processing through the filling-in effect, using a purely psychophysical approach of sound phase-locking. Supporting the first hypothesis, the filling-in phenomenon was found to operate in a cyclic manner of increases and decreases of occurrence. This oscillation was found to strongly correspond to a frequency of 27Hz which falls within a high beta/low gamma range, partially supporting the prediction that the cycling may occur at a frequency within the alpha or gamma range. The outcomes of this study therefore further complicate the currently expanding literature on visual perception and neuronal oscillations.

The findings of the current study aren't wholly unexpected. Although though an active inhibitory role of alpha has been widely reported throughout the study of visual perception in recent years (e.g. Mathewson et al, 2009; VanRullen et al, 2006; Romei et al, 2010; Jensen and Mazaheri, 2010; Busch et al, 2009) there are also significant findings that higher frequencies, such as beta and particularly gamma, have significant roles in perception. These studies range from the influence of higher frequencies on attention and expectation (Wrobel, 2000) through simple object discrimination (Hanslmayr et al, 2007; Piantoni et al, 2010), to more complex motion binding (Lorenceau et al, 2012) and perceptual switching (Engel et al 1997; Doesburg et al 2005).

In addition to the findings of previous investigations the study reported here adds to the progressive investigation into the functional distinctions between frequency bands. To make such distinctions here it is necessary to make comparisons between the results and paradigms used in the current study and similar studies focusing on higher frequencies, with those investigating the role of alpha in visual perception. It can be clearly noted that these previous studies focusing on alpha have been inclined to examine simple aspects of visual processing such as phosphene perception (Romei et al, 2010), apparent motion (VanRullen et al, 2006), simultaneity (Varela et al, 1981) and detection of at-threshold awareness stimuli (Mathewson et al, 2009). In contrast, the paradigm utilised in the current study observes colour spreading through the complex perceptual integration phenomena of the "filling-in" effect. It is therefore perhaps not surprising that neural correlates seem to vary across different perceptual phenomena and it is plausible that the underlying mechanisms across these diverse forms of perception are different.

In an attempt to study the underlying mechanisms of the filling-in effect it is useful to examine the basic principles of general integration of cortical processing, particularly related to that of perceptual integration. While not conclusive, integration is typically believed to occur through the coordination of activity across distributed neural assemblies. Varela et al (2001) defines these neural assemblies as "local networks of neurons transiently linked by reciprocal dynamic connections". It is therefore of value to investigate the neural assemblies which may be linked here. However, in an attempt to avoid invasive procedures and maintain ecological validity, no direct electrophysiological or neuroimaging measures were taken during the research undertaken here. Thus the forthcoming proposition of filling-in occurring through coordination of distributed brain regions is only speculatively suggested by research findings of other studies.

Due to the complexity of the visual system and the lack of research into perceptual filling-in, there are substantial inconsistencies in the proposed anatomical regions suggested to process illusory contours and colour spreading. Nevertheless there is some support coming from electrophysiological and neuroimaging studies to suggest that the illusory contour (Kanizsa square) processing investigated in the current study is associated with activity of early visual areas, particularly V2. Evidence from animal studies suggests both V1 and V2 to be important in processing of illusory contours, however with a stronger association of V2 (Redies et al, 1986; Sheth et al, 1996). Further to this both V1 and V2 activity has been noted in Kanizsa square processing with V2 processing arising earlier (Lee and Nguyen, 2001) and more consistently than V1 (Hirsch et al, 1995). However there is also some evidence to support the further involvement of higher visual areas, particularly when these illusory contours generate shapes. Animal studies have shown the inferotemporal cortex (IT), which may be likened to the human lateral occipital complex (LOC; Tarr and Bulthoff, 1999), may play a role in illusory figure processing (Sary et al, 2007), while fMRI studies noted that Kanizsa squares activated areas V7 and V8, overlapping with LOC (Mendola et al, 1999; Murray et al, 2002; Stanley and Rubin, 2003). Interpretation of these studies therefore suggests that illusory contour processing may occur predominantly at V2 with feedback to V1 but also possible involvement of higher visual areas such as IT and LOC. Unfortunately much less is known about the anatomical regions associated with colour processing (Zeki and Marini, 1998; Shapley and Hawken, 2011) and indeed colour spreading. However, there is some evidence that neon colour spreading may involve early visual processing areas with recent human neuroimaging studies finding activity in V1 (Sasaki and Watanabe 2004). Also, the stimuli utilised, colour spreading to an illusory rather than concrete boundary, further confounds any attempt to define anatomical localisation of regions involved in filling-in. A recent study by Santana-Feitosa (2011) did prove that filling-in occurs to illusory and concrete contours alike, however the authors were unable to provide substantial evidence that the cortical processing of filling-in was identical in the two conditions.

While any attempt to define the brain regions that may be activated by the filling-in noted in this study yields somewhat inconsistent support, attempts have been made to develop network models to account for filling-in. Weil and Rees (2011) cite the Grossberg (1994) model of general perception. This theory proposes that two systems are central to visual processing: the Boundary Contour System and the Feature Contour System. It is through these network models that the authors later examine the anatomical regions which may be involved in all aspects of filling-in, particularly the illusory contours and colour spreading. Grossberg (2003) details pathway of Feature Contour System network from the retina through the LGN, passing through the V1 blob areas and V2 thin stripes to V4, all of which are believed to lie within the ventral stream (Goodale and Milner, 1992). Meanwhile the Feature Boundary System follows this pattern forming a feedback network from the retina; through the LGN to the V1 interblob and V2 interstripe areas. These two systems are proposed to interact with the Boundary System inhibiting and the Feature Contour System facilitating the diffusive spread of surface information. Grossberg's (1994, 2003) model therefore does seem consistent with the proposed regions of activation outlined above. Nevertheless, this model lacks a neurophysiological approach to how such network models interact to transfer information and to generate integrated percepts such as the filling-in effect noted in the current study.

We propose that our findings may add to the investigation into how the network models proposed by Grossberg (1994, 2003) are neurophysiologically linked. The finding of a 27Hz significant cyclic pattern of filling-in may provide a deeper insight into the on-going neuronal oscillations influencing perceptual integration. While speculative, a popular theory is that integration, and thus filling-in, occurs through the distinct neuronal assemblies, firing in synchrony (Llinas et al 1998; Blake and Yang, 1997; Fries, 2005; Womelsdorf et al, 2007). Synchrony between neuronal populations is suggested to occur when multiple assemblies exhibit phase-locked oscillations with constant phase delays matching the condition time from the sending group to the receiving group (Thut et al, 2012). Varela (2001) posits that the study of integration through synchronisation must focus on the temporal dynamics occurring across networks within the millisecond range, thus examining frequencies within beta and gamma range, as in the current study, is of particular relevance.

Although the research that has been conducted into integration through synchronisation is very limited, studies in this area have tended to focus on gamma activity. Investigation into gamma synchrony and integration suggest a role of gamma synchrony in cortical computation (Fries et al 2009), selection and binding of responses (Fries et al, 2007), feature linking (Eckhorn 1988) and top-down processes (Engel et al, 2001) with more general studies illustrating gamma synchrony's involvement in other cognitive functions such as learning (Miltner, 1999) and memory (Carr et al, 2012). The findings of these studies, although not directly linked, do provide some support for our findings on the influence low gamma activity on perceptual integration and filling-in. However there is recent evidence for the possibility of beta synchronisation also influencing integration. In a MEG study Lorenceau et al (2012) found beta activity to facilitate communication between distinct regions coding for form and motion. Thus there currently seems to be some debate over the role of both beta and gamma in facilitating neuronal communication. Studies have been conducted to attempt to make distinctions between the functional significance of synchrony occurring within the beta and gamma bands. Evidence from these studies suggests that beta is of greatest significance for the establishment of long-distance synchrony (Ermentrout et al, 1998; Koppel et al 2000; Lorenceau et al, 2012) while gamma rhythms appear to most representative of local synchrony (Von Stein et al, 1999). This evidence may therefore suggest that any synchrony occurring at 27Hz, as in the current study, may represent the synchrony of neuronal assemblies across an intermediate distance. This concept would also be consistent with models proposed by Grossberg (1994, 2003), in which the processing of colour spreading to an illusory contour appears to occur across distances outside cortical visual columns yet limited to typical visual processing areas, not reaching more distant cortical regions such as the frontal lobe.

The influence on perception by synchrony in different frequency bands is clearly uncertain at the current time. Furthermore, the synchrony of beta and gamma activity is not mutually exclusive, it is entirely plausible that synchrony may be occurring in both frequency bands simultaneously and future research into the role of synchrony on perception may therefore be required to examine multiple frequency bands. It is due to this possibility that we must also address the unexpected absence of a correlation between alpha rhythms and the cyclic filling-in pattern. These findings do not fully reject an involvement of alpha in perceptual integration, as with beta and gamma it is entirely plausible that alpha may have some role that was not detected from the results of this study. It is also of merit to note that, while alpha oscillatory activity was not found to significantly differ from noise, a substantial peak was noted at around 10Hz (alpha) and this peak was just below the significance threshold. Also, similar to functional distinctions between beta and gamma synchrony there is an argument for a clear dissociation of alpha activity with the collective activity of beta and gamma (Hanslmayr et al, 2007). The authors propose that while alpha synchrony seems to inhibit stimulus perception synchrony of both beta and gamma bands appear to facilitate perception.

With the suggestion that different frequencies may signal distinct dimensions of the integration process, some authors have proposed that integration may occur through dynamic links between multiple frequencies mediated by parallel phase synchrony (Varela et al 2001; Bressler et al 1993; Tass et al 1998; Fries et al 2001; Bartos et al 1999). Indeed, Hanslmayer et al (2007) does go on to imply an interaction between these frequencies, operating modulatory effects on each other however the mechanisms proposed for such cross-frequency interaction are not clear. Yet a recent study by Jensen and Mazaheri (2010) takes this argument one step further. Supported by the findings of Hanslmayer(2007) the authors propose perception occurs not only though activation and communication of task relevant areas, mediated by gamma synchrony, but also through the inhibition of task irrelevant areas, through alpha synchrony. Some suggestions have been made that gamma activity may actually be modulated by alpha phase (Osipova et al 2008; Voytek et al 2010) and from these findings Jensen (2010) investigated the neurobiological basis of such modulation. Evidence that the neurotransmitter gamma-aminobutyric acid(GABA) has in important role in alpha activity generation (Jones et al, 2000; Lorincz et al 2009), led Jensen and Mazaheri (2010) to suggest that this GABAergic input may enable alpha to phasically blocking gamma activity through graded inhibition. Similarly GABAergic pharmacological manipulation of the sensory motor cortex yielded evidence of a dissociation between alpha and beta rhythms (Jensen et al, 2005). Such suggestions are further supported by consistent findings that high frequency activity (>25Hz) is found to negatively correlate with activity of alpha (Salari et al 2012; Jensen and Mazaheri, 2010; Fries et al, 2001). Nevertheless, while these conclusions suggest substantial advances in the understanding of ongoing neuronal activity, such claims have yet to be experimentally proven.

The theories outlined above appear to be fairly consistent with the findings of the present study. However it is important to state the problematic nature of the interpretation of literature into the electrical activity of the brain, with assumed frequency band ranges varying greatly between different researchers. Thus while our finding of 27Hz is typically not found within any frequency band, some studies may consider it as beta while other may include it in the gamma range. Furthermore, as research generally focuses on widely accepted segments of frequency ranges relatively little is understood about the functional role of such an intermediate frequency found here. It would therefore be beneficial in the future to fully examine a wide spectrum of frequencies to prevent the exclusion of important data suggesting further oscillatory influences on perception and to investigate the possibility of cross frequency interactions. Indeed there is some speculative evidence of cross frequency interactions (Canolty et al, 2006; Fiebelkorn et al 2012) with approaches including synchrony, cross-frequency coupling (Palva et al, 2005; Bruns et al., 2000) and more in-depth approaches examining neuronal transduction, dynamic activity of neurotransmitters (Jensen and Mazaheri 2010). Thus future research may require novel methodology to examine the possibility of such interactions.

While the literature does suggest a general consistency of the role of neuronal oscillations on perception between individuals there are some studies that have found individual differences of endogenous neuronal oscillations which lead to fairly consistent variations in perception (Edden et al, 2009; Lorenceau et al 2012; Hanslmayr et al, 2007). The entraining sound paradigm and visual stimuli in the current study were identically presented to all participants. While parameters of the stimuli presented was consistent with those found necessary for filling-in across all subjects in a study by Spillman et al (2006), perhaps more care may have been taken into such generalised approach. The complex organisation of the visual system leaves much room for variation between individuals and while some steps were taken to ensure normal participants had visual ability within a normal range it may be necessary to examine visual functioning between individuals more closely. Indeed the study by Feitosa-Santana et al (2011) did allow individual differences in visual processing by calculating isoluminance level for each participant to ensure that any influence of the level of contrast perceived by each subject remained constant. Further studies may therefore aim to also incorporate such measurements into their approach.

This investigation provides some important insights into the study of the effect of endogenous oscillatory activity on visual perception and adds to the findings on the involvement of high frequency (>25Hz) activity in aspects of visual binding and perceptual integration. However while these results appear substantial, the inferences made from them are purely speculative. Therefore future research would be required to revisit more invasive approaches to examine the direct nature of on-going oscillations within the high-beta/low gamma range, through both electrical recordings of EEG and MEG as well as more invasive manipulation of on-going oscillations for example using TMS or tACs.

To conclude, the present study adds to the growing literature on the role of endogenous oscillations on visual perception. Corresponding previous research this study found illusory colour spreading, a form of filling-in, to occur in a cyclic manner. In contrast to recent research on basic aspects of visual perception this cyclic pattern of filling-in was found to arise not within the alpha range but at a higher frequency between the beta and gamma bands. It therefore appears that complex visual processing, as in the featural integration of the current study, occurs at higher frequencies as suggested by previous research examining similarly complex stimuli. This activity of frequencies above 20Hz may therefore suggest communication between regions responsible for processing the different features involved in this colour spreading illusion. Future research should aim to directly examine neural activity, across a large spectrum of frequencies, through electrical recording techniques to attain more conclusive evidence on the role of endogenous oscillatory activity on visual perception.

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References

Alvarenga, D.P., Pessoa, Validir, Couto, Marcia F.C. (2008).Filling-in at partially deafferented visual cortex. British Journal of Ophthalmology 92(9), 1257-60.

Bartos, M., Manor, Y., Nadim, F., Marder, E. and Nusbaum, M. P. (1999) Coordination of fast and slow rhythmic neuronal circuits. *Journal of Neuroscience, 19,* 6650– 6660.

Basar E, Rahn E, Demiralp T, SchurmannM (1998).Spontaneous EEG theta activity controls frontal visual evoked potential amplitudes. *Electroencephalogr Clin Neurophysiol 108*,101–109

Berger, H (1929). Über das Elektrenkephalogramm des Menschen. *Archiv für Psychiatrie und Nervenkrankheiten, 87,* 527-570.

Blake, R. & Yang, Y. (1997) Spatial and temporal coherence in perceptual binding. *Proceedings of the National Academy of Science, 94,* 7115-7119

Bressler, S. L., Coppola, R. & Nakamura, R. (1993). Episodic multiregional cortical coherence at multiple frequencies during visual task performance. *Nature 366*, 153–156.

Bruns, A., Eckhorn, R., Jokeit, H., and Ebner, A. (2000). Amplitude envelope correlation detects coupling among incoherent brain signals. *Neuroreport 11,* 1509–1514.

Busch, N. A., Dubois, J., and VanRullen, R. (2009). The phase of ongoing EEG oscillations predicts visual perception. *The Journal of Neuroscience, 29(24)*, 7869-7876.

Buzsaki G, Draguhn A. (2004) Neuronal oscillations in cortical networks. Review on general principles of neuronal oscillations. S*cience 304*, 1926- 1929.

Canolty, R.T., Edwards, E., Dalal, S.S., Soltani, M., Nagarajan, S.S., Kirsch, H.E., Berger, N.M., Barbero, M.S., and Knight, R.T. (2006). High Gamma Power Is Phase-Locked to Theta Oscillations in Human Neocortex. *Science, 313,* 1626-1628.

Carr MF, Karlsson MP, Frank LMNeuron. 2012 Transient slow gamma synchrony underlies hippocampal memory replay. *Neuron, 23;75(4*),700-13.

Crick, F. and Koch, C .(1990). Towards a Neurobiological Theory of Consciousness. *Seminars in the Neurosciences, 2,* 263–275.

Doesburg S.M., Kitajo K. and Ward L.M. (2005). Increased gamma-band synchrony precedes switching of conscious perceptual objects in binocular rivalry*. Neuroreport. 16(11),* 1139-1142.

Dugue, L., Marque, P., and VanRullen, R. (2011). The phase of ongoing oscillations mediates the causal relation between brain excitation and visual perception. *Journal of Neuroscience, 31(33)*, 11889-11893

Eckhorn, R., Bauer, R., Jordon W., Brosch M., Kruse, W., Munk M., and Reitboeck H.J. (1988)
Coherent oscillations: a mechanism of feature linking in the visual cortex? *Biol. Cybern. 60*, 121-130.

Edden, R.A.., Muthukumaraswamy, S.D., Freeman, T.C., Singh, K.D. (2009)Orientation discrimination performance is predicted by GABA concentration and gamma oscillation frequency in human primary visual cortex. *J. Neurosci., 29*, 15721–15726

Engel, A.K., Roelfsema, P.R., Fries, P., Brecht. M and Singer, W. (1997). Role of the temporal domain for response selection and perceptual binding. *Cerebral Cortex 7 (6)*, 71-582

Engel, A.K. Fries, P. and Singer, W. (2001) Dynamic predictions: oscillations and synchrony in top-down processing. *Nat Rev Neurosci. 2(10)*,704-16.

Ergenoglu, T., Demiralp, T., Bayraktaroglu, Z., Ergen, M., Beydagi, H., Uresin, Y. (2004). Alpha rhythm of the EEG modulates visual detection performance in humans. *Cognitive Brain Research., 20*, 376–383

Ermentrout, G. B.& Kopell, N. (1998). Fine structure of neural spiking and synchronization in the presence of conduction delays. *Proc. Natl Acad. Sci. USA 95,* 1259– 1564

Feitosa-Santana, C., Antona, A.D.D., Shevell, S.K. (2011). What kinds of contours bound the reach of filled-in color? *Journal of Vision 11(2):2*, 1–11

Fries, P., Reynolds, J.H., Rorie, A.E., and Desimone, R. (2001) Modulation of oscillatory neuronal synchronization by selective visual attention. *Science 291 (5508)*, 1560-1563

Fries, P. (2005). A mechanism for cognitive dynamics: neuronal communication through neuronal coherence*. Trends Cognitive Science, 9*

Fries, P., Nikolic, D. and Singer, W. (2007)The gamma cycle*. Trends in neurosciences 30 (7),* 309-316
Goodale MA, Milner AD (1992). Separate visual pathways for perception and action. *Trends Neurosci. 15(1)* 20–25.

Gray CM and Singer W (1989) Stimulus-specific neuronal oscillations in orientation columns of cat visual cortex. *Proc Natl Acad Sci USA 86,* 1698–1702

Greenlee, M.W., Anstis, S. Rosengarth, K., Goldhacker, M., Brandl-Ruhle, S. and Plank, T. (2012).Neural correlates of perceptual filling-in: fMRI evidence in the foveal projection zone of patients with central scotoma .*Journal of Vision*, 12(9),1303

Grossberg S. (1994). 3-D vision and figure-ground separation by visual cortex. *Perception Psychophysiology, 55,* 48–121.

Grossberg S. (2003). Filling-in the forms: surface and boundary interactions in visual cortex. In: Pessoa L., De Weerd P., editors. Filling-in: From Perceptual Completion to Cortical Reorganization. Oxford University Press;. 13–37

Gruber, T. Tsivilis, D., Montaldi, D., and Müller M.M. (2004). Induced gamma band responses: an early marker of memory encoding and retrieval. *Neuroreport 15*,1837–1841

Haig, A.R. and Gordon, E. (1998). Prestimulus EEG alpha phase synchronicity influences N100 amplitude and reaction time. *Psychophysiology, 35(5)*, 591-595

Hanslmayr, S., Aslan, A., Staudigl, T., Klimesch, W., Herrmann, C.S., and Bäuml, K.-H. (2007) Prestimulus Oscillations Predict Visual Perception Performance Between and Within Subjects. *Neuroimage, 37,* 1465-1473.

Hanslmayr, S., Klimesch, W., Sauseng, P., Gruber, W., Doppelmayr, M., Freunberger, R., Pecherstorfer, and T., Birbaumer, N. (2007) Alpha phase reset contributes to the generation of ERPs. *Cerebral Cortex,* 17, 1-8.

Hirsch J., DeLaPaz R.L., Relkin N.R., Victor J., Kim K., Li T., Borden P., Rubin N., and Shapley R. (1995). Illusory contours activate specific regions in human visual cortex: evidence from functional magnetic resonance imaging. Proc Natl Acad Sci USA, 92, 6469–6473.

Jansen, B.H. and Brandt, M.E. (1991)."The effect of the phase of prestimulus alpha activity on the averaged visual evoked response," *Electroenceph. clin. Neurophysiol, 80,* 241-250.

Jensen, 0., Goel, P., Kopell, N., Pohja M., Hari R., and Ermentrout. B. (2005). On the human sensorimotor-cortex beta rhythm: Sources and modelling. *Neuroimage 26(2)*, 347–355

Jensen, O., and Mazaheri, A. (2010). Shaping functional architecture by oscillatory alpha activity: gating by inhibition. *Frontiers in human neuroscience, 4,*186

Jones, K.A., Tamm, J.A., Craig, D.A., Yao, W., and Panico, R. (2000). Signal transduction by GABA(B) receptor heterodimers. *Neuropsychopharmacology. 23(4,)*S41-9.

Kanai, R., Wu, D. A., Verstraten, F. A. J., and Shimojo, S. (2006). Discrete color filling beyond luminance gaps along perceptual surfaces. *Journal of Vision, 6(12):4*, 1380–1395, Kanai , R. Leila C., Antal A., Wals., V., and Paulus, W. (2008). Frequency dependent electrical stimulation of visual cortex. *Current Biology, 18*, 1839-1843.

Kanizsa G. Praeger; New York: 1979. Organization in Vision.

Kayser, C., Petkov, C. I., and Logothetis, N. K. (2008). Visual modulation of neurons in auditory cortex. *Cerebral Cortex, 18(7)*, 1560-1574.

Komatsu, H., Kinoshita, M., and Murakami, I. (2000). Neural Responses in the Retinotopic Representation of the Blind Spot in the Macaque V1 to Stimuli for Perceptual Filling-In. *Journal of Neuroscience, 20(24),* 9310-9319;

Komatsu, H. (2006). The neural mechanisms of perceptual filling-in. *Nature Reviews Neuroscience, 7,* 220–231

Kopell, N., Ermentrout, G. B., Whittington, M. A. & Traub, R. D. (2000). Gamma rhythms and beta rhythms have different synchronization properties. *Proc. Natl Acad. Sci. USA,* 97, 1867– 1872

Lakatos, P. Karmos, G. Ashesh, M. Ulbert, D. Schroeder, I. and Charles. E. (2008). Entrainment of Neuronal Oscillations as a Mechanism of Attentional Selection. *Science, 320(5872)*, 110-113.

Lee T.S., and Nguyen M. (2001). Dynamics of subjective contour formation in the early visual cortex. Proc Natl Acad Sci USA, 98, 1907–1911.

Llinas, R., Ribary, U., Contreras, D. and Pedroarena, C. (1998). The neuronal basis for consciousness. *Phil. Trans. R. Soc. Lond. B 353,* 1841–1849

Logothetis N. K., Pauls J., Augath M., Trinath T., and Oeltermann A. (2001). Neurophysiological investigation of the basis of the fMRI signal. *Nature 412*, 150–157.

Lorenceau et al. (2012). MEG Beta band activity discriminates perceptual form and motion binding, *Perception 41 ECVP Abstract Supplement*, 64

Lorincz, M. L., Kekesi, K. A., Juhasz, G., Crunelli, V., and Hughes, S. W. (2009). Temporal framing of thalamic relay- mode firing by phasic inhibition during the alpha rhythm. *Neuron 63,* 683–696.

Lutzenberger, W., Pulvermüller, F., Elbert, T., and Birbaumer N. (1995). Visual stimulation alters local 40-Hz responses in humans: an EEG-study. *Neuroscience Letters. 183,* 39–42

Makeig, S., Westerfield, M., Jung, T.P., Enghoff, S., Townsend, J., Courchesne, E., Seinowski, T.J. (2002). Dynamic Brain Sources of Visual Evoked Responses. *Science, 295(5555)* ,690-694

Mathewson, K., Gratton, G., Fabiani, M., Beck, D., and Ro, T. (2009). To See or Not to See: Prestimulus alpha Phase Predicts Visual Awareness. *Journal of Neuroscience, 29(9)*, 2725-2732.

Mathewson, K., Fabiani, M., Gratton, G., Beck, D., and Lleras, A. (2010). Rescuing stimuli from invisibility: Inducing a momentary release from visual masking with pre-target entrainment. *Cognition, 115(1)*, 186-191

Meng, M., Remus, D. A., and Tong, F. (2005). Filling-in of visual phantoms in the human brain*. Nature Neuroscience, 8,* 1248–1254.

Mendola J.D., Dale A.M., Fischl B., Liu A.K., Tootell R.B. (1999). The representation of illusory and real contours in human cortical visual areas revealed by functional magnetic resonance imaging. Journal of Neuroscience, 19, 8560–8572.

Miltner, W. H., Braun, C., Arnold, M., Witte, H. & Taub, E. (1999). Coherence of gamma-band EEG activity as a basis for associative learning. *Nature 397*, 434–436

Murray M.M., Wylie G.R., Higgins B.A., Javitt D.C., Schroeder C.E., Foxe J.J. (2002). The spatiotemporal dynamics of illusory contour processing: combined high-density electrical mapping, source analysis, and functional magnetic resonance imaging. *Journal of Neuroscience, 22,* 5055–5073.

Osipova D, Hermes D, Jensen O (2008). Gamma Power Is Phase-Locked to Posterior Alpha Activity. PLoS ONE 3(12): e3990. doi:10.1371/journal.pone.0003990

Oldfield, R.L. (1971). The assessment and classification of handedness; the Edinburgh questionnaire. *Neuropsychologia, 9,* 97-113.

Palva, J. M., Palva, S., and Kaila, K. (2005). Phase synchrony among neuronal oscillations in the human cortex. *J. Neurosci. 25,* 3962–3972

Piantoni, G., Kline, K.A., and Eagleman, D.A. (2010). Beta oscillations correlate with the probability of perceiving rivalrous visual stimuli. *Journal of Vision 10(13):18*, 1–11.

Pfurtscheller, G., Stancak, A. Jr., and Neuper, C. (1996). Event-related synchronization (ERS) in the alpha band-an electrophysiological correlate of cortical idling: a review. *International Journal of Psychophysiology, 24,* 39–46.

Purves D, Paydarfar JA, Andrews TJ (1996).The wagon wheel illusion in movies and reality. *Proc Natl Acad Sci USA 93*, 3693–3697

Redies C., Crook J.M., and Creutzfeldt O.D. (1986). Neuronal responses to borders with and without luminance gradients in cat visual cortex and dorsal lateral geniculate nucleus. *Experimental Brain Research, 61,* 469–481.

Romei, V., Gross, J., and Thut, G. (2010). On the role of prestimulus alpha rhythms over occipito-parietal areas in visual input regulation: Correlation or causation? *The Journal of Neuroscience, 30(25)*, 8692-8697.

Romei, V., Gross, J., Thut, G. (2012). Sounds reset rhythms of visual cortex and corresponding human visual perception. *Current Biology 8;22(9)*,807-13.

Rosanova, M., Casali, A., Bellina, V., Resta ,F., Mariott,i M., and Massimini, M. (2009) Natural frequencies of human corticothalamic circuits. *Journal of Neuroscience,29*, 7679–7685.

Salari, N., Buchel, C. and Rose, M. (2012) . Functional Dissociation of Ongoing Oscillatory Brain States*. PLoS ONE, 7(5),* 1

Sary G., Chadaide Z., Tompa T., Koteles K., Kovacs G., and Benedek G. (2007). Illusory shape representation in the monkey inferior temporal cortex. European Journal of Neuroscience, 25, 2558–2564.

Sasaki Y., and Watanabe T. (2004). The primary visual cortex fills in color. *Proc Natl Acad Sci USA, 101,* 18251–18256.

Sauseng P., Klimesch W., Heise K. F., Gruber W. R., Holz E., Karim A. A., Glennon M., Gerloff C., Birbaumer N., and Hummel F. C. (2009). Brain oscillatory substrates of visual short-term memory capacity. *Current Biology, 19*, 1846–1852.

Shapley, R., Hawken, M.J. (2011) Color in the Cortex: single- and double-opponent cells. *Vision Research, 51,* 701–717

Sheth B.R., Sharma J., Rao S.C., and Sur M. (1996). Orientation maps of subjective contours in visual cortex. *Science, 274,*2110–2115

Singer, W. Engel, A.K., Kreiter, A., Munk, M.H.J., Neuenschwander, and S., Roelfsema, P.R. (1997). Neuronal assemblies: necessity, signature and detectability. *Trends in Cognitive Science 1 Trends*, 252–261

Spillmann, L., Otte, T., Hamburguer, K., & Magnussen, S. (2006). Perceptual filling-in from the edge of the blind spot. *Vision Research, 46*, 4252–4257.
Stanley D.A., and Rubin N. (2003). fMRI activation in response to illusory contours and salient regions in the human lateral occipital complex. *Neuron, 37,* 323–331.

Tass, P. et al. (1998). Detection of n:m phase locking from noisy data: application to magnetoencephalography. *Phys. Rev. Lett. 81*, 3291–3294.

Thut G., Nietzel A., Brandt S. A., and Pascual-Leone A. (2006). Alpha-band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *Journal of Neuroscience, 26,* 9494–9502. .

Thut, G., Miniussi,C., Gross, J. (2012). The functional importance of rhythmic activity in the brain. *Current Biology 22(16)*

Troxler, D. (1804). Ueber das Verschwindern gegebener Gegenstande innerhalb unsers Gesichtskreises. *Ophtalmologisches Bibliothek*. J. Schmidt. Jena, Springer: 431–573.

VanRullen R., Koch C. (2003). Is perception discrete or continuous? *Trends in Cognitive Science. 7,* 207–213.

VanRullen, R., Reddy, L., & Koch, C. (2005). Attention-driven discrete sampling of motion perception. *PNAS Proceedings of the National Academy of Sciences of the United States of America*, 102(14), 5291-5296.

VanRullen, R., Reddy, L., and Koch, C. (2006). The Continuous Wagon Wheel Illusion Is Associated with Changes in Electroencephalogram Power at ~13 Hz. *The Journal of Neuroscience, 26(2)*, 502-507.
VanRullen, R. & Dubois, J. (2011). The psychophysics of brain rhythms. *Front. Psychology* 2(203), 1-10

Varela, F. J., Toro, A., John, E. R., and Schwartz, E. L. (1981). Perceptual framing and cortical alpha rhythm. *Neuropsychologia, 19(5),* 675-686.

Varela F., Lachaux, J.P. Rodriguez, E. and Martinerie, J. (2001). The brainweb: Phase synchronization and large-scale integration. *Nature Reviews Neuroscience, 2,* 229-239

von der Heydt, R., Friedman, H.S., Zhou, H. (2003). Searching For The Neural Mechanism Of Color Filling-In. In: Filling-in: From Perceptual Completion to Cortical Reorganisaiton (Pessoa, L., De Weerd, P. eds),106-127. Oxford: Oxford University Press

Von Stein, A., Rappelsberger, P., Sarnthein, J. & Petsche, H. (1999). Synchronization between temporal and parietal cortex during multimodal object processing in man. *Cereb. Cortex , **9**,* 137– 150

Voytek B., Canolty R. T., Shestyuk A., Crone N. E., Parvizi J., Knight R. T. (2010).Shifts in gamma phase-amplitude coupling frequency from theta to alpha over posterior cortex during visual tasks. *Front. Hum. Neurosci., 4,191*

Wang, W.J. (2010). Neurophysiological and computational principles of cortical rhythms in cognition. *Physiological Review., 90,* 1195–1268

Weil, R.S., Kilner, J.M., Haynes, J.D., and Rees, G. (2007). Neural correlates of perceptual filling-in of an artificial scotoma in humans. *Biological Sciences - Neuroscience. 104 (12)*, 5211-5216

Weil and Rees .(2011).A new taxonomy for perceptual filling-in*. Brain Res Rev. 24; 67(1-2)*, 40–55.

Womelsdorf, T., Fries, P., Mitra, P.P, and Desimone, R. (2006). Gamma-band synchronisation in visual cortex predicts speed of change detection. *Nature. 7077,* 733-6.

T. Womelsdorf, J.M. Schoffelen, R. Oostenveld, W. Singer, R. Desimone, A.K. Engel, and P. Fries. (2007). Modulation of neuronal interactions through neuronal synchronization. *Science, 316,* 1609–1612

Worden M. S., Foxe J. J., Wang N., and Simpson G. V. (2000). Anticipatory biasing of visuospatial attention indexed by retinotopically specific alpha-band electroencephalography increases over occipital cortex. *Journal of Neuroscience, 20,*

Wrobel, A. (2000). Beta activity: a carrier for visual attention. *Acta. Neurobiol. Exp. (Wars). 60(2)*,247-260.

Zeki, S. and Marini, L. (1998). Three cortical stages of colour processing in the human brain. *Brain 121,* 1669-1685