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Do alpha sampling rhythms of visual perception also code for temporal integration to a higher order percept?

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ABSTRACT

Studies on the role of intrinsic cortical oscillations in the organisation of visual perception suggest that cyclic inhibitory influences participate in the temporal coding of incoming sensory information. In terms of behavioural outcome, these inhibitory influences have been related to a cyclic variation in the perceptual fate of a simple near-threshold visual stimulus at a frequency which matches cortical alpha oscillations at around 10 Hz. In the current experiment we seek to demonstrate behavioural rhythms in visual perceptual performance, following cross-modal phase locking of visual cortical rhythms, for a two frame apparent motion stimulus. Our aim was to determine if performance in this more complex perceptual task – which necessitates sampling and integration of features for motion perception – shows a cyclic variation at a similar frequency to that previously demonstrated (~10 Hz) or shows another periodicity. To this end, we assessed oscillatory patterns in near-threshold visual discrimination performance in 20 participants (15 female) while they were viewing the apparent motion and control stimuli. Results show that there was a significant interaction in the perception of the apparent motion stimulus as motion, compared with a control random noise pattern over the time course of a trial (295 ms), which was due to a cyclic oscillatory trend at a frequency of 11Hz with motion perception, which was not the case for noise percepts. This is taken to suggest that the binding of successive static visual stimuli towards an integrated and meaningful percept of apparent motion is influenced in some manner by cortical oscillations in the alpha frequency. Whether this is likely to be an effect of periodicity in sampling or alternately of encoded temporal intraphasic information is considered.

Key words:	Alpha Rhythms	Visual Perception	Sampling	Motion	Oscillations

Contents

1.0 Introduction

While we subjectively perceive the world around us in a continuously updated fashion it can be demonstrated through visual illusions such as that of reverse apparent motion, that perception is discrete (Purves, Paydarfar, and Andrews, 1996; VanRullen and Koch, 2003; VanRullen, Reddy, & Koch, 2006; VanRullen, Carlson, and Cavanagh, 2007). This parsing of the ongoing visual scene into discrete samples over time is understood to be governed by the instantaneous state of excitability in perceptual neural networks. It is thought that this primary visual level process provides a temporal order to encoded sensory information which in turn allows sequencing and integration of events over time (Pitts and McCulloch, 1947; Varela et al., 1981, Buzsáki and Draguhn, 2004; Fries et al., 2007; Busch et al., 2009; Mathewson et al., 2009; Hoogenboom and Romei, 2010). However exactly how this fine temporal organisation of coding is accomplished and how this information is utilised at higher levels in the visual system is not as yet fully understood.

1.1 The role of pre-stimulus alpha oscillations in visual perception: Evidence from electroencephalography (EEG)

Investigation of perceptual sampling at a neural level suggests a strong connection with the amplitude and more recently the phase of oscillatory brain waves. It has been shown that amplitude of pre-stimulus alpha oscillations (8-14 Hz) (Ergenoglu et al., 2004; Thut et al., 2006; Hanslmayr et al., 2007; Kanai et al 2008; Romei; 2008; 2010) and phase of occipital alpha rhythms are associated with accuracy in perception of a near-threshold visual stimulus (VanRullen, Reddy & Koch, 2005; Hanslmayr et al., 2007; Busch et al., 2009; Mathewson et al , 2009; Dugue, Marque and VanRullen, 2011) as well as the probability of neuronal firing (Lakatos et al., 2005; VanRullen et al., 2005; Fries et al., 2007; Whittingstall and Logothetis, 2009). These investigations reveal that alpha-band oscillations play a modulatory role in segmentation of the incoming visual information (Romei, Gross and Thut, 2010; 2012; Foxe and Snyder, 2011) and this is likely to occur via a phase correlated inhibitory influence which gates neuronal firing in a cyclic manner over time (Thut et al., 2006; Klimesch, Sauseng and Hanslmayr, 2007; Thut and Minussi, 2009; Busch, Dubois, and VanRullen, 2009; Mathewson, Gratton, Fabiani, Beck, and Ro, 2009; Jenson and Mazaheri, 2010, Klimesch, 2012; Sauseng, 2012; Haegens, 2011).

While the purpose of this sampling modulation organised by alpha phase is understood to relate to the coding of temporal order, the detail of how this is accomplished is still partially unresolved. It is unclear if alpha's role is solely in the temporal segmentation of the ongoing visual scene into samples of information at a rate of approximately ten per second, or if coding uses oscillatory phase structure to demarcate timing in a manner which operates faster and more accurately than could be achieved through firing rate information alone (VanRullen and Thorpe, 2001; Johansson and Birznieks, 2004; Jensen, Bonneford and VanRullen, 2012; Ng, Logothetis and Kayser, 2012). Certainly this view of phase as a means of encoding additional information about sensory events is supported by evidence which reveals it to be a critical aspect of coding which can subserve detail about stimulus features (Montemurro, et al., 2008; Kayser, Montemurro, Logothetis and Panzeri, 2009). According to this view, within phase coding is thought to be an efficient means for binding fine grained temporal information into the perceptual information stream, which is necessary for integration of scene change over time and crossmodal binding of multisensory information pertaining to an event in time (Sauseng and Klimesch, 2008; Hipp, Engel and Siegel, 2011). Utilizing within phase coding to incorporate additional information into the stream of neural firing increases the power of the neural code and so processing efficiency. It can therefore be seen that oscillatory coding in the visual system while being inhibitory (see above), may also play an active role in information processing (Klimesch, 2012).

Experiments seeking to demonstrate the discrete nature of perception have provided further evidence of a periodicity in attention, perception and conscious updating (VanRullen, Carlson and Cavanagh, 2007; Busch, Dubois and VanRullen, 2009; Mathewson et al., 2009; 2010; Busch and VanRullen, 2010; VanRullen, Busch, Drewes and Dubois, 2011; Chakravarthi and VanRullen, 2012). While findings in general point to an oscillation of ~ 10 Hz over parieto occipital areas being associated with this periodicity, some researchers support the association of a frontal rhythm of a slightly slower frequency of 7 Hz (Busch et al., 2009; Busch and VanRullen, 2010).

1.2 Linking oscillations to behaviour: Causal interventions via phase-locking of alpha by external stimulation

While investigation of the modulatory influence of oscillations in the visual cortex via EEG plays an essential role in revealing how these systems function, it is also of importance to show directly linked behavioural effects and thus to establish a causal relationship between brain oscillations and behaviour (VanRullen and Dubois, 2011; Thut, Miniussi and Gross, 2012). Varela, Toro, John, and Schwartz, (1981) were the first to demonstrate a rhythmic variation in perception at a rate matched to occipital cortex alpha (~10Hz). The paradigm used by Varela, et al., (1981) investigated discrimination accuracy of two briefly presented successive visual stimuli with concurrent recording of occipital oscillations via electroencephalography (EEG). The results showed that the two stimuli were more likely to be perceived as one if they were presented at time points which coincided with the peaks in the recorded alpha cycle i.e. accurate perception had an inverse relationship with the phase of recorded alpha rhythms at stimulus onset. However while this exciting discovery sparked much interest, experimental replication by the same research team and others proofed difficult (i.e. Gho and Varela, 1988).

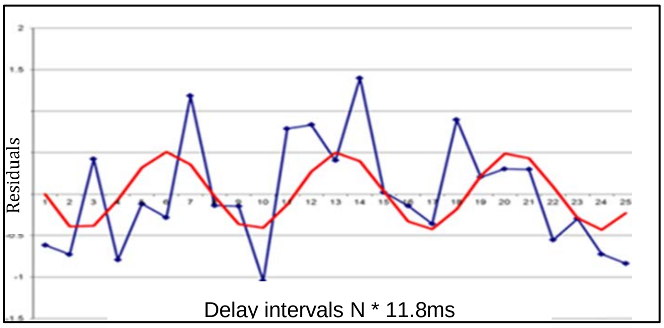
More recent follow-up studies have confirmed that modulation in the excitability of perceptual networks is linked to alpha phase and that prestimulus alpha activity is thus predictive of the perceptual fate of a stimulus (VanRullen et al., 2006; Mathewson et al., 2009; 2010; Busch and VanRullen, 2010). Entraining ongoing cortical oscillations using a rhythmic stimulus has provided an alternative way of examining this facet of perception (Mathewson et al., 2010; 2012; Zauner et al., 2012). However this method led to interpretative difficulties regarding whether the modulation in perception was related to an inherent sampling pattern, a transient sensory response or predictive coding (Lee and Mumford, 2003; Makeig et al., 2004; Sauseng et al., 2007; Martínez-Montes et al., 2008). Rhythmic stimulation was therefore associated with limitations as to the conclusions that could be drawn on the intrinsic organisation of temporal sampling of the visual input.

These issues were resolved by Lakatos, et al., (2008) who utilised intracortical recording in macaque monkeys to demonstrate that phase synchronisation in visual brain oscillations in V1 can also occur in response to an event registered in another sensory modality. In other words, this study showed that crossmodal mechanisms related to attention can reorganise the phase of rhythms in the visual system without any visual input. Following this work Romei, Gross and Thut (2010; 2012) demonstrated crossmodal resetting of occipitoparietal visual alpha in humans after presentation of an auditory stimulus using non-invasive joint EEG and Transcranial Magnetic Stimulation (TMS) techniques. This experiment utilised simultaneous measurement of oscillatory activity and reported phosphenes, which are induced percepts of a visual nature brought about through the administration of TMS pulses over occipital areas. This investigative technique had the significant advantage of avoiding visual input stages of sampling and processing, and thus visually induced cortical activity. It could therefore be demonstrated that there was an alpha phase (~10 Hz) influence on visual perception which originated from an intrinsic cortical rhythm related to the early stages of visual processing, which was not a confounding stimulus induced response.

Using a similar approach as above, Fiebelkorn et al., (2011) demonstrated behavioural modulation effects in detection of a near-threshold sine-wave grating stimulus following crossmodal audio reset of visual cortex oscillations. However the sampling frequency of the experiment was low (2Hz) and as a consequence the experimenter could not comment on the frequency of either behavioural modulation or on the cortical rhythm likely to play a role in this aspect of perception. It is worth noting that Fiebelkorn et al., (2011) reported that the effects of phase-locking extended to 5 seconds post stimulus, which contrasts with the findings from the TMS/EEG experiments of Romei, Gross and Thut, (2010; 2012), who demonstrated an oscillation in perceptual sensitivity at 10Hz extending over the 300ms epoch investigated.

1.3 Cyclic patterns in visual performance revealed by phase-resetting through sounds: Most recent (unpublished) data from this lab

Figure 1 – Overlay of best fit cosine function at 12.03 Hz on to the graph of fast and correct responses in the 2012 student replication of the Varela et al., (1981) experiment



Motivated by the difficulties in replicating Varela et al.'s (1981) finding and by the possibility to phase-reset ongoing oscillations by a sound, an experiment was designed in the University of Glasgow Psychology department (2012), and completed as a student project, which incorporated the audio phase reset of visual perceptual rhythms (Romei et al., 2010) alongside the presentation of two brief, successive visual stimuli (analogous to Varela et al, 1981).

Perception was sampled at a rate of once every 11.8ms over a 295ms experimental time window after sound onset. This paradigm allowed a far greater accuracy of estimation in the likely frequency of cyclic modulation in perception than could be achieved with the design employed by Fiebelkorn, et al., (2011). The experiment succeeded in psychophysically demonstrating a statistically significant rhythm in the perceptual fate of peri-threshold visual stimuli with a frequency comparable to that found in Varela et al., (1981) of 12.03 Hz. The results from that experiment with an overlaid best fit cosine function at 12.03Hz can be seen in Figure 1. The significant result of a perceptual modulation in the alpha frequency range occurred on the condition where two separate presentations of a single dot stimulus were correctly perceived as being presented with an intervening time interval i.e. separately as opposed to simultaneously.

In considering the success of the student replication (2012) in demonstrating behavioural modulation in perception and the previous difficulties encountered in attempts to do the same following Varela et al., (1981), the question was raised if something was different about these later results. A main difference which could hold clues as to why this was the case was that the perceptual modulation demonstrated in 2012 was on a different condition/response set than expected from Varela et al., (1981). Success in demonstrating modulation occurred on separate perception of the dots, which as the stimulus consisted of a dot positioned to the left in one image and to the right in the next (or vice versa), produced the effect of left-to-right (or right-to-left) apparent motion in the observer. This raised the possibility of whether the behavioural finding of perceptual modulation in 2012 was related strictly a sampling effect or if it could be attributed to the particular processing mechanism underlying the perception of apparent motion.

1.4 This experiment: Design and Aims

The aim was to determine if the effect of periodicity found in the student Varela replication (2012) carried out within the department discussed above, was specifically linked to the perception of apparent motion.

The current experiment uses a design similar in all respects bar the visual stimulus to that utilised previously in the student Varela replication (2012) discussed above; the most important features of which are the use of a crossmodal audio reset of visual rhythms and an 85 Hz sampling rate of visual perception i.e. every 11.8ms. However in contrast to the two dot stimulus used in 2012, a set of complex peri-threshold stimulus frames, designed to produce the effect of apparent motion in the observer, were utilised to investigate modulation of an integrated percept. This stimulus was chosen to better represent real world perceptual experience of apparent motion including search and discrimination aspects of perceiving motion from within a complex scene. In addition two alternative stimuli were used to provide matches for the two various ways this motion image set could alternately be perceived. The first was that of the random image set designed to represent those occasions where movement had not been detected, and the second of an image which could represent the integration of the two apparent motion images into a unified static pattern i.e. perceived simultaneously. Thus the stimuli set aims to separate instances of static pattern integration from dynamic temporal motion integration at peri-threshold perceptual levels.

It is proposed that the periodic variation in excitability of perceptual networks enables processing of neural information pertaining to a stimulus at some time points relative to others. If a percept depends on information gathered from two stimulus frames, as in apparent motion, perception should vary over time depending on whether both frames have been successfully sampled and accurately temporally coded. It is hypothesised that once cortical oscillations relating to visual perception have been phase-locked via the use of a cross-modal auditory stimulus, that sampling and integration of two near-threshold stimuli to produce a combined percept of apparent motion will be found to occur with a periodicity of ~10 Hz. It is also hypothesised that cyclic modulation of perceptual sensitivity will not occur when the apparent motion stimulus is not perceived as a motion.

2.0 Method

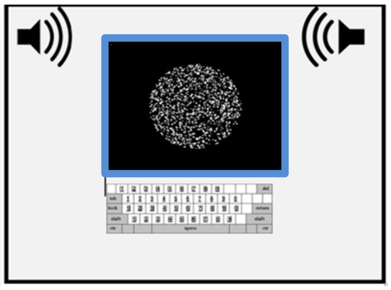
2.1 Participants

Twenty volunteers (mean age 25.05, age range 19–42 years, 15 female, 55 right handed as determined by Oldfield, 1971) with normal/corrected to normal vision, normal hearing and no history of neurological trauma or disease participated in the study. The participants were recruited from the University of Glasgow subject pool, comprised a mix of local people and university students and were compensated for their time with a small cash payment (£10) or course credits. Data from all 20 participants was included in the analyses. Prior to taking part in the experiment each participant received an information sheet regarding the experiment (see Appendix), and gave written informed consent. The experimental procedure was approved by the local Ethical Committee of the Psychology department, University of Glasgow.

2.2 Visual Stimulus

The visual display, which was programmed and presented using E-Prime® software version 1.1 (Psychology Software Tools Inc. http://www.pstnet.com) was displayed on a 21" cathode ray monitor (refresh rate of 85 HZ) which allowed for 11.8ms presentation intervals, as seen in Fig 2.

Figure 2 - Diagram of onscreen presentation of random dot patterns with stereo speakers for sound and keyboard to record discriminant response



This refresh rate was critical as it allowed presentation of a two part stimulus with a frequency of frame change which was greater than the 50-60Hz necessary to produce perception of apparent motion in central vision (Goldstein, 2010). It also allowed for the high frequency sampling rate of perceptual performance (85 Hz) to be employed in the experiment.

Three alternative visual stimulus sets were used, each consisting of a circular pattern of random, white, low-contrast dots on a black background. The circles of random dots in all three conditions were sized at 14cm diameter which represented 8.02 degrees of visual angle and were presented in a central position on the cathode ray monitor for 11.8 ms per presentation. In each condition two images were presented in turn for 11.8ms each with an intervening 11.8 ms interstimulus black blank screen interval.

In the 'Motion' condition the first brief 11.8ms presentation of a circular pattern of random dots was followed by a black blank screen and then a second 11.8ms presentation of a related pattern, in which a percentage of the dots had been rotationally displaced in either a leftward or rightward direction by 5 degrees. This pairing of effective displacement distance between static image presentations and time delay was chosen to induce an effect of apparent rotational motion in the viewer

(Ramachandran and Anstis, 1983; Ramachandran and Inada, 1984). The rotational direction, either leftwards or rightwards, of the second image dot movement pattern was random in order but equal in number. The percentage of the dots that had been rotated in this manner was determined via the titration procedure (see below) which aimed to determine the individual participant's threshold for detection of apparent motion.

In the second condition a 'Glass' pattern stimulus was presented for 11.8ms and was followed by two black blank 11.8ms presentations. A 'Glass' pattern is formed when two identical sets of random dot patterns are superimposed such that the second is offset from the first (Glass, 1969). In the case of our stimulus this was achieved via a rotational deviation of 5 degrees for the same proportion of dots as relocated for the apparent Motion condition and for the Noise condition (determined via titration procedure). This had the effect of producing one stimuli image in which a variety of subtle spiral patterns could be detected. This stimulus set served as the second alternative control for the apparent motion stimulus, representing a match for a combined static integrated pattern perception of the apparent motion stimulus in which all dots were simultaneously perceived.

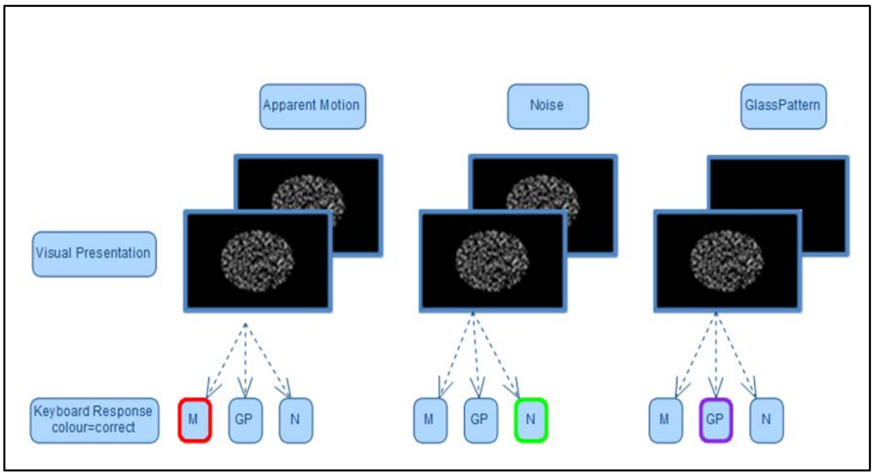
The third visual stimulus, which we named 'Noise', consisted of a circular presentation of random dots for 11.8ms, followed by a black blank screen for 11.8ms and then a second non-identical presentation of random dots for 11.8ms. The second image in this condition had the same proportion of dots relocated as in the Motion condition relative to the first but their placement was random and not in any unified pattern. The proportion of dots relocated was determined by the titration procedure. This stimulus set served as a control for the apparent motion condition by providing two distinct images, being presented for identical intervals, and with the same percentage of dots moving within the pattern.

The three conditions can be described therefore as 1/ Motion - random dot motion pattern and left or right rotated variant (apparent motion set), 2/ random dot 'Glass' pattern paired with a blank screen presentation (Glass pattern set) and 3/ Noise - random dot pattern and second associated random dot pattern with relocations (noise set). Each set of visual stimuli was presented with equal repetitions and randomly with respect to the order of presentation within each condition and overall order of condition.

2.3 Procedure

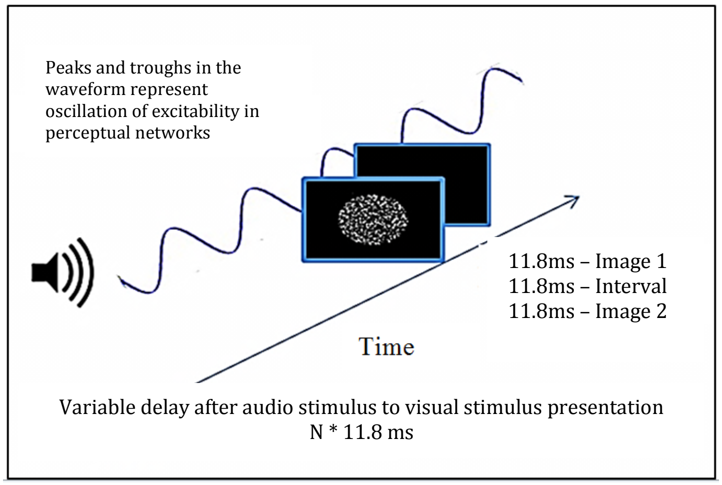
Each participant was tested in a dimly lit room, in a seated position with their chin stabilised via a fixed support at a distance of 100cm from the visual display screen. The participant was required to maintain attention towards the centre point of the screen and was requested to make and input a perceptual response decision regarding the visual stimulus via the computer keyboard as quickly and as accurately as possible after each trial. The visual presentations were described to the participant as 1/ Apparent Motion 2/ Glass Pattern and 3/ Noise and each participant followed a brief training program to allow familiarisation with the stimuli. This involved a demonstration by the experimenter of the three stimulus types using printed images and coaching of the participant through a set of practice onscreen presentation and responses. This process is illustrated in Figure 3 and formed the basis of the judgements of perception carried out by the participant throughout the entire experimental procedure.

Figure 3 - Diagram of the three alternative visual presentation image sets with the correct keyboard response choice denoted in colour for demonstration purposes only



A titration procedure was performed for each participant to determine their individual capacity to differentiate apparent motion from either of the two alternative control stimuli sets. The three stimulus sets were presented as discussed in the section above, and the participant was required to make a discriminant choice according to their perception by selecting the associated keyboard response. This was carried out over 300 trials, using the three varieties of visual stimulus, without any sound. The stimulus images used had varying proportions of relocated dots within the patterns, ranging from the most difficult at only 10%, in regular steps of 5%, to 50%. This variety provided 9 possible levels of difficulty to which the final experiment could be set following this procedure. The program for the experimental trials was adjusted accordingly for each individual participant to set an appropriate level of difficulty in the motion perception task so that it was close to threshold level with 50% of images correctly identified.

Figure 4 - Illustration of temporal delays after ‘BEEP’ for Glass pattern presentation



Following the titration procedure and setting of the appropriate difficulty level the experimental trials were commenced. In the experimental trials there was the addition of an audio stimulus, which was used to induce crossmodal phase locking in visual perceptual rhythms – see Figure 4 for an illustration of the temporal course of the experiment.

The participants were advised that they would hear a ‘BEEP’ sound prior to presentation of the visual stimulus, except for ‘catch’ trials when there would be no sound. The participants were advised that they were not required to pay any particular attention to the sound but that it would occur before each visual presentation. The auditory stimulus, a 900 Hz pure tone, was presented at a 75 dB sound pressure level and lasted for 14 ms.

The visual stimulus was presented at 25 different time delays from the induction of phase locking via the audio stimulus. This served to sample variation in perceptual ability at time points ranging from 11.8ms post ‘BEEP’ to 295ms in intervals of 11.8ms (1 refresh interval of the cathode ray monitor).

The three sets of visual stimuli were presented in a random order for each of the 25 different temporal delays (also random) from the audio stimulus, and the no sound trials. After completion of each trial via selection of a keyboard response by the participant, a pseudorandom delay followed which varied from 0.5 to 2 seconds before the next trial began.

Each participant undertook 5 tests blocks, each containing 312 individual trials. The participants were encouraged to take rests between each block, to compensate for boredom effects. In total over the five blocks there were 20 trials for each sound delay/ stimulus for each of the three visual stimulus conditions (20 * [1 no-sound + 25 different delay periods =26] * 3 = 1560 trials), therefore each participant completed 1560 trials.

2.4 Experimental Design

A within subjects repeated measures design was employed with 3 levels of the visual stimulus condition, either Motion, Glass Pattern or Noise and 25 levels of the time delay condition as independent variables. The main dependent variable was the perceptual response which included correct and two varieties of alternative perception for each condition. Additionally since response timing was considered to be a good proxy for confidence this information was also recorded.

2.5 Method of Data Analysis

Since fast responses were considered to be associated with higher confidence and therefore indicative of ‘true’ subjective perception, the first procedure in data analysis was to separate responses according to speed. ‘Fast’ responses were deemed to be those that lay below the median response speed. In addition all responses which fell out with +/- 3 standard deviations in average response timing were excluded from the analyses as they were considered either to be preemptive guesses or indicative of moments when the participant had lost concentration.

The most evident effect for a number of data sets was a rising trend of increasing response likelihood over the time course of the experiment. However since this effect is not central to our hypothesis it was not examined further and its effect was removed from the data in each condition via the fitting of a linear regression.

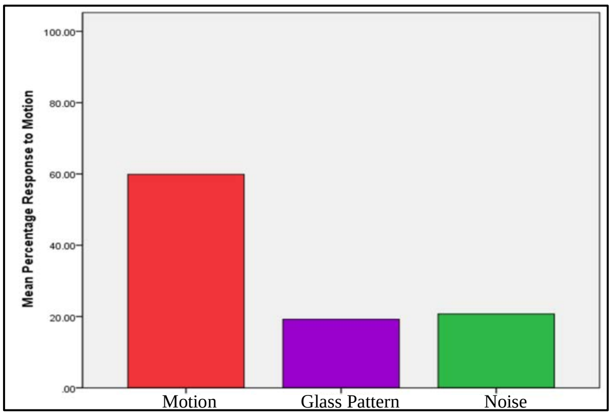
The dependent measure of main interest for further analysis following detrending was the distribution of fast hit rate residuals in the Motion condition when seen as motion, and Motion when seen as Glass pattern, as a function of temporal delay from the crossmodal audio phase reset. As a comparison, the distributions of hit rate residuals in the Noise seen as noise condition were also examined over temporal delays.

3.0 Results

It is hypothesised that once cortical oscillations relating to visual perception have been phase-locked via the use of a cross-modal auditory stimulus, that sampling and integration of two near-threshold stimuli to produce a combined percept of apparent motion will be found to occur with a periodicity of ~10 Hz. It is also hypothesised that this cyclic modulation of perceptual sensitivity will not occur when the apparent motion stimulus is not perceived as a motion.

Prior to turning to comparisons between conditions over the time delays it is necessary to examine the patterns of perceptual results from the Motion condition. There was a large variability between participants in how well the apparent motion stimulus was perceived as motion with an average over all participants of 59.9 % correct with a standard deviation of 33.6. However four participants showed extremely low levels of perception of motion from the apparent motion stimulus ranging from 1% to 14 % and averaging only 7%, correct.

Figure 5 – Bar graph of average percentage responses to the Motion condition showing approximately equal distribution of misses to the Glass pattern and Noise controls

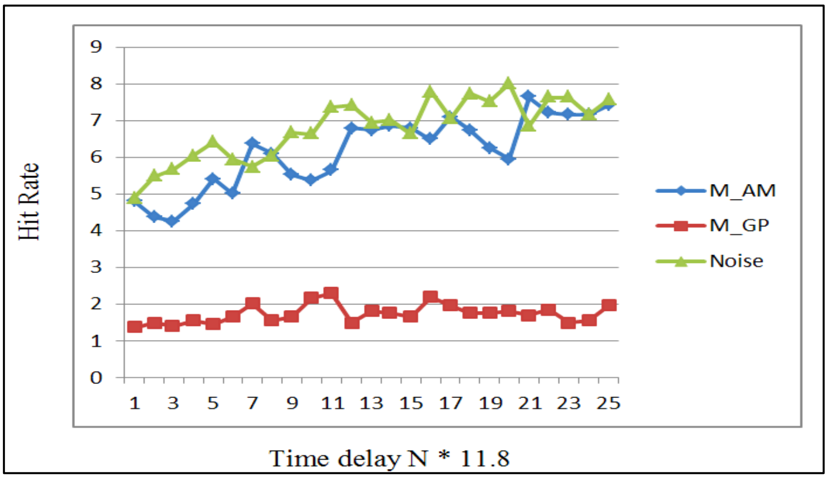


Initial examination of the data both including and excluding these participants, suggested that their removal did not change the overall pattern of results and so a decision was made to include data from all participants within the final analysis. When apparent motion was not perceived from the Motion condition the results were reported as Glass pattern 19.2% of the time on average, st. dev. 26.8, and as a Noise pattern 20.7% of the time on average, st. dev. 22.5, as can be seen in Figure 5. While there was a large interindividual variability in favoured response for missed perceptions of Motion, on average the responses were evenly split between the Glass pattern and the Noise response. This validated the use of the two control conditions as alternatives to the Motion perception, one particularly associated with a blended image and one with a two part stimulus.

Correct perception of the Noise condition occurred on average 69.8% of the time with a st. dev. of 33.2, indicating that it was perceived with a similar success rate to the Motion condition but that there was a greater variance between individuals.
There was an effect of an increasing trend in perceiving the stimuli correctly with longer time delays from the audio stimulus over the 295ms test period for the Motion stimulus seen as apparent motion (M-AM on Figure 6) and for the Noise condition perceived as noise (Noise on Figure 6). However it is worth noting that this isn't the case for the apparent motion seen as glass pattern which is probably due to the small percentage of trials on which this was the selected reponse (M_GP on Figure 6). This result was most likely due to the effect of an increase in attention directing perceptual resources towards the task following the auditory stimulus, such that

longer delays received a greater proportion of overall resources over the time frame of this experiment (Silver, Ress and Heeger, 2006).

Figure 6 - Undetrended data of average results for M_AM – apparent motion seen-as- motion, M_GP – Apparent motion seen-as-Glass pattern, Noise seen as-noise over time in delay periods of N * 11.8ms.



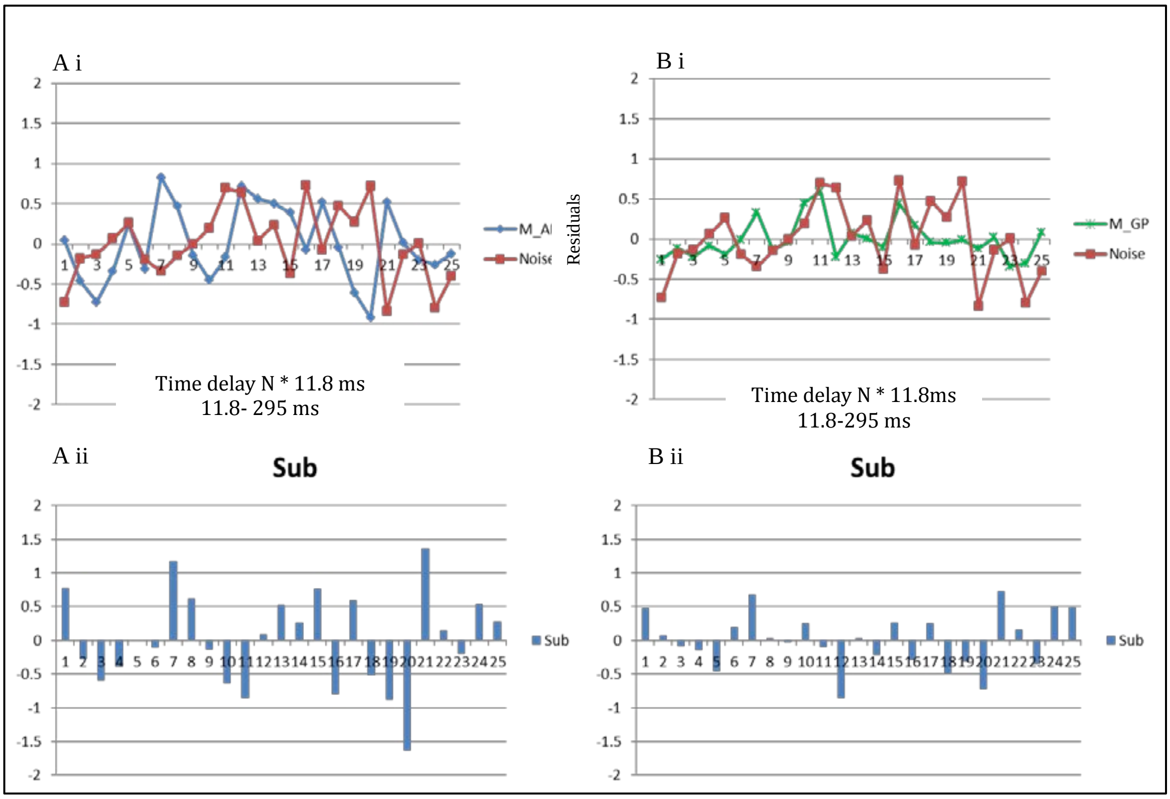
This linear trend is likely unrelated to the cycling of underlying brain oscillations (i,e, the perceptual oscillation hypothesis) and therefore a linear regression was applied to detrend the data in order to examine for more rapid (subtle) effects in perceptual variation (see Figure 7). The final analyses examine the distribution of residuals around these regression lines for perceptual responses which fall into the Motion seen as motion, Motion seen as Glass pattern and Noise seen as noise categories over the 25 different delay periods following the crossmodal reset.

It can be seen from the subtraction of the Motion seen as motion responses (M_AM) from the noise seen as noise response residuals (Noise) (Fig 7 - [Aii]) that there appears to be a pattern of oscillation in perception with 3 peaks within the 295ms time frame. This would appear to suggest that an oscillation in perception with a frequency of approximately 10.2 Hz has an effect on whether apparent motion is seen.

To examine if there is a significant difference from a random distibution of residuals in responses, an ANOVA comparing visual stimulus condition using the two levels - Motion seen as motion and Noise seen as noise, and the delay to visual presentation time with 25 different levels was carried out. The results show that there is a significant interaction between the visual delay and the visual stimulus condition $F_{(24, 456)} = 1.65$, $p = .028$. This indicates that there is difference in the levels of perception of the Motion seen as motion condition when compared to the Noise seen as noise condition which depends upon the time delay tested.

To further examine where the significant differences lie in this interaction, two one way ANOVAs were carried out to examine for differences to random distribution of the residuals within each condition. The results indicate that neither the Motion seen as motion, $F_{(1, 24)} = 1.46$, $p = .074$, nor the Noise seen as noise condition, $F_{(1, 24)} = 1.11$, $p = .292$, showed a significantly different pattern variation over the time delay periods from that which would have been expected randomly when each was considered independently. However the results from the apparent motion condition were showing a trend towards significant modulation over time at the p<.05 level.

Figure 7 - De-trended graphs showing residual oscillation of perception in the fast response subset of responses for [A i Motion seen as motion compared with Noise seen as noise over time delays N * 11.8 and [B i] d Motion seen as Glass pattern compared with Noise seen as noise over time delays N * 11.8.
The corresponding subtracted differences between the two conditions are displayed in the bar charts below each set [Aii] and [Bii] - labelled Sub.



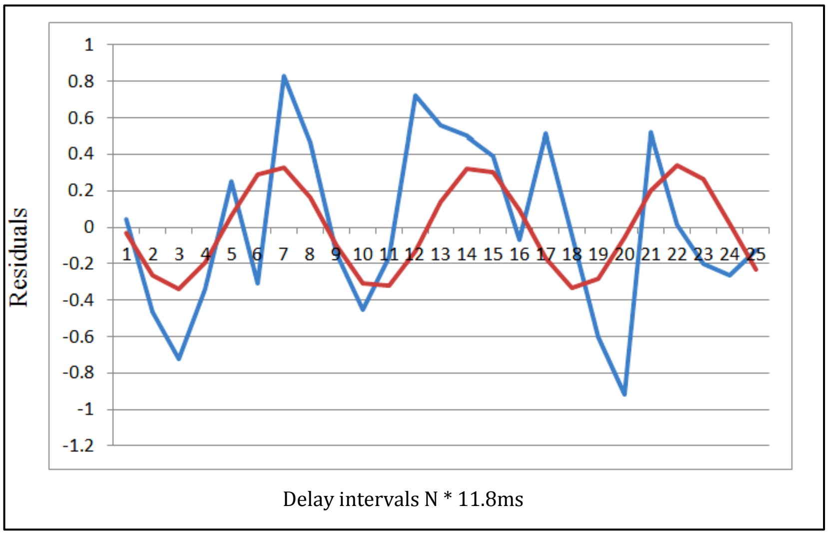
A second two way ANOVA was carried out to examine how the perception of Motion seen as Glass pattern compared with Noise seen as noise over the 25 levels of the time delay factor. In this case there was no significant interaction or main effect of condition or time delay,
$F_{(24, 456)} = 0.738$, $p = .813$.

3.1 Fitting of an oscillation to the Motion seen as motion response residuals

The experimental interest lay in determining if perceptual modulation of apparent motion occurred at a frequency within the alpha frequency band (8-14 Hz). Therefore an oscillatory function was fitted to the pattern of fast response residuals for the Motion seen as motion subset using non-linear regression and least squares estimation in STATISTICA® (Statsoft, Inc., Version 10.0 (http://www. statsoft.com). The cosine function fitted can be defined by the equation, $y = a * \cos (b * 2\pi * x + c)$. Where *y* represents the residuals following detrending of average Motion seen as motion perceptions, x is the time delay from the ‘BEEP’ audio reset stimulus and the presentation of the visual stimuli onset and a, b, and c are constants, was used to represent the results. The constants refer to the attributes of the cosine function, a - representing the amplitude, b - representing the frequency, and c - representing the phase lag. The best fitting cosine function had a significant fit for amplitude at -0.34, *p* = 0.010, and also had a significant fit for frequency at a value of 11, *p* <.001 but not for phase lag at 2.3, *p* = .243. Thus overall the best fitting cosine function was trending towards significance when tested via ANOVA, F = 2.87, *p* = .059.

The best fit cosine function is shown in Figure 8 (overleaf), overlaid onto the graph of residuals following detrending of the Motion seen as motion perceptual results over the 25 time delays.

Figure 8 - Overlay of Alpha wave form (11Hz) in red onto graph of apparent motion seen as motion residuals in blue over time in delay periods of N * 11.8ms.



It can be seen that according to the best fit cosine function peaks in perception of apparent motion from the Motion stimulus occur at delays 5-8 and 13-16 which correspond to timings of 59-94ms and 53-188ms.

4.0 Discussion

The aim of the experiment lay in determining if, once oscillations of visual perception have been phase-locked via a crossmodal audio stimulus, whether perception of apparent motion from two near-threshold sequential displays would demonstrate an oscillation over time, and if so whether that oscillation would fall into the alpha frequency band (8-14 Hz). It was also hypothesised that this cyclic modulation of perceptual sensitivity would not occur when the apparent motion stimulus is not perceived as a motion.

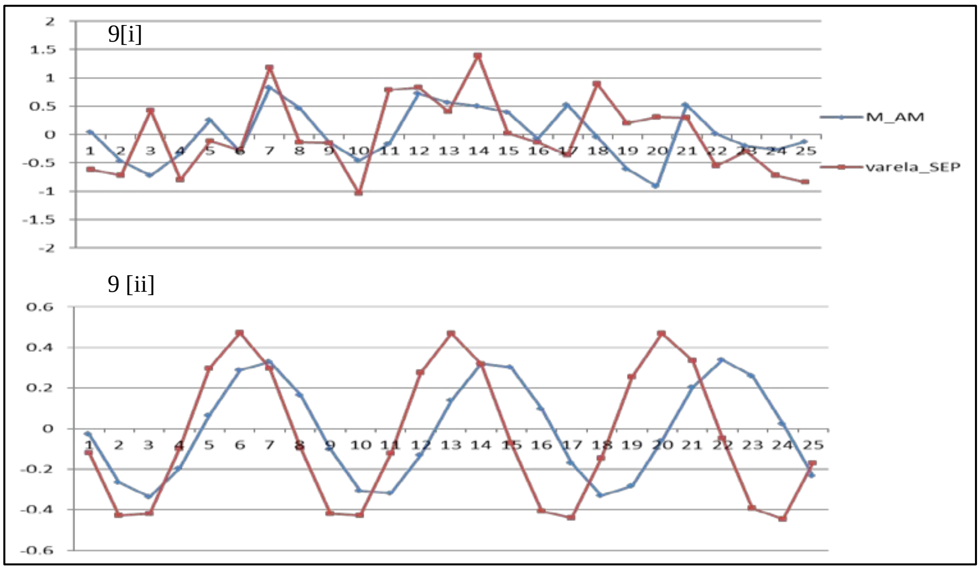
It was found that there was a significant interaction between the stimulus type and the likelihood of perception over the course of the 295ms experimental window for fast responses. This result infers that the pattern of modulation in perception of apparent motion from the Motion stimulus, which is a temporally integrated percept, is affected in a different way to the pattern of perception of alternate complex stimuli, depending on the time delay from the auditory reset. While this result could not be identified as a main effect of apparent motion perception being different to that of the Noise condition, it does offer support for a cyclic modulation of visual perception of apparent motion which has a frequency of 11Hz. The results suggest the existence of an underlying modulation of perception and integration which is specific to higher order percepts requiring a dynamic temporal integration, and which can be related to a cortical oscillation at the frequency of alpha (8-14 Hz). Additionally this finding is in line with previous work that suggested the importance of alpha at 12Hz in apparent motion perception via demonstration of increased power at this frequency during motion perception versus instances of simultaneity in perception (Kompass, Hüfner , Schröger, Kaernbach, and Geissler, 2000).

It should be noted that the interaction was found only in the analysis of variance comparing the effects of perceiving motion from the apparent motion stimulus and from perceiving noise from the noise stimulus. No such similar pattern in perceptual modulation was found for the apparent motion seen as Glass pattern set of results, despite the fact that this was the condition which most closely appropriated the significant result response set reported in Varela et al., (1981) of seeing two separate light sources as simultaneous, which had been so difficult to replicate. The fact that this pattern was once again not demonstrated might now be related to the special characteristics of temporal marking which are utilised when a set of stimuli are perceived as motion, not being invoked on these presentations i.e. that perception of apparent motion invokes a specific timing mechanism in perception which is related to alpha oscillations.

These findings support previous conclusions regarding the importance of alpha oscillations in visual perception particularly with regard to its segmentational organisation over time (Varela, et al., 1981; VanRullen, Reddy and Koch 2005; 2006; Mathewson et al, 2009; Romei, et al., 2010; 2012). However they go further in suggesting that the perception of apparent motion and thus perhaps of other ongoing events which require a dynamic temporal integration for interpretation are specifically organised in some way by alpha modulation.

In this experiment the oscillation which best fitted the behavioural modulation of apparent motion was found to have a frequency of 11Hz, a first peak of heightened perceptual sensitivity at a delay of 59-94ms from the auditory stimulus and a second at 153-188ms. This relates closely to the findings from Romei et al., (2010; 2012) which shows a preferred phase of perception following auditory reset at delays of 75–130ms and 180–225ms, thus in a rhythm of 11.1Hz. However some reticence should be retained in comparing the results of these two experiments, as the cortical origin of the phosphene perception may not have an identical perceptive time path as visual perceptions derived from stimuli. The current results also relate well to the student Varela et al., (1981) replication carried out within the University of Glasgow, Psychology department (2012) despite differences in the stimuli used in the two experiments. The 2012 experiment showed comparable peaks of increased likelihood of identification of a separately presented stimulus as separate at between 54-94ms and 142-177ms. A comparison of the results from the current experiment and that of 2012 can be seen in see Figure 9 - [i] and [ii].

Figure 9 – [i] Line graph of apparent motion stimulus seen as motion in blue and Varela replication in red over time in delay periods of N * 11.8ms. [ii] Superimposed best fit cosine function for the two line charts in 9 [i] over time in delay periods of N * 11.8ms.



In the current experiment the trend towards a significant oscillating modulation of increased likelihood in identifying the apparent motion effect from the Motion stimulus appears strongest up to delay point 18 at 212ms, as can be seen in Figure 9[i]. This may indicate the point at which the synchronization of phase reset alpha oscillations begins to become dissociated. This finding is supported by similar outcomes in the in-department Varela replication (2012) and the work of Romei, Gross and Thut, (2010) which seem to demonstrate that the effects of reset begin to disappear after around 250ms post crossmodal phase resetting of visual perceptual rhythms. This evidence goes strongly against that suggested by Fiebelkorn, et al. (2011) of a 5 second organisation of phase following resetting.

4.1 Discussion of the role of alpha rhythms in the perception of apparent motion

The findings of a tendency towards rhythmicity at a frequency of 11Hz in the perception of apparent motion can be related to the existing literature on the role of alpha rhythms modulation of perception in at least three possible ways which will be discussed below.

The first level of alpha's organisational influence would be considered to be that of a sampling effect brought about through the discrete nature of perception (VanRullen and Koch, 2003; Van Rullen et al., 2006; 2007) and thus representative of the effect of the moderating inhibitory cyclic influence of alpha oscillation on the excitability of cortical perceptual networks (Thut and Minussi, 2009; Busch, Dubois, and VanRullen, 2009; Mathewson, Gratton, Fabiani, Beck, and Ro, 2009; Hanslmayr, Gross, Klimesch and Shapiro, 2011). This sampling mechanism which was called the temporal boundary hypothesis by Varela et al., (1981) is proposed to have the effect of segmenting the incoming stream of visual information and grouping events which happen in one receptive cycle phase i.e. a 30-50ms phase which occurs once during every 100ms phase-locked period (Romei et al., 2012). It is suggested that a visual event, consisting of more than one static image as in this experiment, which is encoded during one of these time frames of high excitability would be both more likely to be perceived and bound into an integrated percept than if that was not the case. It follows that if sequential frames occur such that one fell within the high excitability period and the next fell outwith this time frame, then the first event would be likely to be registered but the second would not. If this was the case then it would be less likely that an integrated perception like that of apparent motion would occur.

However while modulation in perceptual sensitivity at ~10 Hz has been previously demonstrated for simple stimuli and phosphenes (Varela, et al., 1981; Romei et al., 2010; 2012), and is demonstrated here for the Motion seen as motion condition/response set it is not apparent in the pattern of responses in the Motion seen as Glass pattern condition/response set which would have been expected to occur at an alpha frequency but with an opposite phase. This would have been expected if the temporal boundary hypothesis (Varela, et al., 1981), which proposed a segmentation of ongoing visual information into snapshots at a rate of approximately ten per second according to alpha, was complete in its explanatory power.

Since the perceptual modulation result in the current experiment is only demonstrated in the apparent motion condition when seen as motion, and since the time scale of separation between the two stimulus images is only 11.8ms, it seem logical that an additional coding mechanism related to time, of sufficient precision to allow this level of temporal discrimination must be used. It follows that the temporal boundary hypothesis alone cannot provide this level of discrimination and therefore cannot provide a full explanation for these findings.

Alpha's inhibitory modulation of visual processing could also play a role in the processing of temporally integrated event perception via a fine temporal coding mechanism related to precise phase angle within each high excitability sampling window. That is to say, it is not simply the segmentation of the visual information into frames for perception at a rate of around ten per second mediated through alpha inhibition which is important, but also the detailed within phase time code information. It has been suggested that marking of an event according to the exact phase angle of alpha within the high excitability period at which it occurred, could provide a highly discriminative temporal coding mechanism, capable of operating with a sufficiently high speed and precision to match the processing capacity of the human visual system (VanRullen and Thorpe, 2001; Gross et al., 2004; Johansson and Birznieks, 2004; Hipp, Sauseng and Klimesch, 2008; Hipp, Engel and Siegel, 2011; VanRullen and Thorpe, 2001; Jensen, Bonneford and VanRullen, 2012). This method could provide a sufficiently detailed temporal coding to be used for integrating successive frames of a static stimulus into an apparent motion at a higher level in the visual system, simply through within phase alpha sampling, which is therefore a solely feedforward process. However it does not explain why the effect of modulation in perception is not demonstrable for other stimuli.

Another possible mechanism by which alpha’s modulatory influence could effect the modulation in perceptual sensitivity to the apparent motion stimulus is concerned with salience (VanRullen and Thorpe, 2001; Johansson and Birznieks, 2004; Jensen, Bonneford and VanRullen, 2012). According to this theory sequential priority in within phase coding is associated with the stimulus with the highest levels of saliency and therefore associated neural excitability. It is implied therefore that rather than phase coding indicating a strictly sequential temporal orders of events, that it additionally provides a means of prioritising events which are more likely to be relevant to the individual. Since detection of motion in its real form, and apparent motion as an inferred perception is a skill relevant to survival and evolutionary success (Ramachandran and Anstis, 1986), and since it has been shown that movement is treated with the highest salience in visual detection paradigms (Itti, Koch and Niebur, 1998) it is likely that this type of information would be prioritized by the visual system. By this thinking, the salience of motion could give it a preferential advantage in priority for coding within each high excitability episode governed by the oscillatory influence of inhibitory alpha. If this was the case it would be far more likely that an apparent motion stimulus would achieve processing threshold in comparison to a non-motion stimulus. It is noteworthy that if this were the case then even if the motion or apparent motion stimulus fell partly outwith the optimal temporal zone in relation to the ongoing cyclic alpha modulation of perceptual networks it might still reach the threshold for perception. Since perceptual network excitability variation is proposed to be fairly moderate, and Romei et al., (2012) suggest that a variation, oscillating from 35% to 55% is to be expected, it follows that even at low periods of excitability in perceptual networks a sufficiently high influx of neural excitement from a salient stimulus could lead to perception. This mechanism could explain why the perception of apparent motion from the Motion stimulus was more subtle than we might have expected.

In addition saliency based within phase coding could confer a means of organising visual input across sequentially occurring high excitability sampling windows, since an ongoing motion stimulus would be processed with the same phase order ‘tag’ from one window to the next. This temporal ‘tagging’ would allow higher perceptual networks to link ongoing events in a temporal sequence, over the course of consecutive perceptual sampling windows dictated by the alpha modulatory cycle.

This saliency dependent processing incorporated into detailed within phase alpha temporal coding would allow for integrating successive frames of a static stimulus into an apparent motion at a higher level in the visual system. However since it also prioritises the perception of apparent motion relative to other less meaningful stimuli it also explains why the behavioural modulation in perception is not demonstrable for alternate less meaningful stimuli.

Other investigators have emphasised the stochastic nature of the perceptual fate of perithreshold stimuli like these, and take this to indicate that additional as yet unknown process variables exist (Hanslmayr, Gross, Klimesch and Shapiro, 2011). It is possible that stimulus saliency, derived through prior experience and Bayesian probability inference (Lee and Mumford, 2003; Kersten, Mamassian and Yuille, 2004), and fed back to the lowest levels of the visual system could be represented amongst these factors. Other researchers agree that a critical element for perception of apparent motion is mediated through feedback to V1 from motion-sensitive areas MT and V5, which could represent the neural pathway of this feedback input (Sterzer, Haynes, and Rees, 2006).

To summarise this section of the discussion, while it appears from investigations using simple stimuli that sampling organised by alpha phase divides the ongoing stream of visual information into discrete windows (VanRullen and Koch, 2003; Van Rullen et al., 2006; 2007), it seems that a more detailed specificity of coding, still within the alpha rhythm, is utilised to subserve dynamic temporal integration of percepts such as apparent motion.

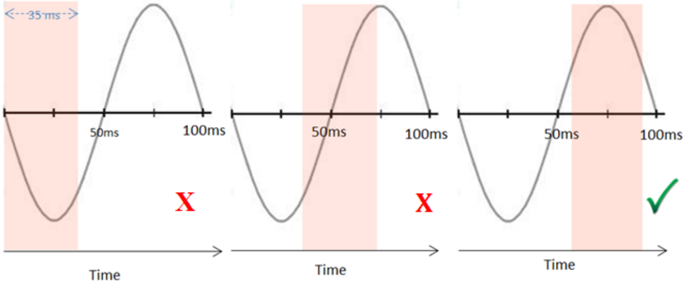
4.2 Methodological evaluation

In terms of evaluating the methodology of the experiment there are a number of issues of concern which may have influenced the results. It appears from the recorded data that there was a large degree of interindividual variation in the capacity to differentiate apparent motion from the control stimuli. While it was attempted to offset this variation via the use of the titration procedure and individualising the difficulty level of the stimuli for detection to near threshold level, it is unclear how well this worked in practice. It seemed that some individuals who scored very highly even at most difficult settings in the titration procedure did not maintain this high level of perceptual discrimination throughout the experiment and vice versa. It may be that while it was possible to maintain superior concentration for the 10 mins of the initial titration test block, that this could not be translated into highly discriminative perception over the total time of the trials which extended over a 60-90 minutes period depending on the individual participant's need for rest. Consequently the conclusion must be drawn that if it had been possible to reduce the time course of the test period for the entire experiment this would have been advantageous.

A second concern was that for a number of individual participants the results from the titration test procedure were not at all clear, such that perhaps they had a good response at a very difficult level and also at a very easy level and nothing at all in between. This was the case in approximately one fifth of participants which caused difficulties in determining how best to set the experimental difficulty parameters. It was also unclear if individuals had specific settings at which they responded best or if they were more suited to one small range of settings, such that choosing the median setting of those in question would give the best response levels. Further investigation of the variability in perceptual response between individuals and in the same individuals over time is necessary in order to develop new designs for investigation of perception which will help to provide more validity to conclusions.

A third issue relates to the timing within the experimental paradigm in comparison of the receptive phase of the alpha cycle and the length of time taken for exposure to the Motion stimulus. A full alpha phase cycle is 100ms long, and contains temporal zones of high and low inhibitory effect which would each likely have a phase length time of around 50ms (however see Zauner et al, (2012) for a more detailed discussion of excitability and phase angle). Additionally the tripartite stimulus set for the Motion stimulus which comprised an image, a blank and then a second image, had a total period which extended to approximately 35ms. The temporal length of the stimulus was therefore relatively wide in comparison to the high excitability phase of the alpha oscillatory cycle. This means that ideal matching of the high perceptual excitability perceptual phase to stimulus timing – where the tripartite stimulus would fall completely within the high excitability period - occurs relatively seldomly- see Figure 10. This could account for why there was less of an apparent motion perception modulation over visual delays than might have been anticipated, since there was a far higher proportion of time point samples at which only one of the two stimulus images would have fallen within high excitability periods than points at which both were.

Fig 10 - Diagram demonstrating infrequency of timing of the 35ms stimuli falling completely within a high excitability phase of an alpha oscillation



Thus for a period of 60ms out of every 100ms alpha cycle the stimulus would be produce a total neural response effect (sensory input + existing network excitability = total neural response to stimulus) of similarly moderate levels of excitement. This is because at any point during this exposure time one of the two stimulus image parts would fall within a high excitability phase and the other would fall within a low excitability phase. Therefore it can be seen that the entire 35ms apparent motion stimulus only fell entirely with the peak excitability phase of alpha's modulation for 15ms out of each full 100ms phase cycle i.e. relatively seldomly.

4.3 Conclusion

Since all visual information, including temporal sequencing is encoded in patterns of neural firing; a systematization of time must exist within the coding structure. The evidence of a behavioural modulation in perception at 11 Hz produced in this experiment, adds further support to the importance played by cortical alpha rhythms in this role. While it is accepted that alpha gates perception in to discrete snapshots over time, it is now suggested that its role may also extend to ordering the fine grained temporal structure and coding for salience.

It appears that stimuli which induce the perception of apparent motion are preferentially ordered into an alpha sampling rhythm or achieve a prioritisation for conscious perception at a higher level, relative to stimuli that are not designed to induce this percept. Further investigation is necessary to determine if perceptual modulation in perception of apparent motion stimuli is related to the saliency of the percept (mediated through feedback from V5 and/or other regions) or temporal dynamic integration of stimuli (mediated at a coding level and feeding forwards). Either of these two mechanisms could still be bound into the organisation of within phase alpha coding and it may be the case that both play critical roles in the organisation of motion perception.

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