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Investigating the temporal and phase relations of oscillatory mechanisms involved in auditory binding.

Thesis submitted for the Degree of Doctor of Philosophy

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Abstract

Introduction: Auditory binding refers to the integration of the components of a sound to form a wholistic percept. The present research explores similarities within visual and auditory binding mechanisms by testing two theories grounded in visual binding research: The General Phase Angle Hypothesis (GPAH), and the Return Phase Hypothesis (RPH). Informed by the findings, differences in the structure of the auditory binding mechanism dependent on music training were examined using a combination of experimental and neuroimaging techniques. The findings contribute to our knowledge of anticipatory coding as a dynamic system, necessary to navigate within a dynamic environment.

Methods. All experiments employed an auditory priming/stimulus entrainment paradigm to evoke an auditory gamma-band response (aGBR) that is phase locked to the frequency of the primed target stimulus. Trials required a forced choice reaction time (RT) response, thus providing a psychophysical measure of the internal oscillatory mechanism involved in auditory cognition. The third study incorporated Magnetoencephalography (MEG) neuroimaging.

Results. The GPAH proved a better predictor of an anticipatory effect, beyond an effect of priming – emphasised by the findings from a study guided by a capacity sharing relation derived from the Time Quantum Model (TQM). Regarding the second phase, musicians and non-musicians demonstrated differential priming effects.

Conclusions. The TQM capacity sharing relation provides a template for the optimal experiment-stimulus parameters with which to investigate the phase interactions within the auditory oscillatory mechanisms required for binding. While priming enhances early bottom-up (gamma) carrier frequencies, the process also shifts critical gamma frequencies involved in auditory binding mechanisms by ~2 Hz, considered to be due to delta superimposition resulting from task demands. Furthermore, musicians demonstrate a reduced effect of priming. The implication is this population rely more on top-down processes as training strengthens the corticofugal system, allowing for more efficient feedback from higher auditory processing areas.

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Declaration

I, the candidate, assert that this thesis is my own work, and that I have not obtained a degree in this university or elsewhere on the basis of any of the thesis content.

Naomi du Bois

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List of Works

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Book chapter: du Bois, N., & Elliott, M. A. (2017). The temporal dynamics involved in object representation updating to predict change. In *Progress in brain research* (Vol. 236, pp. 269-285). Elsevier.

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Book chapter: Elliott, M. A., & du Bois, N. (2018). Dynamical Constants and Time Universals: Relating and Resolving Two Theories of Cognitive Microstructure. In *Invariances in Human Information Processing* (pp. 51-62). Routledge.

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1 The Importance of Anticipatory Coding in Object Representation Updating to Predict Change

1.1 Introduction

Scene analysis involves the segregation of the components of stimuli arising from distinct environmental events into separate perceptual representations, or streams (Bregman, 1990; Elliott & Müller, 1998; Elliott, Shi, & Kelly, 2006). The components of these visual and auditory stimuli, such as the colour and contour of objects, and the pitch¹, timbre², and loudness³ of sounds, are coded in different neural assemblies⁴. Binding is the term given to the integration of these separate neural systems and is achieved via synchronised oscillatory activity, whereby rhythmic vibrations in neural assemblies arising from neural feedback connections result in a synchronisation of their firing patterns (Gray & Singer, 1989; Michalareas et al., 2016; von der Malsburg, 1981). It is considered that this type of dynamic system structure underlies psychological processes such as sensation, perception, attention, learning, and memory, all contributing to the mind and human behaviour. Such processes are therefore complex, non-linear, self-organising, and emergent (Fusella, 2013). To integrate the components of each percept in the visual or auditory scene efficiently, thus promoting a stable environment, requires the prediction of outcomes based on the given input. Accordingly, anticipatory coding promotes the communication of the representations of events or perceptions predicted to occur in the immediate future to the motor and sensory cortices in advance of the conscious perception or event (Bubic, Yves von Cramon, D., & Schubotz, 2010). This is achieved via integrated bottom-up and top-down processes whereby the neural carriers of stimulus information and prediction errors are modulated by the feedback carriers of the expected representations (Bubic et al., 2010; Engel, Fries, & Singer, 2001; Michalareas et al., 2016; Sauseng, Klimesch, Gruber, & Birbaumer, 2008). Thus, cognition is not a direct process of piecing together information, rather it

¹ Pitch is the perceptual property associated with the frequency characteristic of sound. Pitch perception allows us to order sounds on a frequency related scale.

² Also referred to as tone colour/quality, timbre is the perceptual property associated with the sound spectrum and envelope.

³ Loudness is the perceptual property attached to amplitude, which is determined by the height of the sound wave.

⁴ A neural assembly refers to a group of spatially separate neurons participating in self-generated and phase-locked network oscillations.

occurs in real time and develops over the life-span, arising as the most probable outcome of many possible alternatives. The thesis presented here seeks to examine the frequency and phase relations underlying the oscillatory mechanism intrinsic to the binding process in the auditory domain, both experimentally and using neuroimaging techniques.

1.2 Synchronisation: Support and Controversy

Subjective experience does not match the neural circuitry of the brain, and thus a large explanatory gap remains between the way in which information is received and coded in the brain and our perception of a stable world. Auditory illusions are examples of this correspondence mismatch. For example, the Deutsch scale illusion occurs when two melodies (M1 and M2) are played, with the first note an octave apart, on two separate instruments. However, each melody comprises alternate notes from either the descending or the ascending scale, taking the first note in the melody as the tonic (first note in a scale), depending on which end of the scale the melody began (Deutsch, 1975; Janßen, Bramsløw, Riis, & Marozeau, 2017). The illusion occurs when the instruments and the timing of the notes are the same, and therefore the timbre and rhythm remain stable. If the scale is in the key of C, the first instrument plays C1, B2, E1, G1, G1, E1, B2, and C1 (M1), while the second instrument simultaneously plays C2, D1, A2, F1, F1, A2, D1, and C2 (M2). Beginning with C1 in the first sequence, and alternating between both sequences, results in C1, D1, E1, F1, G1, A2, B2, and C2, while beginning with C2 and following the same pattern results in C2, B2, A2, G1, F1, E1, D1, and C1 – one ascending scale and one descending scale. Even though the alternating notes of the ascending scale and equally the alternating notes of the descending scale, are dislocated in space, the perceived melody is usually that of a scale that either first ascends, or first descends, and then changes pitch direction, half way through, i.e., the perceived M1 is C1, D1, E1, F1, F1, E1, D1, and C1, while the perceived M2 is C2, B2, A2, G2, G2, A2, B2, and C2. Even when each melody is presented to the listener monaurally, for example, with the notes from M1 to the right ear and the notes from M2 to the left ear, the same illusion is usually perceived with each scale lateralised to one side. The melodies do not change physically when listened to separately or played together, and again they do not change when presented to each ear separately or to both ears in a real-world setting – however in both instances, the

perceived melody changes completely. This illusion occurs due the fact that the auditory system fuses sounds binaurally, and streams sound according to similarities such as common onset time and harmonicity (Darwin, 1997). Johann Sebastian Bach's Violin Partita no. 2 in D minor is an excellent example of the reverse effect, referred to as auditory stream segregation, due to the punctuation of a musical piece with notes that are separated by more than an octave, thus with a marked dissimilarity in pitch, resulting in the perception of two separate streams rather than a continuous melody played on one instrument (Disbergen, Valente, Formisano, & Zatorre, 2018). Auditory cognition differs from the visual modality, where light from the same object stimulates adjacent retinal regions. Two separate sounds can have frequency⁵ components that are interspersed across a wide frequency spectrum, and sounds enter both ears to form a composite sound wave. The neural substrates of auditory cognition deal with the problem of integrating the components of each sound into separate percepts using bottom-up cues such as pitch and/or timbre similarity and onset time etc., coupled with top-down processes based on context and past learning experience. Interesting in this regard is the McGurk effect, which emphasises the importance of audiovisual integration in speech interpretation, and the propensity for visual information to interfere with auditory information when there is ambiguity (Basu Mallick, Magnotti, & Beauchamp, 2015; McGurk, & MacDonald, 1976). If the sound source is physically a voice saying, for example 'Bah' repeatedly, but the visual image is that of a person saying 'Gah' repeatedly, in time with the physical sound, the listener will perceive an illusory 'Dah', due to a blending of the auditory and visual information. As with vision however, auditory cognition performs a very complicated process of piecing together sound percepts from the vast array of sound components such as pitch and timbre, heard at any given time in the auditory scene, to provide a stable perception of the world around us, despite, and at times due to, failures under certain conditions.

Research examining the neural mechanisms underlying this process of integration has advanced our understanding of the temporal dynamics involved greatly in the last forty years. Von der Malsburg (1981) put forward the correlation theory of brain function, which describes a dynamic system dependent on and

⁵ Frequency refers to the rate per second of a resonant wave, either in a material (as in sound waves), or in an electromagnetic field (as in radio waves and light).

CHAPTER ONE: ANTICIPATORY CODING

controlled by correlations in the fine temporal structures of neural responses. Support for this theory arrived a few years later when it was discovered that by presenting grating stimuli to the visual receptive fields of anaesthetised cats, stimulus-evoked (SE) oscillatory responses are generated and are coherent in locations that are functionally close yet spatially separated, i.e. when local oscillators share a common coding property such as movement direction, or proximity in spatial location, they resonate coherently with the SE oscillation (Eckhorn et al., 1988). Thus it was proposed that these synchronous oscillatory responses could provide a mechanism with which coded information in spatially distributed areas of the cortex could be temporally coordinated (Eckhorn et al., 1988; Gray & Singer, 1989). The idea of 'Binding by Synchrony' offered empirical as well as neurophysiological support for von der Malsburg's theory of binding via correlative brain function. Neural oscillations refer to the rhythmic (repetitive) activity of neurons in the central nervous system, generated by mechanisms within the individual neuron or by interactions between neurons. Oscillations in an individual neuron's membrane potential, or in the rhythm of the firing of the action potentials, produces oscillatory activation of the post-synaptic neurons. These interconnected neurons form neural assemblies, which are self-generated and phase-locked network oscillations, resulting in synchronisation of their firing patterns. The temporal and phase parameters involved in the dynamic mechanism of auditory cognition necessary for this process are the focus of this contribution.

Since its conception, binding by synchrony has received a variety of support and criticism. Von der Malsburg (1999) refers to this process as a general mechanism for brain function, which classic neural networks cannot completely explain, while proponents of the neural network approach argue that it holds as a means of explaining how binding is signalled but not computed (Shadlen & Movshon, 1999). It has been argued that neurological findings support the concept of binding as a higher order process. For instance, Balint syndrome, resulting from bilateral damage to the occipitoparietal cortex and areas of the posterior parietal cortex, causes visual binding deficits (Rizzo & Vecera, 2002). One example is simultanagnosia, which is the inability to perceive more than one object at a time. Damasio (1985) noted that lesions to the cortex involved in early visual representations (V1 for example) results in deficits to vision and perception, but not specifically to binding. Thus, it was argued that synchronous firing in primary visual

cortex should not be necessary. Shadlen and Movshon (1999) suggest that firing rate provides the perceptual input, and synchronous activity is merely an elaborate description of coincidence detection – binding by synchrony activates post-synaptic neurons that act as coincidence detectors, which they propose is analogous to generating cardinal neurons (neurons that are selectively activated by specific objects). However, in support of binding by synchrony, von der Malsburg (1999) proposed that ratios of activity (rather than firing rate alone) in separate but overlapping neural assemblies allow for coding of intermediate values on perceptual dimensions to maximise neural economy and discriminability. Shadlen and Movshon (1999) also dispute the methodology normally used to examine correlated spike activity and suggest that the corrections used cannot remove correlations due to events such as slow response variability, response latency, and visual responses connected to fixational eye movements, which produce peaks in cross-correlograms, thus confounding the significance of the synchronicity reported. However, regarding the influence of fixational eye movements, in some instances, the temporal information may well be contained in the perceptual input. For example, eye and body movements can impose a temporal signal structure (von der Malsburg, 1999). While it was agreed that synchronous firing in primary visual cortex could be a result of feedback projections necessary for the tagging of neurons coding the same object, it was argued that these projections would require a level of absolute precision, not only to topographically relevant areas of V1 but to specific columns and laminae, which had not been found. Since this argument was made, hierarchical laminar patterns of feedforward and feedback projections have been demonstrated in the visual cortex of non-human primates (Barone, Batardiere, Knoblauch, & Kennedy, 2000; Markov et al., 2014; Michalareas et al., 2016). Typically, laminar layer 4 has been demonstrated to carry feedforward activity while layers 1 and 6 carry feedback activity. Michalareas et al. (2016) used magnetoencephalography (MEG) to examine correlations in the laminar projection patterns of seven homologous macaque and human areas of visual cortex, particularly in the direction of these projections and their inter-areal influence. The findings of this research show that communication along feedforward projections is subserved by gamma-band activity [gamma wave range = 30-70 Hertz (Hz)], while that along feedback pathways is subserved by alpha-beta activity [alpha wave range = 7.5-12 Hz, beta wave range = 12.5-30 Hz]. Cognitive architecture promotes correlation – neurons connected to each other

(discounting short delays) induce temporal correlations in their activity, and also neurons that are connected to a common source of activity (even though they are not directly connected), become temporally correlated via complex synaptic connections. Von der Malsburg (1999) realised the importance of temporal correlation between the sending and receiving neurons – now empirically described by Engel, Fries, & Singer (2001) as temporal coherence. This finding also explains how cognition can be altered flexibly through inhibition, thus disrupting coherence. The production and evaluation of networks of functional neural firing patterns require a self-organising system established via synaptic plasticity (see von der Malsburg, 1999; von der Malsburg, 1985; von der Malsburg, 1981). Thus, a single neuron can provide different functions, taking part in different activities, depending on the neural assembly it is part of at a given time, and the network firing pattern thus induced.

Communication through coherence (CTC) proposes active neural assembly oscillations are modulated by rhythmic excitability fluctuations resulting in temporal windows of coherence through which communication occurs. Such modulations affect the probability of both spike output and synaptic sensitivity to input, thus resulting in phase-locking between oscillatory neural assemblies allowing for communication, due to shared temporal windows for input and output. Prior to the proposal of CTC, it was considered that the action potential rate, and strength of synchronisation between neurons forming an assembly, provided the code for neural communication. However, Fries (2005) argued that this form of communication was constrained by the anatomical structure of the brain and did not allow for effective, flexible communication given the timescale at which cognitive demands change. The control and coordination of inter-areal interactions required for most brain functions operate on timescales faster than that of synaptic change (Battaglia, Witt, Wolf, & Geisel, 2012). CTC describes binding by synchrony as the mechanism by which the cognitive system forms a representational code and extends this hypothesis to include the consequences of such a mechanism for communication – modulation of these oscillatory mechanisms depending on cognitive demands, allows for effective and flexible communication. Research based on feedforward models of neuronal communication have found that increasing synaptic input rate decreases the size of the postsynaptic excitatory potential to such an extent that in some cases there is a null effect of increased rate on the postsynaptic potential, which contradicts the firing rate modulation theories (Tsodyks & Markram, 1997). Azouz and Gray (2003)

found that increases in input rate (measured as the average subthreshold membrane potential in the 250 milliseconds (ms) period prior to a spike) causes a linear increase in the membrane potential at the time a spike is elicited – the spike threshold, thus reducing the effect of input rate. However, the spike threshold decreased with increasing slope of the pre-spike membrane potential suggesting sensitivity to the density of input rate within a very short temporal window. Thus it is suggested, as proposed by von der Malsburg (1999), that a neuronal assembly sending a message will maximise the effectiveness of the message getting through if each neuron in the assembly groups its spikes in bundles, and if all neurons in the assembly then synchronise so as to maximally increase the number of bursts at the receiving neuron within a very short window of time. This is exactly what appears to happen when neurons engage in synchronised gamma oscillatory activity (Pascal Fries, 2009). CTC argues that this results in regular and predictive communication windows within the sending neural groups. In addition to this, however, the conduction delay, or travelling time between each sending group and the receiving group, must also be the same. In fact, it has been demonstrated that this delay is regulated in different parts of an axon such that synchronous arrival of these spikes at the receiving neuron is ensured regardless of physical disparities (Salami, Itami, Tsumoto, & Kimura, 2003). Finally, effective communication depends on the arrival of synchronous bursts at a time when the receiving neuronal group is maximally excited. As the receiving assembly will also oscillate modulated by fluctuations of excitability within the assembly, communication requires phase-locking between the sending and receiving assemblies for effective communication – and this is described by CTC.

1.3 Support from an Oscillatory Priming Paradigm

Initial psychophysical attempts to demonstrate perceptual binding used temporal cues in perceptual report tasks (Fahle, 1993; Lee & Blake, 1999; Usher & Donnelly, 1998). The premise of these experiments was that externally manufactured temporal synchrony could induce a temporally synchronised response in neural populations coding figure-ground information. This temporal coordination leads to feature binding and has a direct, first-order effect on perception. However, these experiments have been demonstrated to contain unintended cues due to temporal contrast and motion inducing spatiotemporal signals (Farid, 2002; Farid & Adelson, 2001). Elliott and Müller (1998), and Elliott, Shi and Kelly (2006) argued that neural

bindings, especially in early visual processes may not be directly related to that which is perceived. In addition, Elliott (2011) argued that perceptual synchrony paradigms such as these fail to consider the interval of time over which events appear to be simultaneous (the perceptual moment). Pöppel (1997) refers to this moment as a perceptual unit of 30 ms duration. This period of perceived simultaneity is the minimal amount of time required for figure-ground segregation (Kandil & Fahle, 2001). In consideration of the perceptual moment, as well as neurophysiological issues, the gamma-band range of frequencies was suggested as the most likely brain rhythm to subserve the feedforward mechanism of perceptual information as these frequencies are slow enough to withstand the conduction times of coupled assemblies, and yet can carry signals rapidly (Singer, 1993). For example, one oscillation at 33 Hz takes 30.3 ms to complete (1000/33 = 30.3) compared to a 7 Hz oscillation (theta range) that takes 143 ms, which is slow enough to establish synchronisation but too long to allow for rapid scene analysis given that much of perceptual processing occurs at this time if not ahead. In support of this, a study conducted by Conci, Gramann, Müller, & Elliott (2006) used electroencephalography (EEG) during a visual search task to investigate the interference effect posed by shape-information provided by distracters upon target detection. The findings of this experiment suggest that even under difficult conditions scene analysis is largely complete within 340 ms, and much of the required investigation occurs between 60 and 120 ms. Perhaps most importantly however, experiments using temporal cues alone failed to provide a means with which to investigate the temporal parameters of the mechanisms involved in binding feature information, therefore not permitting an investigation of research questions regarding specific frequency interactions, and the role of phase relations within these interactions. Cognition requires coherence between the sending and receiving neural assemblies, modulated by slower endogenous brain rhythms, which results in precisely timed windows of communication. A psychophysical investigation therefore requires a means of providing a temporal code that can be manipulated, which will result in an output that will allow the effects of the manipulation to be examined.



Figure 1.1. Illustration of the premask-matrix paradigm employed by Elliot (2014). The first panel in **A** shows all possible positions for the flickering crosses, while the second panel shows a target present condition, with the Kanizsa square presented in the top left corner. The top row of panels in **B** illustrates the intraphase condition, which primes the location of the Kanizsa target, and the bottom row illustrates the interphase condition, which does not prime the location. For example, a 1 second premask comprising 40 frames, each presented for 25 ms, with <1 ms duration between frames, results in a 40 Hz rate of flicker.

Source taken from Elliott, M. A. (2014). Atemporal equilibria: pro- and retroactive coding in the dynamics of cognitive microstructures. *Frontiers in Psychology*, *5*, 990.

Elliott and Müller (1998) developed an oscillatory priming⁶ paradigm which used synchronized and oscillating visual stimuli in a premask to entrain and prime an oscillatory response. They then measured the effect of this response on participants' reaction time (RT) responses to targets present (or absent) at the primed location. The target was a Kanizsa-type figure; a square defined only by the corner junctions. The premask matrix consisted of flickering crosses (see figure 1.1). This matrix was hypothesized to entrain an internal oscillatory response matching the frequency of the priming stimulus – in other words, an oscillatory response with a frequency corresponding to the rate of flicker. Entrainment is an important characteristic of

⁶ Presenting a stimulus for durations below levels of conscious detection.

interactions between brain rhythms, and refers to the coupling of two independent oscillatory systems in such a way that their periods of oscillation become related by virtue of phase alignment (Cummins, 2009). By manipulating the rate of flicker, the oscillatory response could be altered correspondingly. The global frequency of the premask was determined by the number of frames presented in a premask of one second duration, therefore 40 frames per second equated to a 40 Hz premask, as illustrated in figure 1. Elliott and Müller (1998) initially found an enhancement effect for RTs to targets present under synchronous conditions when presented specifically at 40 Hz. Enhancement refers to an increased gap between absent and present RTs. A few points regarding the paradigm should be emphasised prior to discussing further developments, to appreciate its utility as a psychophysical measure of the internal synchrony binding mechanisms underlying the integration of visual information.

1.3.1. Avoiding unintentional artifacts. To remove spatial and attentional artifacts a 75% threshold for detecting a synchronous premask was established through a pilot programme – resulting in presentations above 21 Hz rate of flicker. In addition to being unaware of the presence or absence of the Kanizsa figure, participants also reported being unable to detect a difference between the synchronous and random conditions. Premask presentation times were varied between 300 and 4800 ms, as beta and gamma frequency oscillatory activity requires ~100 ms to become established (Elliott & Müller, 1998). Due to the dynamic structure of the stimuli in this paradigm, Elliott and Müller (2001) investigated whether the effects of priming were influenced by motion signals induced by the flicker or the transition from the premask matrix to the target matrix. It was found that induced motion did increase target saliency but did not statistically alter the effect of prime synchrony (which remained constant – reaction times in random conditions did not converge with those in synchronous conditions).

1.3.2 Evidence for the persistence of the evoked oscillatory response. Inference of phase interaction between the target and the oscillatory trace requires that the entrained oscillation be demonstrated to persist during the interval between the last frame to be presented containing the target (in the synchronous condition) and the time of target presentation. Elliott and Müller (2000) examined the duration and structure of the synchronous response to the premask entrainer to ascertain whether it performs as a short-term memory store for figure-ground information in a

similar way to visually accessible stimuli. Based on evidence from EEG studies demonstrating a stimulus-locked 40 Hz response to the presentation of visual stimuli, approximately 100 ms post stimulus onset (Schürmann, Başar-Eroglu, & Başar, 1997; Tallon-Baudry, Bertrand, Delpuech, & Permier, 1997), it was hypothesised that inter-stimulus intervals (ISIs) which corresponded with a 0° phase difference between the 40 Hz premask rhythm and the presentation of the target figure would enhance reaction timed responses. For example, at 40 Hz each frame lasts for 25 ms and therefore a 0° phase angle⁷ would correspond with an ISI of 25 ms or an integer multiple of 25, such as 50 ms, following a 1 second premask, whereas an ISI of 12 ms would correspond with a 180° phase angle (stimulus presentation would be out of phase with the synchronous prime). Persistence effects were demonstrated to be similar to those of visible stimuli (200 - 300 ms). More specifically, for premask displays presented at a 40 Hz rate of flicker, persistence endured for 150 - 200 ms post-stimulus off-set, which when the time of the final presentation of the premask display (-100 ms) is accounted for, implies that the synchronous prime inherits the persistence of the 40 Hz premask display as a whole, despite the synchronous premask remaining un-detected by participants. Counter to expectations, an advantage for ISIs corresponding to a 180° phase angle was revealed, as opposed to the hypothesised 0° phase angle advantage.

1.3.3 Reconciling persistence effects with the non-detectability of the prime. The details of the premask are not detected by participants – meaning the RT responses to a synchronous prime are pre-attentive - which is inconsistent with the evidence that the persistence of the oscillation evoked by the premask display matches that of visible, and therefore attended to, stimuli. Visual experience occurs later in the visual system, and yet because the premask remains outside of the participant's awareness, this precludes areas beyond the inferotemporal (IT) cortical area. The receptive fields of neurons in V4 and IT are wide enough to encode the entire display (Elliott & Müller, 2000), yet Elliott and Müller (1998), found the enhancement effect is conditional on the presentation of the target at the location previously occupied by the entrainer and not when the target is present at a different location (synchronous target present trials). This spatial-specificity suggests that the

⁷ Phase angle is the difference in phase between two frequencies expressed as an angle, such that 360 $^{\circ}$ (2 π radians) corresponds to one complete cycle (oscillation).

synchronous prime is principally active in early visual processing (in regions where the receptive fields encode small areas of the visual field) such as V1. Given the synchronous prime demonstrates persistence properties consistent with the premask display as a whole, a derivative would be that it also maintains the same temporal structure (e.g. a synchronous prime generated by a premask presented at 40 Hz, will oscillate at 40 Hz). Elliott and Müller (2000) thus suggest that individual frames do not persist long enough to be separable consciously (they are processed as simultaneous events). Also, and consistent with this, due to the < 1 ms delay between individual frames, in the IT area of cortex neural responses to each frame become integrated so that they generate an average sustained response maintained by the premask rhythm. Therefore if the premask was presented at a 40 Hz rate of flicker, this would result in a low amplitude 40 Hz response in IT, the minima of which would not reach the sensory threshold. Fries, Reynolds, Rorie, and Desimone (2001) suggest that neural gamma activity generated in IT will induce oscillatory activity of the same frequency in earlier visual processing neurons that cover the same receptive field. This may result in a shift in phase between the induced and the evoked rhythms (equal in frequency), which would explain the enhancement effect when the target is presented at a phase angle of 180° compared to the persistent oscillatory trace of the premask, despite the details of the synchronous prime remaining outside of participants conscious awareness.

1.3.4 Theories grounded in this research. While initial results highlighted a frequency specific enhancement effect for a 40 Hz premask presentation rate, when the frequency range was extended, analyses revealed significant priming effects at other frequencies also; specifically at 32-33, 39-40, and 46-47 Hz, indicating priming effects for frequencies each separated by ~6.75 Hz (Elliott & Müller, 2004). Two related theories have emerged from this research; the generalised phase angle hypothesis (GPAH) and the return phase hypothesis (RPH) (Elliott, 2014; Elliott & Müller, 2004; Kompass & Elliott, 2001). The former predicts an anticipatory response to a primed stimulus, while the latter explains this type of anticipatory response but also responses that are synchronised or lag the primed event (Elliott, 2014). While RTs are enhanced significantly for target present responses in the synchronous condition, Elliott and Müller (2004) found that the trends for synchronous absent/present, and random absent/ present (all four conditions), depicting maximum and minimum RTs, are strongly similar. In fact, when scaled to

account for the larger (x3) priming effect and the faster overall RT's in the synchronous premask condition, the trend for target present maxima and minima RTs in both the random and synchronous conditions were found to be statistically the same (rank order correlation $r_s = .79$), with reaction time enhancement occurring at the minima of the trend. Evidence of these regularities in the data led Elliott and Müller (2004) to propose the Generalised Phase Angle Hypothesis; if a constant time delay is assumed then critical priming frequencies and corresponding reciprocal periods of time ($\tau = 1/f$) will be facilitated at specific points in time for which the temporal period between occurrences is an integer multiple (n) of the priming frequency.

$$J(\tau) = \left(n\tau + \frac{1}{2}\right)\tau - T$$



Figure 1.2. Modelled data.

Illustration of the predicted data modelled on the assumption that the maxima and minima of RTs reflect the difference between the negative peak of the hypothetical stimulus-evoked frequency and a quantal timing parameter of 138±2 ms.

Source taken from Elliott, M. A., & Müller, H. J. (2004). Synchronization and stimulus timing: Implications for temporal models of visual information processing. In *Psychophysics Beyond Sensation: Laws and Invariants of Human Cognition*.

It was calculated that if T, and multiples of T, were assumed to correspond with the points in time at which the frequencies located at the minima of the RT by frequency function occur, then $T = 138\pm2$ ms. Interestingly, when predicted data were modelled, based on the assumption that the maxima and minima of RTs reflect the difference between the negative peak of the hypothetical stimulus-evoked frequency and a quantal timing parameter of 138 ± 2 ms, both the trend in the maxima and minima data, and the overall pattern of decreasing amplitudes with increasing frequency, were described by the predicted function (see figure 1.2).

However, while the enhancement effects occur at the minima of the RT by frequency function, this priming effect is only evident for trials containing a synchronous prime, and therefore cannot be explained entirely by the GPAH (Elliott, 2010). Kompass and Elliott (2001) proposed the RPH which explains this effect as a consequence of the temporal segmentation of the priming frame from the distractor frames within the premask matrix, due to the repeated presentation of the premask forming a short-term memory which persists for a period comparable to persistence of visible stimuli (240-300 ms, post-stimulus offset).



Figure 1.3. Return Phase Hypothesis (RPH) – predicted enhancements. The RT enhancements occur at the minima of RT responses on target present trials when target presentation occurs immediately prior to the synchronous prime in the oscillatory trace of the premask.

Source taken from Kompass, R. & Elliott, M. A. (2001). Modelling as part of perception: A hypothesis on the function of neural oscillations.

The hypothesis was based on modelled data acquired from previous experiments by Elliott and Müller (2001). For each of the frequencies which had previously produced priming effects (32-33, 39-40, and 46-47 Hz) a reaction time enhancement for target present conditions only occurred when termination directly preceded the presentation of the synchronous frame. As the magnitude, or the strength of the enhancement effect, is maximal when the target stimulus is presented at a point in the evoked oscillatory response that just precedes the frame with the primed target had the entrainer continued, the RPH thus predicts an anticipatory response to a primed stimulus established by the rhythm of the premask matrix, (Kompass & Elliott, 2001, see figure 1.3). The data suggest this is achieved via resonance between two different stages of information processing; one being 'model generation' which consists of bottom-up processing, while the other, 'model evaluation', consists of top-down processing. Kompass and Elliott (2001) presumed that the model generation was performed by a rhythm matching the periodicity of the four-frame prime within the premask, while the model evaluation depended on the backpropagation of the established response matching the premask presentation rate from neurons within the IT area of visual processing. Within a 40 Hz premask presentation, four frames with a corresponding 25 ms duration would last 100 ms which has a periodicity matching a 10 Hz rhythm, referred to as the local response, while the overall rhythm depends on the rate of flicker, arising in this case from the presentation of 40 frames of equal duration (25 ms), in a one second period, referred to as the global response. By this account, the neural oscillations are considered a resonance between both stages of processing and are therefore a result of processing rather than the processing mechanism itself. However, it is also possible that the enhancement is partly due to the interaction of the premask evoked response, and the backpropagation of the induced response, equal in frequency, but shifted in time, and the modulation effect of a theta rhythm – such as the 6.69 Hz wave identified according to the GPAH. This would be consistent with recent research demonstrating gamma activity to be involved in carrying stimulus information and prediction errors, modulated by slower rhythms that carry information about the expected representation, and update the predictions (Bubic, von Cramon, & Schubotz, 2010; Engel et al., 2001; Michalareas et al., 2016; Sauseng, Klimesch, Gruber, &

Birbaumer, 2008). A closer investigation of the effect of return phase (RP) on primed responses also supports this conclusion (Elliott, 2014).

1.3.5 Findings from this paradigm to date. The GPAH accounts for an interaction in phase between priming frequencies and a slower brain rhythm due to enhancement effects that occur when primed with specific frequencies whose phase would regularly align with that of a slower rhythm, estimated to be 6.75 Hz, when the target is presented in phase with this slower rhythm. However, the enhancement also depends on the target being presented out of phase with the oscillatory trace of the premask, and it only occurs during the synchronous condition, and therefore does not completely explain the oscillatory mechanism involved in visual binding. The RPH explains the enhancement effect based on resonance arising from the process, whereby this effect further depends on the position of the priming frame in the oscillatory trace of the premask, and thus does not explain the process. Up to this point, target presentation coincided in phase with the wavelength of a 6.75 Hz rhythm. Elliott (2014) again expanded on the frequency range (27.75-67.5 Hz) and further manipulated the ISIs used to present the target at specific times in the oscillatory trace of the premask to investigate the effect of phase alignment with this slower theta rhythm, and the effect of RP, on RT responses. The first study, therefore, focused on the GPAH and the later study on the effect of the RP on priming.

1.3.5.1 Study 1. The ISI in the first study was kept at a constant 600 ms (to present the target in phase with a possible theta rhythm of 6.75 Hz, 600/ (1000/6.75) = 4.05 complete cycles of a 6.75 Hz wave. The combined results of this large-scale study found that the GPAH predicts an anticipatory response when targets are presented at entrainment frequencies that regularly align in phase at intervals that are multiples of 149 ms, due to a presumed modulation of a 6.69 Hz rhythm rather than a 6.75 Hz wave (the duration of one cycle at 6.69 Hz is 1000 ms/.6.69 = 149.48 ms). A bootstrap estimate of significance at $p \le .05$, which was set at power values of ≥ 7.5 , was applied to data from premask presentations at frequencies ranging from 27.75 – 67.5, 600 ms in duration, therefore with a target presentation time that was in phase with a 6.69 Hz rhythm (149 ms x 4 = 596 ms).



Figure 1.4. Periodogram.

Illustrating the spectral analysis, using the Lomb-Scargle method, of data from premask presentations at frequencies ranging from 27.75 - 67.5 Hz, in phase with a 6.69 Hz rhythm, when a bootstrap estimate of significance at $p \le 0.05$, set at power values of ≥ 7.5 , had been applied.

Source taken from Elliott, M. A. (2014). Atemporal equilibria: Pro- and retroactive coding in the dynamics of cognitive microstructures. Frontiers in Psychology.

A spectral analysis using the Lomb-Scargle method produced a periodogram with a single highly significant peak separation at 6.69 Hz (see figure 1.4). The usual premask duration of 600 ms remains in phase with this rhythm also (600/(1000/6.69) = 4.01 complete cycles of a 6.69 Hz wave). These results suggest that oscillatory prime formation can occur across the EEG gamma band of frequencies when target presentation occurs aligned with zero phase-lag to a 6.69 Hz rhythm.

1.3.5.2 Study 2. Two experiments manipulated the ISIs to present the target at specific points in the oscillatory trace of the premask display. Firstly, the ISI was kept constant to present the target out of phase with a 6.69 Hz rhythm (700 ms), resulting in a weaker priming effect – but none the less an effect of priming at frequencies of approximately 1 Hz greater than previously found. Secondly, the ISIs were manipulated to present the target at three specific times in the oscillatory trace

of the premask: corresponding with the following frames, 23.8 frames – slightly ahead of the beginning of frame one (which contains the prime in the synchronous condition), 21 to coincide with the end of the first frame, and 22.4, during the third frame. Therefore, the ISI varied depending on the rate of flicker and was not necessarily in phase with a 6.69 Hz rhythm.

Overall the results demonstrate that according to the RPH when target presentation is phase-aligned with a 6.69 Hz rhythm, an anticipatory response is facilitated, that is responses to targets presented slightly ahead of the priming frame in the oscillatory trace of the premask are enhanced. However, when target presentation is not phase-aligned with this rhythm and occurs at, or slightly after, the primed event, there is an enhancement effect at entrainment rates that are not separated by the period of a 6.69 Hz rhythm (35, 36, 37, 38, and 39 Hz). Thus, with regard to the RPH, the rate of premask presentation serves to facilitate a response that is dependent on the location of the prime within the matrix. Importantly, this needs to be considered both when designing the parameters of the experiments and interpreting the results of primed responses. Anticipatory coding in more general terms appears to rely on the modulation effect of a 6.69 Hz rhythm. Estimates for these priming frequencies span between 32.25-33.5 Hz; 38-40 Hz; 45.75-46.5 Hz; 53.25-53.75 Hz; 59-60.75 Hz, and 65.75-67.5 Hz (Elliott, 2014). It can also be concluded that this anticipatory code is not generated in the absence of this phase interaction. However, it cannot be assumed that this is the only endogenous brain rhythm with which feedforward gamma activity interacts during perceptual organisation processes.

1.3.6 The effects of presentation rate and harmony on auditory perception. A similar auditory priming paradigm has been used to examine the dynamic system of auditory binding. Galambos, Makeig, & Talmachoff (1981) discovered the effect of repeatedly presenting 25 ms 'clicks' of different frequencies [250, 350, and 500 Hz] to the auditory system was to produce a stable composite 40-Hz event-related potential (ERP) 8 - 80 ms post-stimulus onset. This sustained oscillatory response to the click sequence is termed a steady-state response (SSR). From this research pip-train stimuli have been developed; a sequence of pips with each pip carrying its own frequency, while the number of pips in the train dictates the overall frequency of the evoked auditory gamma-band response (aGBR). Individual pips are onset and offset ramped so that essentially the number of pips in the train provides an amplitude modulation frequency for the tones carried by the pips. Therefore pips-per-second (pps) refers to the rate at which the pips are repeated but is functionally equivalent to frequency (see figure 1.5).



Figure 1.5. Illustration of the stimulus used by Aksentijevic and colleagues, (Aksentijevic, Barber, & Elliott, 2011; Aksentijevic, Northeast, Canty, & Elliott, 2013; Aksentijevic, Smith, & Elliott, 2014). Each click evokes a sinusoidal wave response. In the 33 pps priming stimulus illustrated here, the duration of the oscillation is 30.3 ms; repeated clicks generate 33 such responses in one second giving rise to a 33 Hz oscillation (1000/30.3 = 33). In this way, pip-trains can be easily manipulated with very specific parameters. The original auditory priming paradigm was designed by Aksentijevic, Barber, and Elliott (2011), using pip-train stimuli hypothesised to externally entrain a gamma-band response considered to be phase-locked to the stimulus (Aksentijevic et al., 2011, 2013, 2014). The entrainer contained a repeated priming stimulus comprising a four-pip sequence of one 1,000 Hz deviant pip followed by three 500 Hz baseline pips (DBBB).

Aksentijevic, Barber, and Elliott (2011) designed an auditory priming paradigm using these pip-train stimuli. Each trial comprised a one-second entrainer embedded with a repeating four pip prime, the sequence of which was one 1000 Hz pip and three 500 Hz pips, followed by a 100 ms ISI and then a target stimulus (requiring a forced choice response), as described in figure 1.5. Based on research by Kadia & Wang (2003), which found that multi-peaked neurons (i.e. having more than one excitatory spectral peak in their frequency tuning curve) in primary auditory cortex, can be activated by a combination of harmonically related tones, Aksentijevic et al. (2011) proposed the unique template hypothesis, which posits that it can logically be inferred from this that a pure tone could thus activate and synchronise a harmonic template (representation) with the same fundamental frequency - same lowest oscillation frequency (of a periodic wave form) – in primary auditory cortex. In the case of the four-pip prime used in the entrainer, the 500 Hz pip is considered to activate and synchronise the corresponding unique template. The authors further proposed the Harmonic Reset (HR) model based on this premise, which states that due to the 180° phase difference between the 500 Hz wave and that of the 1000 Hz wave, the deviant 1000 Hz pip thus desynchronizes, or 'resets' the 500 Hz unique template, therefore this precise mismatch in phase is necessary to distinguish between harmonics which are related, yet distinct, such as 500 Hz and 1,000 Hz. Support for this model stems from the findings of the research employing this paradigm (Aksentijevic et al., 2011; 2013; 2014). Inharmonic targets comprise deviant pips with frequencies which are fractional multiples of the entrainment frequency, increased by an octave and a minor third (i.e. entrainer and inharmonic target deviant pips are related in the ratio 5:12; 1000:2400(/200) as 5:12), while harmonic targets contain deviant pips that are harmonically related by integer multiples (in the ratio 1:2; 1000:2000 as 1:2). Ratios represent the ratio between the entrainer deviant (1000 Hz) and target deviant (HTP = 2000 Hz, ITP = 2400 Hz). Participants reported being unaware of a harmonic relation between the entrainer and target stimuli which suggests that the effects of priming were pre-attentive as was the case in the visual priming experiments. The results of their investigations indicated a specific rate and time response-time advantage for target stimuli which were inharmonically related to the priming stimulus; that is when primed at a presentation rate of 33 pps, there was strong evidence of a coherence window at 106 ms and again at 258 ms, post-stimulus off-set, during which RTs to targets containing an inharmonically related frequency (a semi-tone relation) were enhanced. The rate of 33 Hz is consistent with other research (Pantev et al., 1991; Pöppel, 1997; Schulte, Knief, Seither-Preisler, & Pantev, 2002). The coherence windows following interstimulus interval's (ISI's) of 106 ms and 258 ms have been replicated (Aksentijevic et al., 2013, 2014). The 106 ms window is understood to be the behavioural threshold for the 500 Hz representation (template) established by the entrainer, above which coherence is reached. This coherence window was found to be asymmetric and lasted less than 20 ms (Aksentijevic et al., 2011). The second coherence window

at 258 ms post-stimulus offset was postulated to be the result of resynchronisation through a feedback loop originating in secondary processing areas which resonate at frequencies in the theta range (6 - 10 Hz), as it occurs after the natural decay of an evoked gamma-band response (eGBR) and is possible evidence for the encoding of the 500 Hz representation (template) into working memory.



Figure 1.6. 33 pps 'pop-out' effect.

Top: Illustration of the 33 pps condition which resulted in the 'pop-out' effect described. The entrainment duration was a constant 1000 ms followed by an interstimulus interval (ISI) of 100 ms – unlike the visual experiments a break is required between the sound stimuli to separate them. At this point in the oscillatory trace, the target is presented during the first (deviant) pip in the 9th cycle of the four-pip sequence (one cycle = $4 \times (1000/33) = 121 \text{ ms}$), shifted in phase by 130° with a presumed 6.69 Hz rhythm (out of phase). Bottom: Graph of the results reported by Aksentijevic et al., (2011), illustrating the pop-out at 33 pps entrainment: Mean
response times (and standard error means (SEM) for HTP and ITP conditions plotted (on the *y*-axis) against presentation rate (*x*-axis).

This effect is referred to as a pop-out due to the slowing of harmonic responses and simultaneously fast inharmonic responses resulting in a gap in the RT trends, and it has been found (and replicated) when the target is presented at 1100 ms post-stimulus onset (Aksentijevic et al., 2011, 2013, 2014), see figure 1.6). Interestingly, musicians have not demonstrated this effect. Aksentijevic et al. (2014) tested a group of (contemporary) musicians and a control group who had no music training and found that musicians respond faster overall compared to non-musicians, but the RT trend for harmonic and inharmonic targets did not deviate.

According to the HR model, the deviant pip 'resets' the 500 Hz representation, and therefore at this point in the entrainment oscillation of a 33 pps prime the 500 Hz representation is desynchronised (the target is presented during the oscillatory trace of the deviant pip: 1100 ms/(1000/33) = 36.3, the beginning of the 10th cycle of the prime). The pop-out suggests a facilitation of responses to a deviant stimulus at a 33 pps rate of entrainment when the target is out of phase with a 6.69 Hz rhythm. This paradigm provides a unique method with which to investigate the precise timing of interactions between specific frequencies. To illustrate this point, the results arising from both the visual and auditory priming paradigms discussed highlight anticipatory effects at specific frequencies in the gamma range, while at the same time revealing a complete absence of an effect at frequencies just one integer value above and below.

1.4 The Importance of Anticipatory Coding

Arguably predictive processing is one of the most basic functions of neural computations with prediction errors driving brain processes and behaviour. While there are differences in interpretations of the terms predictive processing, expectations and anticipatory processing, it is generally agreed that expectations are representations of events or perceptions predicted to occur in the immediate future, and anticipatory processing communicates these expectations to the motor and sensory cortices in advance of the realised perception or event (Bubic et al., 2010). LaBerge's (1995) definition of anticipation as increased processing in sensory or motor areas which precedes, and facilitates, the processing of an expected motor or

perceptual occurrence, offers a clear description of the role of anticipation in cognition at the micro level. For example, in order to perceive a visual world that is stable, an efference copy of motor commands controlling eye movement is sent to other areas of cortex to report the impending movement. The brain uses this copy of the motor command, operating on the eye muscles, to predict the gaze position in order to calculate an objects location relative to head position - which must account for both the retinal location of the object and the gaze position of the eye within the orbit (Wolpert & Flanagan, 2001). This is a form of specific anticipatory processing. Anticipation is now widely accepted to be at the core of brain functioning (Pezzulo, Butz, & Castelfranchi, 2008). Many cognitive functions and neural systems such as motor control (Wolpert & Flanagan, 2001), visual processing (Enns & Lleras, 2008), language (DeLong, Urbach, & Kutas, 2005), and music (Keller & Koch, 2008), have been demonstrated to be characteristically anticipatory. At the macro level anticipation is the key to predicting events as they unfold and thus allows for efficient person-environment interaction. According to Rohrmeier and Koelsch (2012) prediction is fundamental to processing music information, and for musicians to synchronise and harmonise as they play. The phenomenon of tapping to the beat demonstrates the listener's anticipation of the accents within the rhythm of a musical piece and highlights the predominant influence of auditory feedforward interactions on the motor output – this is an example of the role of anticipation in predictive coding (Zatorre, Chen, & Penhune, 2007). At a micro level, anticipation essentially prepares the motor and sensory functions required for action in advance of the actualisation of an expected perception or event. At this level anticipation has been conceptualised as a bias signal (Rees & Frith, 1998) – the sources of this bias are the brain regions which generate the expectancies, and the sites of this bias are the areas that are influenced by it – which requires a form of communication to mediate the process (Bubic, Yves von Cramon, & Schubotz, 2010). Modulated neural activity facilitates this communication. The predictive coding model describes visual processing as an integration of information between bottom-up stimulus-driven feedforward connections, and top-down expectation, or hypothesis-driven feedback connections, across multiple layers of a hierarchical structure (Friston & Kiebel, 2009).

Predictions have been demonstrated to emerge based on associations (DeLong et al., 2005). A real-world event that illustrates this point would be hearing

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a voice that is known to the listener behind a door that is opening, which generates the listener's expectation to see the face of the speaker matching the voice enter the room. A corollary of anticipatory processing involves mechanisms that react to deviations in the expected event. In the above example, if the listener's expectations are not met, a response must be made to update the listener and feedback the revised prediction. We have evolved to generate expectancies so that we are alerted to events that are out of character. Evidence of this has been empirically demonstrated.

With regard to harmonic and melodic prediction, neurophysiological music research has demonstrated that syntactically irregular chords elicit event-related potentials (ERPs) with negative polarity and peak latencies of around 150-350 ms post-stimulus onset (Rohrmeier & Koelsch, 2012). Unexpected harmonies (musicsyntactically irregular chords) elicit brain potentials in electroencephalography (EEG) and MEG studies, with negative polarity in the right anterior frontotemporal regions of the scalp, which have peak latencies of around 150-250 ms post-stimulus onset. One of these early responses to harmony violations is referred to as the ERAN response (early right-anterior negativity response; Koelsch, Schroger, & Gunter, 2002). While the ERAN is most often observed with right hemisphere weighting, a similar response is elicited in musicians that is localised solely in the right hemisphere and is maximal at around 350 ms. This response is referred to as the RATN response (right anterior temporal negativity response; Koelsch et al., 2002). The homologue of the ERAN response, the early left anterior negativity response (ELAN) is elicited by syntactic language violations and has been investigated to examine the role of predictive mechanisms in order to explain how the brain can make a response to violations in expectancies so rapidly, given known stimulus processing speeds (Lau, Stroud, Plesch, & Phillips, 2006). This research concluded that predictions constrain the number of probable outcomes and therefore speed up the syntactical analysis. Given the importance of anticipatory processing, the relevance of the visual and auditory entrainment research discussed above can be fully realized. This simple paradigm offers a unique way to examine very precise temporal relations between feedforward and feedback projections of oscillating neural assemblies.

1.5 Synchronisation of Neural Assemblies as a Temporal Code

Afferent signals induce local patterns of activity in areas of cortex specific to the input. However, these patterns are modulated constantly by long-range interactions with cell populations, either within the same area or a disparate assembly, resulting in synchronisation or desynchronisation, depending on the phase relation. This modulated temporal patterning across long-range inputs, expresses predictions about specific feature arrangements, with various influences competing for a stable resonance within an assembly. A successful match of the input to the expected output amplifies the synchronised pattern and thus influences other neural populations and leads to larger patterns of temporal coherence. The precision of spike synchrony has been demonstrated to increase with growing stimulus expectancy during the delay period prior to stimulus presentation. Also, neurons participating in a coherently oscillating assembly just before stimulus onset results in a precisely synchronised response when stimulated by the expected stimulus, due to top-down influences which selectively enhance the coherence for subsets of oscillating neurons in the network (Engel et al., 2001). This process fits with the description of anticipatory processing, suggesting the system prepares for an expected event by narrowing the range of possibilities resulting in very precise synchronisation within the delay period prior to an expected event. The inhibitiontiming hypothesis explains the role of inhibition in this process at the neural level (Klimesch, Sauseng, & Hanslmayr, 2007). Oscillatory activity induced by inhibitory neural activity alternates rhythmically between phases of maximum and minimum inhibition, influencing the firing pattern of pyramidal cells depending on the amplitude of the oscillation and the cells state of excitation. If the level of excitation exceeds the influence of inhibition (amplitude of the oscillation), it will fire tonically (with regularly spaced spikes), resulting in general inhibition. However, if the level of excitation is low, or the amplitude of the oscillation is high - it will fire rhythmically (entrained to the oscillation), with greater precision being achieved during oscillatory coherence at the negative peak. Therefore, while an increase in the amplitude of the inhibitory oscillatory activity reflects an increase in inhibition, depending on the level of excitation of the cell and the amplitude of the oscillation, this may result in either very precise temporal neural activity due to the short time window allowed by the oscillation for the firing of a large neural population, or

general suppression of firing. While event-related synchronisation (ERS) reflects inhibition, event-related desynchronisation (ERD), or decrease in alpha band power, particularly in the upper alpha range, 10-13.5 Hz, is functionally related to excitatory cognitive processes and therefore active information processing. The synchronisation of neurons in disparate networks in the alpha frequency range allows for the effective activation of common target cells. Thus, inhibition controls the precise timing of an oscillation to establish a very selective activation pattern (Klimesch et al., 2007). With regard to the influence of theta coupling, an increase in frontal midline EEG theta activity in conjunction with theta phase synchrony between frontal and posterior brain regions is associated with executive function (Griesmayr et al., 2014). In support of this theta networks such as frontal theta as a mediator in the deployment of attention, and fronto-posterior theta coupling for the efficient monitoring and coordination of parallel processes – in particular posterior networks for processes involving the manipulation of information, have been empirically demonstrated to subserve working memory processes in the human brain (Griesmayr et al., 2014). Both theta and alpha phase synchronisation coordinate feedback activity to exert top-down control over memory processes. Sauseng, Griesmayr, Freunberger, & Klimesch (2010) have found that theta phase synchronisation ($\sim 4 - 6$ Hz) controls the access and retrieval of episodic and new information, while alpha oscillations (in the upper band, 10 - 13.5 Hz) control semantic memory access and retrieval. Theta synchronisation has also been implicated in the encoding of episodic memory (Summerfield & Mangels, 2005).

Binding by synchrony was initially proposed based on oscillatory activity in the gamma-band range of frequencies [approximately 30 - 70 Hz] as an evoked response to sensory stimuli (Singer, 1993). Singer (1993) suggested that oscillatory activity in the gamma-band range may be optimal for synchronisation due to the speed of the oscillatory cycle simultaneously allowing for rapid signal transmission whilst withstanding the conduction times of coupled assemblies required to establish synchronisation. Fries (2009) proposes that the influence of gamma-band synchronisation can be either general or specific depending on how it is modulated. Within a cortical network, gamma-band synchronisation increases the strength of entrainment on target neural networks, establishing exclusive neural communication links essential for cortical computation. According to Axmacher, Mormann, Fernández, Elger, and Fell (2006), the function of gamma band activity with regard

to memory processes could lie in the fine temporal precision required for the induction of neural coupling and long-term potentiation to create learning-dependent changes (Axmacher et al., 2006). However, gamma-theta synchronisation is necessary for the temporal ordering of memories, including the sequence of items to be remembered and spatial locations. Gamma-theta synchronisation is an example of cross-frequency coupling, which refers to the modulation of one frequency band of activity by another frequency band (Canolty et al., 2006). Canolty et al. (2006) found that transient coupling between gamma (in the range of 80 - 150Hz) and theta (in the range of 4 - 8 Hz) coordinates activity between disparate neural assemblies thus providing an effective mechanism of communication for cognitive processes. Contrary to gamma, theta oscillations undergo phase-reset, which is a change in its dynamic behaviour due to a perturbation in its phase which changes the period of the oscillation. This characteristic allows gamma and theta activity to synchronise and is thus considered the neural mechanism involved in matching an expected representation to an external visual stimulus (Sauseng et al., 2008). In support of this, the successful maintenance of information in short-term memory has been associated with cross-frequency coupling between theta (~ 5 Hz) and gamma activity (> 50 Hz) in posterior parietal areas of cortex, suggesting a neural substrate involved in the retention of relevant information. However, EEG recorded alpha activity (~ 10 Hz) has been implicated in the successful suppression of irrelevant information. Sauseng et al. (2009) demonstrated, in the human EEG, that gamma phase coupling to the negative peak of theta oscillations increased contralaterally to the visual hemifield containing the relevant items in a visual short-term memory task. Synchronisation was enhanced for memory loads of four items or less (average capacity) and even predicted individual memory capacity. Using repetitive transcranial magnetic stimulation (rTMS), Sauseng and colleagues (2009) evidenced a similar pattern for alpha modulated activity except that the results were ipsilateral to the hemifield containing relevant items and resulted in an increased ability to suppress irrelevant information. Both mechanisms were found to be independent of one another, suggesting a double dissociation of correlated oscillatory mechanisms in short-term memory. Thus, a complex interplay between fast frequencies in the gamma range and the modulating effects of slower rhythms is well supported and documented. The fast frequencies carry the feedforward information such as stimulus input and prediction errors, and the slower frequencies feedback templates

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and update the predictions. In this way, anticipatory coding prepares the system to interact with the environment based on continuously updated object representations and predicted events. For example, Sauseng et al. (2008) found that in the interval prior to target presentation there was evidence of coherent theta activity distributed in a fronto-centro-posterior network, reflecting a reactivation of a representation in memory in anticipation of the expected target. About 100 ms post target presentation there was a reset of the ongoing phase in theta activity at local parieto-occipital sources, thus enabling the synchronisation in phase with local gamma activity necessary for the processing of the visual input. This theta-gamma coupling was demonstrated at parieto-occipital sources from approximately 100 to 200 ms post target onset, and is considered to represent the binding of information from top-down memory and bottom-up stimulus input (Sauseng et al., 2008). In line with this research, the visual and auditory binding findings related above also illustrate gamma-theta coupling which enhances anticipatory coding. Key to the code is in the interaction in phase between gamma-band cortical responses and slower endogenous theta rhythms, and therefore the timing of these interactions. This line of research potentially provides a method with which to examine the temporal parameters involved very precisely.

1.6 Summary

To engage with our environment based on our learning histories and behavioural goals, it is necessary to segregate and amalgamate, to perceive objects but also to recognise those objects and predict, or decide, on the most probable next event. To navigate our environment, therefore, the most basic perceptual processes (in primary cortical areas), need to connect with higher-order processes such as attention, memory and decision making (von der Malsburg, 1999). The temporal dynamics of anticipatory coding triggers the cortical systems involved in perceiving the environment, and updating the representations therein, to predict change. Feedforward and feedback influences are central to the theory of predictive coding. Areas further up in the hierarchy derive predictions based on the incoming information and past learning experience. They, in turn, feed these predictions back to lower areas, where they are compared to the sensory data. Thus the prediction errors are calculated and fed forward. An accumulation of prediction errors over time results in updated predictions, and as a result, the prediction errors change more

rapidly than the predictions. Therefore, mediation of predictions and prediction errors via inter-areal synchronisation would require higher frequencies (gamma band) to communicate prediction errors compared to predictions (subserved by lower frequency bands) (Michalareas et al., 2016). Here we focus on evidence which reinforces this theory, including support for the modulatory effects of slower brain rhythms on gamma oscillatory activity, which explains the mechanisms behind the processes of anticipatory and predictive coding. However, much remains to be discovered regarding the fine scale-temporal relations underlying these interactions. The visual and auditory priming research discussed provides a window into the precise timing of interactions between very specific frequencies. The entrainment paradigm offers a straightforward and effective way to investigate these temporal parameters, which are essential to extrapolate more precise measurements of the frequencies, within respective bandwidths, that engage in cross-frequency coupling, and the phase alignments optimal for communication. The following chapters will outline the methods employing the auditory priming paradigm used to manipulate the temporal and phase relations between these fast and slow brain rhythms and discuss the findings pertaining to the contributions made to our understanding of anticipatory coding, required to predict changes in our dynamic environment.

1.7 Thesis Preface

The first study will examine similarities and/or differences between visual and auditory priming effects. The research question addressed is whether the effects of entraining the auditory system with frequencies in the gamma range provides evidence of specific gamma-theta interactions facilitating a response to a primed target, similar to the interactions supported by the visual priming effects.

Table 1.1. Predicted Experimental Effects.

Column one details the study and the experiment number, while column two indicates both the theta wave presumed to modulate the entrained auditory gammaband response (aGBR), and the phase of this wave at target presentation time. The third column states the theme of the study and gives a brief description of the predicted effects. It should be noted that all hypothesised results are expected to be

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facilitated by specific entrainment frequencies – those frequencies that are critical for the binding process.

Experiment	θ phase	Hypotheses					
Study 1	6.69 Hz	Examine auditory priming effects					
Exp 1	130°	A facilitation of responses to inharmonic targets will depend on presentation during the deviant pip trace					
Exp 2	(a) 95.5°	(a) Target presentation during the deviant pip trace will result in faster HTP RTs					
	(b) 24.5°	(b) Target presentation early in the theta cycle will influence a facilitatory response					
Exp 3	0°	Target presentation at zero phase lag with theta will disrupt harmonic salience					
Exp 4	0°	Frequency range precedes range in Exp. 3 - target presentation at zero phase lag with theta will disrupt harmonic salience					
Exp 5	0°	Frequency range proceeds range in Exp. 3 - target presentation at zero phase lag with theta will disrupt harmonic salience					
Study 2	7.29 Hz	TQM as a guide					
Exp 1	0°	Guided by TQM parameters, target presentation at zero phase lag with theta will disrupt harmonic salience					
Exp 2	270°	Guided by TQM parameters, target presentation at a 270° phase lag with theta will disrupt harmonic salience					
Study 3	6.69 Hz	Magnetoencephalography (MEG) study					
	130°	There will be differences in priming effects dependent on music ability					
Study 4	6.69 Hz	Auditory Masking Study					
	130°	Priming the auditory system with a gamma-band frequency does not facilitate musicians' responses to a harmonic					

These experiments will be exploratory, building on each other. The expected outcomes are listed in table 1.1. Previously, the priming paradigm, in both the visual and auditory binding research, has used a wide range of frequencies and interstimulus intervals to manipulate the stimulus parameters to examine the gamma-theta phase relations that facilitate an invariant response. As this is a time-consuming method of investigation, the second study takes a different approach, to establish a suitable temporal model for the stimulus parameters, thus reduce the number of probable relations. Time Quantum Model (TQM) posits there is a very precise temporal architecture, related to a host of cognitive functions such as temporal thresholds and perceived durations, the structure of which is built on basic units of time (Geißler, 2009; Stevens, 1957, 2017; Teghtsoonian, 1971; Teghtsoonian & Teghtsoonian, 1997). Elliott and du Bois (2017), demonstrated a link between the time-based priming effects evidenced from the visual and auditory priming data and the TQM taxonomy, which this second study will build on. Previously, musicians have not demonstrated priming effects consistent with their non-musician counterparts (Aksentijevic et al., 2014). Based on this research, the third study will combine the behavioural techniques employed using the priming paradigm and magnetoencephalography to investigate differences in priming effects dependent on musicianship. The final study will again use a musician and a non-musician group, and the same stimulus parameters. However, a counter balanced two block procedure will present the trials as usual in one block and will use a simultaneous white gaussian noise masker to eliminate stimulus entrainment in the other block. In this way differences in the effect of priming on the musically trained compared to the musically naïve brain will be examined. The predicted outcomes for each experiment in all four studies are presented in table 1.1. It is anticipated that the resultant findings will provide a rudimentary, yet wholistic understanding of the basic frequency interactions involved in the integration of the components of sound, and differences in the structure of this dynamic-system as a consequence of music training.

2 Are Visual Priming Effects Generalisable to the Auditory Domain?

2.1 Introduction

Evidence from visual binding research, discussed in the previous chapter, suggests the effect of priming is influenced by the phase relation of an internally generated cortical theta rhythm of 6.69 Hertz (Hz) at target presentation time. Persistence of the stimulus entrained oscillation has been demonstrated to endure for 150-200 milliseconds (ms) post-premask (entrainer) offset. Elliott (2014), posits that the consequence of phase alignment with a 6.69 Hz theta rhythm at the time the target is presented is that responses to the primed event in the entrained oscillation occur slightly ahead of time in anticipation of the synchronous frame. Whereas, if target presentation is out of phase with a 6.69 Hz wave, responding occurs at the same time or slightly after the primed event.

The initial phase of this research thesis investigated a generalisation of the visual priming effects to auditory binding as a means of explaining similar frequency-specific effects of priming, using a similar but not procedurally identical paradigm to that used in visual priming. In the auditory priming research described previously, the entrainer contains a repeated priming stimulus comprising a four-pip sequence of one 1,000 Hz deviant pip followed by three 500 Hz baseline pips (DBBB). The entrainer is designed using the Harmonic Reset (HR) model, derived from the 'unique template hypothesis', which asserts that a pure tone activates and synchronises a harmonic template that has the same fundamental frequency as that of the stimulus. In the case of the four-pip prime used in the current entrainer, the 500 Hz pip activates and synchronises the corresponding unique template. Due to the 180° phase difference between the 500 Hz wave and that of the 1000 Hz wave, the deviant 1000 Hz pip desynchronises, or 'resets' the 500 Hz unique template. The initial investigation using the original (DBBB) paradigm, which tested and subsequently validated the HR model, found a facilitation for responses to the inharmonic target (Aksentijevic, Barber, & Elliott, 2011), or perhaps more accurately a slowing of responses to the harmonic target (Aksentijevic et al., 2014), which was rate specific (when stimuli were presented at 33 pips per second (pps)). This effect was found when the target was presented during the oscillatory trace of the deviant,

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and therefore lags the beginning of the four-pip prime in the oscillatory trace of the entrainer (Aksentijevic et al., 2011; Aksentijevic, Northeast, Canty, & Elliott, 2013; Aksentijevic et al., 2014). Trace refers to the persistence of the phase-locked evoked auditory gamma-band response (aGBR) to the external sound stimulus. The timing of target presentation at this point lags the phase of a 6.69 Hz wave by 130° (1100 ms post entrainer onset, 1100/ (1000/6.69, duration of one cycle of a 6.69 Hz wave) = 7.36, .36 x 360° = 129.6°). This facilitation effect provides support for a retroactive response according to the Return Phase Hypothesis (RPH), presuming the same temporal dynamics underlie the oscillatory binding mechanisms in both the visual and auditory sense modalities. However, this is not necessarily the case, and it is possible that the 33 Hz rate specific pop-out effect could be interpreted as an anticipatory response to the expected 500 Hz pip.



Figure 2.1. Harmonic Reset (HR) arising from the unique-template hypothesis. Bottom: Acoustic waveform of the original DBBB entrainer. Three 500 Hz pips (B) synchronise the 500 Hz template. The representation is reset by a 1,000 Hz deviant pip (D). Top: The consequence of this is a periodic oscillatory representation with an asymmetric period.

Source taken from Aksentijevic, A., Barber, P. J., & Elliott, M. A. (2011). Process timing and its relation to the coding of tonal harmony. *Journal of Experimental Psychology. Human Perception and Performance*, *37*(5), 1628–1642.

The rationale again stems from the HR model. A triplet of 500 Hz pips will generate an oscillatory cycle that increases in coherence with successive pips due to

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the phase alignment of the individual oscillations. A deviant 1000 Hz pip must inhibit odd harmonics of 500 Hz (1,500, 2,500...Hz) to establish its own oscillatory cycle, which disrupts the 500 Hz oscillation. The re-introduction of the 500 Hz pip re-activates the 500 Hz oscillatory representation. However, the disruption to the 1000 Hz oscillatory cycle is not as pronounced as inhibition of odd harmonics is not required. According to the HR model, this results in a representation that has an asymmetrical amplitude (see figure 2.1). Thus, it is hypothesised that the first baseline 500 Hz pip following a deviant pip is correspondent with the first frame in the synchronous condition of the visual paradigm. This study modified the paradigm by rearranging the pip sequence so that the deviant pip was last (from DBBB to BBBD), thereby allowing for a comparison to be made between the findings of the auditory and visual experiments using a procedurally different, yet functionally similar, stimulus entrainment paradigm. With this aim, over the course of five experiments, the target presentation time was manipulated to investigate an effect of phase alignment with a 6.69 Hz rhythm, and to study the role of RP as a determinant of a priming effect.

2.2 Stimuli.

Individual pips and pip-train stimuli for these experiments were created by the author in Audacity, using sampling rate (not duration) – 44100 samples per second – and were accurate to two decimal places of a millisecond (ms). Individual pip tones were onset- and offset-ramped with ramps that were symmetrical and had a plateau of 33% of the overall pip duration, resulting in a frequency oscillation equivalent to an amplitude modulation frequency. The number of cycles per second for such an oscillation is therefore equal to the number of pips in a one-second interval. Thus, the number of pps in the pip-train stimuli on a given trial dictates the entrainment frequency (or rate of entrainment) for that trial, i.e., the frequency in Hertz, and rate in pps, of the entrained aGBR, are equivalent (e.g., 30 Hz = 30 pps).



Figure 2.2. Pip trains.

Illustration of the sequence of pips in the entrainer and target present trials. In this case, the inter-stimulus interval (ISI) was 100 ms. The carrier frequencies were as follows; for the entrainer B (baseline) = 500 Hz and D (deviant) = 1000 Hz, for the HTP targets B = 1000 Hz and D = 2000 Hz, for the ITP targets B = 1000 Hz and D = 2000 Hz, for the ITP targets B = 1000 Hz and D = 2400 Hz, and for the TA targets there are only baseline pips – B = 1000 Hz.

The entrainer pip-train comprised a repeated four-pip sequence of three 500 Hz pips followed by a deviant 1000 Hz pip. The target pip-train consisted of a target absent stimulus or one of two target present stimuli. The target absent pip-train contained only 1,000 Hz pips. Target present trains were harmonic (harmonic target present – HTP) and inharmonic (inharmonic target present – ITP), and consisted of a repeated baseline-deviant pip sequence (BDBD; Aksentijevic et al., 2014). Target present baseline pips carried a frequency of 1,000 Hz. The deviant frequency for the HTP stimulus was 2,000 Hz (harmonically related to the priming frequency and target baseline frequency; fourth harmonic of 500 Hz and second harmonic of 1,000 Hz; the target deviant and the prime deviant were in the ratio 1:2). The deviant frequency for the ITP stimulus was 2,400 Hz (inharmonically related to the priming frequency and the target baseline frequency; increase in pitch by an octave plus a minor third; the target deviant and the prime deviant were in the ratio 5:12). Target stimuli were presented at the same rate as the entrainer for that trial, i.e., when the entrainer was presented at a rate of 40 pps, the target for that trial was also presented at a rate of 40 pps. Rate of entrainment was varied randomly across all trials in each experiment. Stimulus generation and the embedded harmonic relations were

consistent with the original auditory priming paradigm designed by Aksentijevic et al. (2011; see figure 2.2).

2.3 Apparatus.

2.3.1 Experiment 1. Experimental trial and stimulus generation were controlled by a Dell OptiPlex 780 computer with sound signals generated by an internal stereo sound card. Stimuli were presented electronically, and the data were collected using SuperLab (v.4, Cedrus) software (Abboud, Schultz, & Zeitlin, 2008). Reaction time (RT) was measured via an RB-840 response pad (an experimental interface device – XID) which offers 2-3 ms RT resolution.

2.3.2 Experiment 2 and 3. Experimental trial and stimulus generation were controlled by a Dell OptiPlex 755 computer with sound signals generated by an internal stereo sound card, and again RT was measured via an RB-830 response. Stimuli were presented electronically, and the data were collected, using E-prime 2.0 (PST-101339) (Schneider, Eschman, & Zuccolotto, 2002).

2.3.3 Experiments 4, and 5. Experimental trial and stimulus generation were controlled by a Dell Latitude E5450, Intel Core i7-6700HQ 2.60 GHz laptop. Sound stimuli were presented electronically via Chronos PST-101600, a multifunctional response and stimulus device, which also measured RT, offering an RT resolution of <1 ms, achieved by preloading the sounds onto the Chronos box. Experiments were programmed in E-Prime 2.0 (Professional, SP2, build 2.0.10.356) (Schneider et al., 2002).

2.4 General methods

All experiments took place in a sound-attenuated chamber, with a background noise level < 30 dB SPL, located in the School of Psychology building at the National University of Ireland, Galway. Lighting was kept at a constant low level. The stimuli were presented diotically via Sennheiser HD 25 headphones. Using a Gold Line sound level meter (model SPL120), stimulus intensity was kept at an average 50 dB sound pressure level (SPL) (A-weighting; average error 3 dB SPL), to achieve a stable steady state response (SSR) and yet avoid aural harmonics (Aksentijevic et al., 2011). Before commencement of the first session, participants completed a brief questionnaire to ensure they were eligible for inclusion and to provide details on gender, age, handedness, and music experience (if any).

Instructions were provided on the computer screen as prompts for the participant. Experimental sessions began with a practice block (between 20 and 40 trials, depending on the number of conditions, to avoid the repetition of any one condition during the practice session). Each trial was cued by a grey cross, the display duration of which was 500 ms, with stimuli presented immediately following cross offset. Targets were presented for 2000 ms. A 500 ms interval followed either a stimulusresponse or termination of the trial in the case that a response was not made. Participants were required to attend to, but not to respond to the first sound stimulus. Following the ISI specific to the experiment, participants were instructed to respond as rapidly and accurately as possible to a second sound stimulus. The experimental exercise was a forced choice response task based on the target stimulus properties. Stimulus amplitude modulation results in a sound that waxes and wanes and can be described as warbling as it varies regularly in pitch. If the overall pitch of the sound was flat, the target was absent, and the response was 'No'. If the sound alternated in pitch, the target was present, and the response was 'Yes'. During the practice only, in the event an incorrect response was made, a red x appeared on the screen to provide participants with feedback. RTs were recorded from the onset of the second sound stimulus by keypress (not release). Sessions were run on different days and lasted between 40 minutes and one hour, depending on the number of conditions in an experiment. Previous binding research has found that under examination, the effects found using the original paradigm replicate and are stable with relatively small numbers of participants N >10<16 see, e.g. Aksentijevic et al., 2011, 2013, 2014; Elliott, 2014; Elliott & Müller, 1998, 2000, 2001, 2004. Therefore, the sample size for each experiment was between 12 and 16. Ethical approval was obtained for this study from the National University of Ireland Galway Research Ethics Committee. A repeated measures design was used. Factors included rate, ISI, and target. Rate refers to the number of pps in the stimuli, equivalent to frequency, and was randomised across trials. The factor ISI was used to manipulate the phase relations, as required, at target presentation time, i.e., to present the target when a given frequency, such as a theta rhythm, was in a specific phase alignment. ISI was constant in all but one of the following experiments. Target was asymmetrical with two levels – target absent (TA) and target present (TP), within this latter condition were two levels of harmony - harmonic target present (HTP) and inharmonic target present (ITP). The trials were proportioned as follows: TA = 50%, TP = 50% (HTP = 25%, ITP = 25%). An equal

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number of repetitions were required for each trial condition. Therefore, when calculating the number of trials per experiment, the number of levels for the factor target were four, denoted as x 2(2), as the ratio between targets was 2:1:1 (TA: ITP: HTP). For example, forty repetitions required eighty TA trials as the TP trials contained forty repetitions of both the harmonic and the inharmonic target.

2.4.1 Statistical Analyses. Trials resulting in a response error were removed from the data prior to subsequent analyses. Examination of the raw RT data using the Statistical Package for Social Sciences (IBM SPSS statistics 23.0) revealed nonnormal distributions with pronounced positive skew. Based on a Kolmogorov-Smirnov (D) test and a Shapiro-Wilk's (W) test, subsequent analyses were conducted on the exponents of the means of log-transformed RT distributions, calculated in Matlab using an in-house script (for supporting ideas see Box, & Cox, 1982; Box & Cox, 1964). A repeated-measures analysis of variance (ANOVA) was conducted on the corrected RT data using SPSS. Degrees of freedom were corrected for Greenhouse-Geisser estimates of sphericity when a violation of this assumption was indicated. Bonferroni correction was applied to all pairwise comparisons. The target absent condition serves to provide a discernible response for the participant, as the difference between the harmonic and inharmonic targets are not easily distinguishable. Therefore, target absent RTs are not included in analyses testing the principle hypotheses. The error data was subjected to the same ANOVA analysis as the corrected RT data, and error reports for each experiment are included in the results section.

2.5 Experiment 1

2.5.1 Research question. The first experiment presented the target at a phase angle of 130 ° with a presumed 6.69 Hz rhythm – consistent with the trial parameters which brought about the (33 pps) rate-specific frequency effect, i.e., a one-second entrainer followed by a 100 ms ISI, therefore presenting the target at 1100 ms into the oscillatory trace of the entrainer (Aksentijevic et al., 2011).



Figure 2.3. Experiment 1; phase relation of a 6.69 Hz theta wave. Illustration of the phase relation between a 6.69 Hz theta wave at target presentation time, presuming a zero phase-lag with the onset of the entrainment oscillation.

At this point in time, a 6.69 Hz rhythm has completed .36 of its eighth oscillation, presuming a zero phase-lag between this and entrainer onset, resulting in a 130° phase angle at target presentation time (.36 of 360° = 129.6) (see figure 2.3). The parameters were designed to test the effect of return phase (RP). Given that the previously documented 'pop-out' effect occurred under these stimulus conditions (Aksentijevic et al., 2011, 2013, 2014), and at this point in the 6.69 Hz theta wave cycle suggested to modulate the entrained gamma activity (Elliott, 2014) – any difference in the pattern of responding would be due to the position of the deviant pip. It was hypothesised there would be a facilitation of responses to inharmonic stimuli under temporal conditions which are dependent on the position of the deviant pip at the time of target presentation. As the 33 pps pop-out effect has been found for target presentations that are out of phase with a 6.69 Hz rhythm, suggesting the effect is retroactive and not anticipatory, this tests the strength of RP as a determinant of a facilitatory effect on responses to stimuli that are harmonically related to a primed template.

2.5.2 Sample and design. Fourteen participants recruited in the Galway area took part in this study. Two were left-handed (male n = 4, female n = 10, *M* age 27.43 years, *SD* 8.48). All participants reported normal hearing, no formal music training, and provided informed consent.

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A repeated measures design was used with two factors, rate (10 levels; 30 - 39 pps) and target (asymmetrical with two levels – TA (50% of trials) and TP; HTP (25% of trials) and ITP (25% of trials)). The ISI was kept constant at 100 ms. Participants were presented with 40 trials per condition which resulted in 1600 trials per participant, ($10 \ge 2(2) \ge 40 = 1600$). Trials were presented over the course of two sessions (45 minutes in duration, on separate days) in blocks of 40 trials. Individual sessions began with a 40 – trial practice block. Experimental conditions were completely randomised within and between blocks. The dependent variable was corrected RT – the exponents of the means of the log-transformed data.

2.5.3 Results. The data were analysed to examine the effect of moving the deviant pip in the entrainment sequence. It was hypothesised that the effect was due to RP rather than a retroactive response due to the phase relation of a 6.69 Hz theta wave at target presentation time involved in modulating the effects of priming in visual binding research. The effect remains coincidental with the position of the deviant pip. However, under entrainment with the new pip sequence, rather than revealing a pop-out due to slower harmonic responses, the effect dependent on presentation during the deviant pip in the oscillatory trace of the entrained rhythm results in a facilitation of harmonic responses. Therefore, the results suggest as hypothesised, that the original pop-out and the facilitation of harmonic responses found here, are an effect of RP. Initially, a 10x 2(2) repeated measures ANOVA was conducted on corrected RT data to evaluate the effect of presentation rate (pps; 30-39 pps), and target (TA, HTP, and ITP) on RT responses. A significant main effect of rate was found due to a roughly linear decrease in RTs as rate increased; $F_{(4.12, 53.4)}$ = 3.02, p = .003, $\eta_p^2 = .19$. To test the principle hypothesis, a further 10 x 2 repeated measures ANOVA was conducted to evaluate the effect of presentation rate (pps: 30-39 pps), and harmonic relation (ITP and HTP targets) on RT responses. Significant main effects were found for harmony, and rate; $F_{(1,13)} = 13.65$, p = .003, $\eta_p^2 = .51$, $F_{(9,117)} = 2.58, p = .01, \eta_p^2 = .17$ respectively.

Rate	Harmony		Mean Difference	Std. Error	Sig. ^b	Sig. ^b 95% Confidence In for Difference		
	2 = HTP	P, 1 = ITP	(2-1)			Lower	Upper	
pps						Bound	Bound	
30	2	1	30.931*	6.226	.000	17.480	44.382	
31	2	1	22.565^{*}	8.197	.016	4.857	40.273	
32	2	1	14.171^{*}	6.374	.045	.402	27.941	
33	2	1	25.192^{*}	8.064	.008	7.771	42.613	
34	2	1	26.760	12.789	.057	869	54.389	
35	2	1	16.942^{*}	7.352	.038	1.059	32.826	
36	2	1	8.979	13.099	.505	-19.320	37.278	
37	2	1	16.958	8.623	.071	-1.670	35.586	
38	2	1	16.441^{*}	5.750	.013	4.018	28.864	
39	2	1	17.801^{*}	7.237	.029	2.167	33.436	

Table 2.1. Study 1, Experiment 1, Pairwise Comparisons for the Effect of Rate on Harmony.

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

2 = HTP; harmonic target present.

1 = ITP; inharmonic target present.

The main effect for harmony was due to faster RTs to ITP targets (MD = 19.67, SE = 5.33, p = .003), while a pairwise comparison revealed that the effect for rate was due to a significant difference between RTs to HTP and ITP RTs (faster ITP responses) at all levels of rate except at 34 (p = 0.06), 36 (p = 0.51), and 37 pps (p = 0.07).

2.5.4 Error analysis. The percentage number of errors was 4.84%. The arcsine of the square root of the proportion of errors for each condition were analysed and a significant main effect of target was found ($F_{(1.4, 18.1)} = 9.2$, p = .004, $\eta_p^2 = .42$), due to fewer ITP errors compared to both TA (p = .013) and HTP errors (p = .025). Given the low ITP error rate, the implication is the facilitation of ITP responses, and related effects, in the statistical analyses of the corrected RT means, were owing to the effect of entrainment on performance and not a speed-accuracy trade-off.

2.5.5 Discussion. The least difference in RTs to both harmony targets (HTP-ITP RTs) occurs at a rate of 36 pps (MD = 8.98, SD = 13.1, p = .51). The corresponding presentation time for 36 pps entrainment conditions occurs during the

oscillatory trace of the deviant pip, as can be seen from the trend of the data in figures 2.4 and 2.5 below.



Figure 2.4. Graphed Harmony RT data.

Illustration of RT responses (y-axis) for both harmonically related targets, harmonic (circle legend) and inharmonic (diamond legend), at each rate of entrainment (legend labels), mapped over the four-pip prime within the entrainer at the time of target presentation (top *x*-axis), when out of phase with a 6.69 Hz rhythm. The bottom *x*-axis illustrates the number of repetitions of the four-pip prime at target presentation time (TPT). For example, targets presented at an entrainment rate of 32 pps coincided with the deviant pip in the oscillatory trace of the four pip prime sequence, during the ninth repeat of the sequence.



Figure 2.5. Experiment 1, priming as a function of Return Phase (RP). The RP depends on the rate of entrainment as it refers to the periodicity of the fourpip sequence. RP contains the code for the priming four-pip sequence, and therefore, any effect of RP is relative to the entrainment rate of the prime. The magnitude of priming is the strength of the effect of the prime, which is calculated as the difference between the RTs for each level of harmony (HTP-ITP, as inharmonic RTs are faster -y-axis) at the same level of entrainment. In this case, the target was presented when a 6.69 Hz wave was aligned at an angle of 130°. The top x-axis is a measure of the completion of the pip in the oscillatory trace of the entrainer coinciding with target presentation time (CNP; completion of next pip). The middle x-axis defines the last fully presented pip (LFPP). The bottom x-axis defines the current pip in the four-pip sequence, at target presentation time. For example, targets presented at an entrainment rate of 33 pps occurred a quarter of the way into the first pip of the oscillatory trace of the four-pip prime sequence, therefore the last fully presented pip tone was the fourth in the sequence. This model is taken from the design used to illustrate the magnitude of priming in the visual research using a similar stimulus entrainment paradigm (Kompass & Elliott, 2001).

Previous research using the original (DBBB) paradigm reported the pop-out effect following 33 pps entrainment when target presentation occurred at this point in the oscillatory trace. While the HTP-ITP difference is marginally significant following 32 pps entrainment (MD = 14.17, SD = 6.37, p = .045), under 32 and 36 pps entrainment conditions, the HTP-ITP RT difference is smaller compared to other

rates, and in both cases target presentation occurs during the deviant pip trace (see figure 2.5). The trend of the data in figure 2.4 illustrates a deviation in the function for RT responses to both harmonics at these entrainment rates due to faster responses to harmonic targets. Therefore, consistent with the findings from research using the original paradigm, RP predicted a facilitation effect, i.e., in both cases differences in the pattern of target-related responses were found when target presentation coincided with the deviant pip, indicating this is an effect of RP. However, the results from the current experiment reveal an effect of RP that is evident as a deviation in the trend of ITP and HTP responses when targets are presented during the oscillatory trace of the deviant pip, as a consequence of faster harmonic responses rather than the previously reported delay for harmonic responses (Aksentijevic et al., 2014). This result supports the hypothesis that the pop-out effect is an effect of RP. The target in both cases was presented out of phase with a 6.69 Hz theta wave cycle, and therefore the shift from a facilitation of inharmonic to harmonic responses is due to the position of the deviant pip. In visual binding, the phase of a 6.69 Hz theta rhythm at target presentation time shifts the priming effect from a facilitation of an anticipatory response to a response that occurs at the same time as, or slightly after, a primed event in the oscillatory trace of the entrainment stimulus. The results of this analysis do not support a similar effect of theta modulation in audition and raise the question as to why the move resulted in a facilitation rather than a delay of a harmonic response. One possible answer is that the new arrangement of the pip sequence desynchronises a 500 Hz representation at the end of the RP resonant cycle rather than near the beginning, due to the position of the deviant pip. The new sequence perhaps primes the auditory system better for a harmonic of the 500 Hz template as coherence rises steadily during the overall cycle. In this way, the sharp drop in coherence at the end of the cycle due to the inhibition of odd harmonics (e.g., 1500, 2500...Hz) may facilitate a response to a harmonic target as the carrier frequencies [1000 and 2000 Hz] are not inhibited.

2.6 Experiment 2

2.6.1 Research question. Owing to the findings of the previous experiment, this experiment was designed to further examine the effect of RP, and to test the effect the phase relation of a 6.69 Hz theta wave at target presentation time, will have on RP. A facilitation of responses to targets presented during a deviant pip will

reveal an effect of priming due to RP, while the effect of the phase relation of a 6.69 Hz rhythm on this priming effect can be investigated by presenting the same targets under two separate 6.69 Hz phase conditions – aligned at phase angles of 24.5° and 95.5°. The parameters were chosen to manipulate the phase of a 6.69 Hz theta wave at target presentation time, while simultaneously ensuring a target presented at a rate of 32 pps will be positioned approaching the deviant pip in the oscillatory trace of the entrainer under both phase conditions, as opposed to during the trace deviant in the previous experiment. Furthermore, a target presented at a rate of 29 pps (not included in the previous experiment) will coincide with the trace deviant during the 95.5° phase condition and will be presented approaching the deviant trace during the 24.5° condition. There are thus two hypotheses; One, presentation times coinciding with the deviant pip will determine any observed advantage to harmonic, or inharmonic responses, and two, the phase angle of a 6.69 Hz theta rhythm at target presentation time will influence responses based on the harmonic relation between the target and the entrainer. The first hypothesis is based on the observed dip in the trend of the HTP RT data following 32 and 36 pps entrainment rates (see figure 2.4), indicating a facilitation of HTP responses for targets coinciding with the deviant pip in the oscillatory trace of the entrainer. Presuming this is due to the position of the deviant pip in the entrainment oscillations RP cycle, this trend should continue for other entrainment frequencies depending on the RP at target presentation time. The second hypothesis aims to examine the effect of a 6.69 Hz phase relation at target presentation (implicated in modulating visual binding frequency specific effects) on RP. The results from the visual binding research using a similar entrainment paradigm demonstrate faster responses in anticipation of the priming frame in the oscillatory trace of the premask, when target presentation is in phase with 6.69 Hz rhythm. However, when this rhythm is out of phase alignment, responses are faster when the target is synchronous with, or slightly lags, the priming frame. Therefore, shifting the phase alignment of the target with a 6.69 Hz rhythm using the auditory paradigm is expected to influence the RP that leads to a facilitation of a harmonic response. The range of presentation rates [28 to 32 pps] overlapped with the previous range [30 to 39 pps].



Figure 2.6. Illustrations of the phase relation between a 6.69 Hz theta wave and the target, at target presentation time (TPT).

All five diagrams above are illustrations of the phase relation between a 6.69 Hz theta wave and the target, at TPT. All targets, for illustration purposes, are ITP targets. The ISI manipulates this phase relation by adjusting TPT to coincide with a specific point in the oscillatory cycle of the slower rhythm. Each diagram shows the repeated BBBD pip-sequence in the entrainer stimulus. In all cases, the x-axis represents the trial timeline, with an entrainment duration of 1000 ms, followed by an ISI, and then the target stimulus. Thus, in diagram (a) it is observed that the TPT of 1100 ms employed in experiment 1 resulted in a 130° phase alignment between a 6.69 Hz theta wave and the target – which, when presented at a rate of 32 pps, is positioned during the deviant pip in the oscillatory trace of the entrainer. Diagram (b) demonstrates a shift in this alignment to a 24.5° phase-lag at a TPT of 1206 ms, which presents the target approaching the trace deviant pip for targets presented at a rate of 32 pps. Again, approaching the trace deviant pip at this presentation rate, diagram (c) illustrates a TPT of 1086 ms, resulting in a shift in phase alignment to a 95.5° angle. Diagram (d) illustrates the same 24.5° phase alignment achieved at a TPT of 1206 ms, but for a 29 pps entrainer, which results in a target presentation that is synchronous with the deviant trace. Finally, diagram (e) illustrates the 95.5 ° phase

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alignment with a 6.69 Hz theta, using a TPT of 1086 ms, which presents the target at a rate of 29 pps during the deviant trace.

Experiment 1 used a target presentation time of 1100 ms post entrainer onset. Therefore, target presentation at a rate of 32 pps occurred during a deviant pip, and 130° phase-aligned with a 6.69 Hz rhythm (see figure 2.6 (a)). This experiment presented the target during the 32 pps condition approaching the deviant pip in the oscillatory trace, when aligned in phase with a 6.69 Hz wave by both 95.5° (at the peak amplitude of the wave, see figure 2.6 (b)), and 24.5° (close to zero phase-lag, see figure 2.6 (c)). The same temporal conditions (controlled by the length of the entrainer and the ISI) presented the target at 29 pps, with the same 6.69 Hz phase alignments, half way through the deviant pip trace at the peak of the slower rhythm (see figure 2.6 (e)), and on the cusp of the deviant pip when at a phase angle of 24.5° (close to zero phase-lag, see figure 2.6 (d)). This allowed for an examination of a minor change to the 32 pps condition within the RP of the pip sequence compared to the previous experiment, while simultaneously examining the effect of target presentation at the same location at a different rate of entrainment (29 pps), both during phase alignment at the peak amplitude of a 6.69 Hz wave and with a close-to zero phase-lag. It was hypothesised that the facilitation of a response to harmonic targets observed in the trend of the HTP and ITP RT data in the first experiment would be shifted to the harmonic targets presented at a rate of 29 pps at the peak amplitude of a 6.69 Hz wave. The 24.5° phase aligned condition tested the phase relation of a 6.69 Hz theta modulation frequency on the RP priming effect. The findings from experiment 1 suggest that RP is a strong determinant for a priming effect – including the salience of a harmonic target. However, this differs from the visual priming research results which have found a consistent priming effect due to RP that facilitates a response to the primed frame dependent on the phase of a 6.69 Hz rhythm at the time a synchronous target is presented. To date the auditory priming research has not examined the effect of a theta modulation on auditory priming effects. Based on the visual priming research findings, it was hypothesised that phase manipulation would influence the RP priming effect.

2.6.2 Sample and design. Sixteen participants recruited in the Galway area took part in this study. Two were left-handed (male n = 6, female n = 10, *M* age 24.63 years, *SD* 7.29). All participants reported normal hearing and provided

informed consent. Five participants had some experience playing an instrument. They did not have formal music training, and they did not practice regularly. A repeated measures design was used with three factors, rate (5 levels; 28 - 32 pps), target (asymmetrical as described for experiment 1), and ISI (2 levels; 86 and 206 ms). Participants were presented with 40 trials per condition which resulted in 1600 trials per participant, (5 x 2 x 2(2) x 40 = 1600). Trials were presented over the course of two sessions (45 minutes in duration, on separate days) in blocks of 40 trials. Experimental conditions were completely randomised within and between blocks. The dependent variable was corrected RT.

2.6.3 Results. This experiment was designed to answer two questions. Firstly, does target presentation during the deviant pip in the oscillatory trace of the entrained rhythm facilitate a response to a harmonic target (faster HTP RTs)? If so, HTP responses should be faster during the 29 pps entrainment condition, as opposed to the 32 pps condition, for targets presented when aligned with a 6.69 Hz theta wave at a 95.5° phase angle, i.e., there will be an observed dip in the trend of HTP RTs at 29 pps compared to other entrainment rates. Secondly, is the facilitation of a harmonic response influenced by the position of the target in the cycle of a 6.69 Hz theta wave? Should the results support this second hypothesis, a 24.5° phase alignment between the target and a 6.69 Hz theta rhythm will result in different priming effects. The findings do not support the first hypothesis, as a similar facilitation effect was not found at 29 pps as expected. However, the phase alignment between the target and a 6.69 Hz rhythm influenced responses depending on the harmonic relation between the target and the entrained carrier frequencies. While the results suggest this is an effect of RP, the facilitated response was to the inharmonic target as presentation approached the trace deviant pip (contrary to the effect of RP found in the results for experiment 1).

Initially, a 5 x 2 x 2(2) repeated measures ANOVA was conducted on corrected RT data to evaluate the effect of presentation rate (pps; 28, 29, 30, 31, and 32 pps), ISI (86 ms; 95.5° phase angle, and 206 ms; 24.5° phase angle), and target (TA, HTP, and ITP) on RT responses. A significant main effect was found for target and rate; $F_{(1.11, 16.68)} = 8.88$, p = .007, $\eta_p^2 = .37$, and $F_{(4, 60)} = 4.32$, p = .004, $\eta_p^2 = .22$, respectively. The former effect was due to slower HTP RTs compared to TA RTs (MD = 27.14, SD = 9.27, p = .031), and compared to ITP RTs (MD = 22.34, SD = 3.64, p < .001). The effect for rate was due to faster RTs following 32 pps

entrainment compared to 28 pps (MD = 6.55, SD = 1.74, p = .018) and 31 pps (MD = 5.88, SD = 1.43, p = .009).

To examine the principle hypotheses regarding the influence of the temporal parameters of the trial configurations on responses dependent on the harmonic structure of the target (harmonic and inharmonic), a 5 x 2 x 2 repeated measures ANOVA was conducted on corrected RT data to evaluate the effect of presentation rate (pps; 28, 29, 30, 31, and 32 pps), time between prime and target stimuli (ISI; 86 ms; 95.5 ° phase angle, and 206 ms; 24.5 ° phase angle), and harmonic relation (ITP and HTP targets) on RT responses. Significant main effects were found for harmony, rate, and ISI; $F_{(1,15)} = 37.65$, p < .001, $\eta_p^2 = .72$, $F_{(4,60)} = 3.5$, p = .012, $\eta_p^2 = .19$, and $F_{(1, 15)} = 33.04$, p < .001, $\eta_p^2 = .69$, respectively. Also the interaction effect between harmony and ISI was found to be significant ($F_{(1, 15)} = 10.25$, p = .006, $\eta_p^2 = .41$), due to faster RTs to inharmonic targets at both ISIs (p < .001 for both ISIs), and faster RTs overall at an ISI of 206 ms. The effect for harmony was due to faster RTs to inharmonic targets (MD = 22.34, SE = 3.64, p < .001). The effect for ISI was owing to faster RTs overall at an ISI of 206 ms (M = 421.16, SE = 23.15, MD = 16.44, SD = 2.86, p < .001).

ISI	Rate	Harmony		Mean	Std.	Sig ^b	95% Co	nfidence
		5		Difference	Error	U	Interval for	
							Difference ^b	
	pps	2 = HTP, 1 = ITP					Lower	Upper
							Bound	Bound
186 ms	28	2	1	24.624*	5.342	.000	13.239	36.010
	29	2	1	26.934*	6.841	.001	12.353	41.516
	30	2	1	27.733*	6.531	.001	13.812	41.654
	31	2	1	25.531*	7.515	.004	9.513	41.550
	32	2	1	25.113*	4.734	.000	15.023	35.203
206 ms	28	2	1	9.998	7.740	.216	-6.499	26.495
	29	2	1	20.392*	5.990	.004	7.625	33.160
	30	2	1	16.268*	5.028	.006	5.552	26.985
	31	2	1	16.964*	5.313	.006	5.639	28.289
_	32	2	1	29.874*	5.283	.000	18.614	41.134

Table 2.2. Study 1, Experiment 2, Pairwise Comparisons: ISI by Rate by Harmony.

Based on estimated marginal means

* The mean difference is significant at the .05 level.

b Adjustment for multiple comparisons: Bonferroni.

2 = HTP; harmonic target present

1 = ITP; inharmonic target present

A pairwise comparison revealed that ITP RTs were significantly faster than HTP RTs at all rates and for both ISIs, except for at 28 pps in the 206 ms ISI condition (in phase condition, and middle of RP) (see table 2.2).



Figure 2.7. Experiment 2; graphed harmony RT data.

(a) Illustration of the RT responses for targets (*y*-axis = RTs in milliseconds), both harmonic (circle legend) and inharmonic (diamond legend), at each rate of entrainment (legend labels), and the RP (*x*-axis = RP, determined by the pipsequence of the entrained oscillation) at the time of target presentation, when aligned

with the peak amplitude of a 6.69 Hz rhythm (phase angle of 95.5°). (b) Illustration of the same target-entrainer relation at target presentations at the beginning of a 6.69 Hz rhythm (phase angle of 24.5°).



Figure 2.8. Experiment 2; priming as a function of Return Phase (RP). Illustration of the strength of the effect of the prime – calculated as the difference between the RTs for each level of harmony (*y*-axis = HTP-ITP RTs in ms), at the same level of entrainment (legend labels), as a function of the RP for the four-pip prime sequence (the top *x*-axis = completion of the pip, and the middle *x*-axis = the sequence of the pip), given target presentation aligned in phase with a 6.69 Hz rhythm, at angles equal to 95.5° (circle legend), and 24.5° (square legend).

Given the significant interaction effect between harmony and ISI, a third analysis was performed to examine each level of the ISI separately, using an adjusted alpha of .025 – the factors of interest were harmony and rate. As seen in figure 2.7 (a), at an ISI of 86 ms, which presents the target out of phase with a presumed 6.69 theta rhythm, RTs to inharmonic stimuli are faster compared to harmonic targets (pvalue falls between < .001and .004). However, the function mapped by each target is the same. At an ISI of 206 ms, when target presentation is in phase with the same presumed rhythm, a Bonferroni corrected pairwise comparison of rate by harmony revealed significant differences in RTs between each level of harmony at all levels of entrainment except 28 Hz (28 Hz, p = .216; 29 Hz, p = .004; 30 Hz, p = .006; 31 Hz,

p = .006; 32 Hz, p < .001, see table 2.2). These differences are qualified by a significant harmony by rate interaction ($F_{(4, 60)} = 2.59$, p = .045, $\eta_p^2 = .15$), which is illustrated by the difference in the functions of both types of harmonic response (see figure 2.7(b)), and by the graph of the difference in RTs to both targets (see figure 2.8).

2.6.4 Error analysis. The percentage error reported was 4.71%. The arcsine of the square root of the proportion of errors for each condition were analysed and a significant main effect was found for target ($F_{(2, 30)} = 11.53$, p < .001, $\eta_p^2 = .44$), due to fewer ITP errors compared to HTP errors (p = .001). Thus, the indication is a speed-accuracy trade-off does not contaminate the results.

2.6.5 Discussion. The empirical findings do not allow for the rejection of the null hypothesis regarding the facilitation of a harmonic response when target presentation coincides with the deviant pip in the oscillatory trace of the entrainer. However, in the 24.5° phase-lag condition, as can be seen from figure 2.8, the largest deviation between ITP and HTP RTs occurs for targets presented at 29 and 32 pps, approaching the deviant pip trace (also refer to figure 2.6 (b) and (d) for illustration). The results of experiment 1 found that targets presented at the latter entrainment rate aligned in phase with a 6.69 Hz frequency at an angle of 130° resulted in a facilitation of harmonic responses (faster HTP RTs). Adjusting target presentation so that the timing shifted the alignment in phase with a 6.69 Hz rhythm from 130° to ~90° completely removed any obvious effect of RP, while a near zero phase-lag with this rhythm resulted in a disruption of the harmonic salience – or perhaps a facilitation for inharmonic responses – given the dips in ITP RTs at these presentation rates compared to the smooth curve of the HTP RT function, when RP approached the deviant pip trace. This supports the hypothesis that, as in vision, modulation effects of a theta rhythm of 6.69 Hz may contribute to auditory binding, with the phase of this rhythm coinciding with target presentation influencing the salience of a harmonic target.

2.7 Experiment 3

2.7.1 Research question. This experiment was designed to test the hypothesis that a zero phase-lag between target presentation time and a 6.69 Hz theta rhythm will disrupt a response to harmonic targets. Previously this pop-out effect was found when the deviant pip was first in the entrained prime sequence, and

therefore during the desynchronisation of the 500 Hz harmonic template, for a target presented out of phase with a 6.69 Hz rhythm by 130°. Rearranging the pip sequence, desynchronising the 500 Hz template at the end of the sequence, and therefore manipulating the information stored in the RP resonance, led to a facilitation of harmonic responses. However, from the results of experiment 2, there is some suggestion that the phase of a 6.69 Hz rhythm at target presentation time influences the salience, and therefore the facilitation or disruption of responses to the harmonic target. This experiment was designed to test the disruption to harmonic salience when the target is presented synchronously with a 6.69 Hz rhythm (zero phase-lag) over the same range of frequencies used in the first experiment, 30 to 39 pps. Experiment 1 used these entrainment frequencies and presented the target out of phase alignment with a 6.69 Hz rhythm (again at a phase angle of 130°), resulting in a facilitation of harmonic responses at 32 and 36 pps entrainment, when target presentation coincided with the deviant pip trace.

2.7.2 Sample and design. Sixteen participants recruited in the Galway area took part in this study. Three were left-handed (male n = 7, female n = 9, *M* age 29.68 years, *SD* 8.75). All participants reported normal hearing and provided informed consent. Five participants had some experience playing an instrument (one formally; piano for four years), however, they did not practice regularly. A repeated measures design was used with two factors, rate (ten levels; 30 - 39 pps) and target (asymmetrical as described in experiment 1). The ISI was kept constant at 196 ms. Participants were presented with 40 trials per condition which resulted in 1600 trials per participant, ($10 \ge 2(2) \ge 40 = 1600$). Trials were presented over the course of two sessions (45 minutes in duration, on separate days) in blocks of 40 trials. Individual sessions began with a 40 – trial practice block. Experimental conditions were completely randomised within and between blocks. The dependent variable was corrected RT.

2.7.3 Results. The data were analysed to examine the effect of priming on harmonic responses when targets are presented at zero phase-lag with a 6.69 Hz frequency. Initially, a 10x 2(2) repeated measures ANOVA was conducted on corrected RT data to evaluate the effect of presentation rate (pps; 30-39 pps), and target (TA, HTP, and ITP) on RT responses. Significant main effects were found for target and rate; $F_{(1.23, 18.47)} = 5.26$, p = .028, $\eta_p^2 = .26$, and $F_{(9, 135)} = 4.87$, p < .001, $\eta_p^2 = .25$. The effect for target was due to significantly faster responses to inharmonic

targets compared to harmonic targets (MD = 14.6, SD = 2.24, p < .001), while the effect for rate was due to an almost linear decrease in RTs with increased rate. To test the principle hypothesis, a further 10 x 2 repeated measures ANOVA was conducted on corrected RT data to evaluate the effect of presentation rate (pps), and harmonic relation (ITP and HTP targets) on RT responses. The results support a disruption to the salience of harmonic targets presented synchronously with the beginning of a 6.69 Hz theta wave cycle, thus allowing rejection of the null hypothesis. Significant main effects were found for harmony, and rate; $F_{(1,15)} = 42.44$, p < .001, $\eta_p^2 = .74$, $F_{(9,135)} = 4.34$, p < .001, $\eta_p^2 = .22$ respectively. The main effect for harmony was due to faster RTs to ITP targets (MD = 14.6, SE = 2.24, p = .000).

(I) Rate	(J) Rate	Mean	Std. Error	Sig ^b	95% Confidence Interval	
		Difference		-	for Difference ^b	
		(I-J)				
					Lower	Upper
pps	pps				Bound	Bound
36	30	-7.508	2.792	.757	-18.735	3.719
	31	-2.198	3.541	1.000	-16.435	12.038
	32	-5.757	2.875	1.000	-17.315	5.802
	33	.696	2.836	1.000	-10.707	12.098
	34	391	2.293	1.000	-9.612	8.829
	35	-2.015	3.027	1.000	-14.186	10.156
	37	4.580	3.720	1.000	-10.376	19.536
	38	5.322	2.920	1.000	-6.418	17.062
	39	2.006	2.741	1.000	-9.016	13.028
37	30	-12.088	3.841	.299	-27.533	3.357
	31	-6.778	3.350	1.000	-20.248	6.691
	32	-10.337	3.400	.372	-24.006	3.333
	33	-3.884	3.383	1.000	-17.486	9.718
	34	-4.971	2.970	1.000	-16.915	6.973
	35	-6.595	3.007	1.000	-18.686	5.496
	36	-4.580	3.720	1.000	-19.536	10.376
	38	.742	2.559	1.000	-9.548	11.033
	39	-2.574	2.718	1.000	-13.504	8.356
38	30	-12.830*	2.267	.002	-21.944	-3.716
	31	-7.521	3.065	1.000	-19.843	4.802
	32	-11.079^{*}	1.895	.001	-18.700	-3.457
	33	-4.626	2.212	1.000	-13.520	4.268
	34	-5.713	1.486	.072	-11.689	.262
	35	-7.337	2.606	.586	-17.814	3.139
	36	-5.322	2.920	1.000	-17.062	6.418
	37	742	2.559	1.000	-11.033	9.548
	39	-3.316	2.301	1.000	-12.567	5.934
39	30	-9.514	2.660	.124	-20.211	1.183
	31	-4.204	2.888	1.000	-15.818	7.409
	32	-7.763*	1.730	.020	-14.720	805
	33	-1.310	2.956	1.000	-13.196	10.576
	34	-2.397	2.478	1.000	-12.362	7.568
	35	-4.021	2.286	1.000	-13.213	5.170
	36	-2.006	2.741	1.000	-13.028	9.016
	37	2.574	2.718	1.000	-8.356	13.504
	38	3.316	2.301	1.000	-5.934	12.567

Table 2.3. Study 1, Experiment 3, Pairwise Comparisons for Rate.

Based on estimated marginal means *. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

Rate	Harmony		Mean Difference (2-1)	Std. Error	Sig. ^b	95% Confidence Interval for Difference	
	2 = HTP, 1 = ITP					Lower	Upper
						Bound	Bound
30	2	1	13.292*	4.027	.005	4.710	21.875
31	2	1	11.514*	5.060	.038	.730	22.299
32	2	1	10.337*	4.379	.032	1.003	19.671
33	2	1	10.854*	3.577	.008	3.230	18.479
34	2	1	11.501*	5.047	.038	.745	22.258
35	2	1	19.407*	3.714	.000	11.491	27.322
36	2	1	15.888*	7.210	.044	.520	31.255
37	2	1	14.311*	4.338	.005	5.066	23.557
38	2	1	18.868*	4.698	.001	8.854	28.882
39	2	1	19.983*	5.364	.002	8.549	31.417

Table 2.4. Study 1, Experiment 3, Pairwise Comparisons: Rate by Harmony.

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

2 = HTP; harmonic target present.

1 = ITP; inharmonic target present.

A pairwise comparison revealed that the effect for rate was due to a decrease in RTs as rate increases (see table 2.3). While ITP RTs were found to be faster at all levels of rate, the significance value is greatest for the difference at rates 35 and 38 pps (p = .000, and p = .001 respectively, see table 2.4).

2.7.4 Error analysis. The percentage error reported was 6.16%. The arcsine of the square root of the proportion of errors for each condition were analysed and a significant main effect was found for target and rate ($F_{(2, 30)} = 28.66$, p < .001, $\eta_p^2 = .66$, and $F_{(9, 135)} = 2.49$, p = .012, $\eta_p^2 = .14$ respectively). The former was due to fewer ITP errors compared to both TA (p = .02) and HTP errors (p < .001), and the latter stemmed from fewer errors at 37 and 39 pps entrainment compared to 36 pps, (p = .006 and p = .003 respectively). Again, the indication is the results are not contaminated by a speed-accuracy trade-off.

2.7.5 Discussion. Figure 2.9 illustrates a deviation in the data trend for both harmonics at 35 and 38 pps, due to either faster ITP responses or slower HTP responses at both rates. The physical characteristics resemble that of the 33 Hz popout effect found previously when the deviant was first in the sequence. In both cases, the target is presented mid-cycle (between baseline pips 2 and 3). Thus, it is suggested that when the target is presented in phase with a 6.69 Hz rhythm, and

halfway through the RP resonance, when the coherence of the 500 Hz representation is peaking, the harmonic becomes less salient.



Figure 2.9. Experiment 3; Graphed harmony RT data.

Illustration of RT responses to both harmonic (circle legend) and inharmonic (diamond legend) targets (*y*-axis), mapped over the entrainer at the time of target presentation (top *x*-axis), when aligned with the beginning of a 6.69 Hz wave cycle (i.e. zero phase-lag). The number of four-pip sequence oscillations from entrainment onset is illustrated on the bottom *x*-axis.

This experiment presented the target at 32 pps mid-way through the RP sequence, and although this resulted in disruption to the salience of harmonic targets in experiment 2, when the target was presented approaching the deviant pip trace, when also very close to a zero phase-lag with the beginning of a 6.69 Hz rhythm, the functions for ITP and HTP responses did not deviate. This suggests the effect of RP is strongly influenced by the phase of a 6.69 Hz wave at the time a target is presented.

2.8 Experiment 4

2.8.1 Research question. Experiments 4 and 5 were designed to present the target at the beginning of a 6.69 Hz theta wave cycle (with zero phase-lag), to examine the trend of the ITP and HTP data mapped over RP across a larger
frequency range. Experiment 3 examined the effect of this manipulation for presentation rates 30 - 39 pps. Experiment 4 worked backwards from this range, using presentation rates 26 - 30 pps. Target presentation midway through the RP cycle was hypothesised to result in a pop-out effect of priming.

2.8.2 Sample and design. Sixteen participants recruited in the Galway area took part in this study. One participant was left-handed (male n = 4, female n = 12, M age 28.25 years, *SD* 7.72). All participants reported normal hearing and provided informed consent. Seven participants had some experience playing an instrument (one formally; piano grade 1), however, they did not practice regularly.

A repeated measures design was used with two factors, rate (5 levels; 26 - 30 pps) and target (asymmetrical as described for experiment 1). The ISI was again kept constant at 196 ms. Participants were presented with 30 trials per condition which resulted in 600 trials per participant, (5 x 2(2) x 30 = 600). At the end of each block, the experimental programme presented the first two trials, any error trials, and the trial directly proceeding an error trial, again. Thus, the number of repetitions were reduced. These trials were removed during the analysis, and the repeated trials were retained. RTs are often delayed at the start of a block and following an error, and for this reason the design was changed. Trials were presented in one session (approximately 45 minutes in duration) in blocks of ~ 42 trials. Individual sessions began with a 10 – trial practice block. Experimental conditions were completely randomised within and between blocks. The dependent variable was corrected RT.

2.8.3 Results. The results do not support the rejection of the null hypothesis. An initial 5 x 2(2) repeated measures ANOVA was conducted on corrected RT data to evaluate the effect of presentation rate (pps; 26 – 30 pps), and target (TA, ITP and HTP targets) on RT responses. A significant main effect was found for harmony; $F_{(2, 30)} = 12.52$, p < .001, $\eta_p^2 = .46$, due to slower HTP RTs compared to both ITP and TA RTs (MD = 20.16, SE = 3.5, p < .001, and MD = 23.23, SE = 6.04, p = .005 respectively).

To examine support for the principle hypothesis, a 5 x 2 repeated measures ANOVA was conducted on corrected RT data to evaluate the effect of presentation rate (pps; 26 – 30 pps), and harmonic relation (ITP and HTP targets) on RT responses. A significant main effect was found for harmony; $F_{(1,15)} = 33.2$, p < .001, $\eta_p^2 = .69$, due to faster RTs to ITP targets (MD = 20.16, SE = 3.5, p < .001).



Figure 2.10. Experiment 4; graphed harmony RT data.

Illustration of the RT responses to both harmonic (circle legend) and inharmonic (diamond legend) targets (*y*-axis), mapped over the entrainer at the time of target presentation, when aligned with the beginning of a 6.69 Hz wave cycle (i.e. zero phase-lag). The top *x*-axis represents the position of the target in the oscillatory trace of the entrainer, while the bottom *x*-axis illustrates the number of oscillatory cycles completed.

Targets were presented during the first baseline pip in the oscillatory trace of the four-pip entrainment sequence at a presentation rate of 27 pps, coinciding with the re-synchronisation of the 500 Hz template. The HTP RT data demonstrates a sharp dip at this entrainment rate.

Rate (pps)	Harmony		Mean Difference (2-1)	Std. Error	Sig b	95% Confid for Dif	ence Interval ference ^b
<u>(PP³)</u>	2 = HTP, 1 = ITP		(2-1)			Lower Bound	Upper Bound
26	2	1	21.605*	5.745	.002	9.360	33.850
27	2	1	9.431	4.697	.063	580	19.441
28	2	1	24.176^{*}	7.234	.004	8.757	39.596
29	2	1	23.311*	5.970	.001	10.586	36.035
30	2	1	22.281^{*}	5.734	.001	10.059	34.504

Table 2.5. Study 1, Experiment 4, Pairwise Comparisons: Rate by Harmony.

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

2 = HTP; harmonic target present.

1 = ITP; inharmonic target present.

A pairwise comparison revealed that the difference between harmony responses was not found to be significant at a rate of 27 pps (MD = 9.43, SE = 4.7, p = .063). The implication is that a harmonic response is facilitated (resulting in similar HTP and ITP RTs) early in the RP as odd harmonics no longer require inhibition (see figure 2.10). However, the hypothesised slowing of harmonic responses and facilitation of inharmonic responses (pop-out), when the target was presented mid-way through the RP cycle, was not found. Therefore, the results do not support the rejection of the null hypothesis.

2.8.4 Error analysis. The percentage error reported was 6.19%. The arcsine of the square root of the proportion of errors for each condition were analysed and a significant main effect was found for Target ($F_{(2, 30)} = 18.5$, p < .001, $\eta_p^2 = .55$), due to fewer ITP errors compared to both TA (p = .021) and HTP errors (p < .001). As before, the indication is the results are not contaminated by speed-accuracy tradeoffs.

2.8.5 Discussion. Under the 27 pps entrainment condition, the target is positioned during the first pip (500 Hz) in the oscillatory trace and appears to result in either a slowing of responses to the inharmonic, or a quickening of responses to the harmonic (see figure 2.10). According to the HR model at this point in the entrainer the 500 Hz template has been 'reset' and as inhibition of odd harmonics is not required, it is reasonable to assume that the auditory system expects a harmonic. The facilitation of harmonic responses was observed when the target was presented at a 130° phase angle with a 6.69 Hz cycle for presentation rates of 32 and 36 pps

(see experiment 1, figure 2.4). However, this was not the case when targets were presented at these same rates at the beginning of a 6.69 Hz cycle (see experiment 3, figure 2.9). It is suggested that possibly RP is a stronger determinant of a priming effect at slower gamma frequencies.

2.9 Experiment 5

2.9.1 Research question. Again experiment 5 was designed to present the target at the beginning of a 6.69 Hz theta wave cycle (with zero phase-lag), to examine the trend of the ITP and HTP data mapped over RP across a frequency range extending upwards from 39 Hz, as was previously examined in experiment 3. Target presentation midway through the RP cycle was hypothesised to result in a pop-out effect of priming.

2.9.2 Sample and design. The sample and design were as per experiment 4. A repeated measures design was used with two factors, rate (11 levels; 39 - 40 pps) and target (asymmetrical as described in experiment 1). The ISI was kept constant at 196 ms. Participants were presented with 30 trials per condition which resulted in 1320 trials per participant, (11 x 2(2) x 30 = 1320). Trials were presented over the course of two sessions (approximately 50 minutes in duration, on separate days) in blocks of ~46 trials. Individual sessions began with a 15 – trial practice block. Experimental conditions were completely randomised within and between blocks. The dependent variable was corrected RT.

2.9.3 Results. The data were analysed to examine the effect of manipulation of target presentation time with the beginning of a 6.69 Hz wave cycle on harmonic responses. An 11 x 2(2) repeated measures ANOVA was conducted on corrected RT data to evaluate the effect of presentation rate (pps; 39-49 pps), and target (TA, ITP and HTP) on RT responses. A significant main effect was found for target; $F_{(1.32, 19.76)} = 8.37$, p = .006, $\eta_p^2 = .36$, due to slower HTP RTs compared to both ITP and TA RTs (MD = 16.99, SE = 3.12, p < .001, and MD = 17.76, SE = 6.29, p = .039 respectively). A significant interaction effect between target and rate was also found; $F_{(20, 300)} = 1.66$, p = .038, $\eta_p^2 = .1$, due to HTP RTs that were slower compared to ITP RTs at entrainment rates of 41, 42, 43, 44 and 48 pps, and slower compared to TA RTs entrainment rates of 39, 41, 42, 44 and 48 pps.

To test the principle hypothesis, an 11 x 2 repeated measures ANOVA was conducted on corrected RT data to evaluate the effect of presentation rate (pps; 39-

49 pps), and harmonic relation (ITP and HTP targets) on RT responses. The results support a disruption to the salience of harmonic targets presented mid-way through the RP cycle and synchronous with a 6.69 Hz theta wave cycle, thus allowing rejection of the null hypothesis. Significant main effects were found for harmony, and rate; $F_{(1,15)} = 29.92$, p < .001, $\eta_p^2 = .66$, $F_{(10,150)} = 2.1$, p = .032, $\eta_p^2 = .12$ respectively. The main effect for harmony was due to faster RTs to ITP targets (*MD* = 16.99, *SE* = 3.11, p = .000).

Rate	Harmony		Mean	Std.	Sig. ^b	95% Confidence	
	5		Difference	Error	-	Interval for	Difference ^b
			(2-1)				
pps	2 = HTP, 1 = ITP					Lower	Upper
						Bound	Bound
39	2	1	13.344	6.388	.054	271	26.960
40	2	1	11.174*	4.818	.035	.904	21.444
41	2	1	26.666*	4.714	.000	16.617	36.714
42	2	1	20.592*	4.485	.000	11.032	30.151
43	2	1	16.257*	5.294	.008	4.974	27.541
44	2	1	17.956*	6.330	.013	4.463	31.449
45	2	1	16.006*	7.231	.043	.594	31.418
46	2	1	8.079	4.567	.097	-1.655	17.813
47	2	1	15.095*	5.743	.019	2.855	27.335
48	2	1	28.289*	4.937	.000	17.767	38.812
49	2	1	13.374*	5.506	.028	1.639	25.109

Table 2.6. Study 1, Experiment 5, Pairwise Comparisons: Rate by Harmony.

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

2 = HTP; harmonic target present.

1 = ITP; inharmonic target present.

However, a pairwise comparison revealed that the difference between harmony responses was not found to be significant at a rate of 39, or 46 pps (MD =13.34, SE = 6.39, p = .054, and MD = 8.1, SE = 4.57, p = .097 respectively).

2.9.4 Error analysis. The percentage error reported was 5.85%. The arcsine of the square root of the proportion of errors for each condition were analysed and a significant main effect was found for target ($F_{(2, 30)} = 30.3$, p < .001, $\eta_p^2 = .67$), due to fewer ITP errors compared to both TA (p = .01) and HTP errors (p < .001). The error analyses for all five experiments have consistently found ITP responses to be significantly more accurate, which suggests the observed ITP RT advantage in all cases is due to improved performance rather than a speed-accuracy trade-off.



2.9.5 Discussion.



Illustration of the strength of the effect of the prime – calculated as the difference between the RTs (y-axis = HTP-ITP RTs) for each level of harmony at the same level of entrainment (legend labels) as a function of the RP for the pip sequence (bottom x-axis), given target presentation aligned in phase with a 6.69 Hz rhythm, with zero phase-lag. The middle x-axis defines the last fully presented pip (LFPP). The top x-axis is a measure of the completion of the pip represented on the bottom axis (CNP; completion of next pip).



Figure 2.12. Experiment 5; graphed harmony RT data.

Illustration of the RT responses to targets, both harmonic (circle legend) and inharmonic (diamond legend), and the entrainer at the time of target presentation, when aligned with the beginning of a 6.69 Hz wave cycle (i.e. zero phase-lag).

There are two points of interest in the results of this experiment. Firstly, is the finding that ITP responses are faster compared to HTP responses at all rates of entrainment – except at 39 and 46 pps, at which point the target is presented approaching, and in the case of the 46 pps target condition synchronous with, the deviant pip trace (see figure 2.11). Secondly, as illustrated in figure 2.12, there is a deviation in the trend of the function for both harmonic responses when the target is presented halfway through the resonant four-pip cycle, for presentation rates 41/42, and 48 pps. Again, this deviation in the data resembles the physical appearance of the pop-out effect. Therefore, the results add support to the suggestion that when the target is presented in phase with a 6.69 Hz rhythm, and halfway through the resonant RP cycle, when the coherence of the 500 Hz representation is peaking, the inharmonic becomes more salient. The findings suggest that when there is zero phase-lag between a target and a 6.69 Hz rhythm, RP generates a listener's expectancies, thus determining the salience of a given harmonic structure. When

target presentation time approaches, or is synchronous with, the deviant pip in the oscillatory trace of the entrainer, a response to a harmonic target is facilitated – presumably because the deviant pip prompts the inhibition of odd harmonics (e.g., 1500, 2500...Hz). Consequently, the harmonic carrier frequencies of 1000 and 2000 Hz will not be inhibited, resulting in faster HTP RT responses. Target presentation times approaching maximum coherence of the 500 Hz representation in the oscillatory trace of the entrainer (midway through the three baseline pips) may increase the salience of an inharmonic, with carrier frequencies of 1000, and 2400 Hz, as this violates the expected 500 Hz harmonics of the established template. Also of interest, is that 39 Hz and 46 Hz, as well as 41 Hz and 48 Hz, are separated by 7, which adds support to the modulation of a 6.69 Hz wave resulting in this priming effect.

2.10 General discussion

The paradigm for these experiments manipulated the sequence of pips in the original paradigm designed by Aksentijevic et al. (2011), from a deviant-baselinebaseline-baseline (DBBB) sequence to a baseline-baseline-baseline-deviant (BBBD) sequence. The premise for this change was grounded in the HR model. It was hypothesised that this sequence would correspond with the four-frame sequence used in the visual priming paradigm designed by Elliott and Müller (1998), which used rate of flicker rather than tone bursts to entrain specific gamma-band responses. The HR model predicts that the coherence of the acoustic waveform of the DBBB entrainer is asymmetric, rising over the course of the three baseline pips, peaking at the end of the third baseline pip, levelling at the start of the deviant pip, and sharply dropping by the end of the deviant. The sharp drop in coherence during the deviant pip is due to the inhibition of odd harmonics (1500, 2500...Hz) resulting from the established 500 Hz template. However, the reactivation of the 500 Hz 'unique template' does not require the inhibition of odd harmonics and therefore coherence begins to rise immediately following presentation of the first baseline pip. It was considered that altering the sequence so that the baseline pips were followed rather than preceded by the deviant would entrain the auditory system to anticipate the 500 Hz tone following the deviant pip's reset of the 500 Hz coherence. The previously reported pop-out effect occurred when the target was presented out of phase with a 6.69 Hz rhythm and during the deviant (first) pip in the oscillatory trace of the

entrainer – a phase relation with this theta wave at target presentation time has been found to facilitate a response to targets presented at a primed location (in the oscillatory trace of the premask) in the visual binding experiments (Elliott, 2014). According to these research findings, when the target is presented out of phase with this rhythm a response is facilitated that is synchronous with or slightly lags the primed event, and when presentation is in phase with this theta wave there is a facilitation of an anticipatory response, occurring slightly ahead of the primed event. Presuming the pop-out effect is a facilitatory response due to the position of the target in the phase of the slower theta rhythm of 6.69 Hz, would entail the response was retroactive rather than anticipatory. Therefore, altering the sequence of the pips also tests the GPAH in relation to auditory binding. By presenting the harmonic and inharmonic targets both in phase and out of phase with this rhythm, it was hypothesised that the RP established by repetition of the BBBD pip sequence would yield results comparable to those found for visual binding, i.e., a zero phase-lag facilitation of responses to targets presented slightly ahead of the first 500 Hz baseline pip and an out of phase facilitation when presented synchronous with, or slightly after this pip.





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experiments. The dashed vertical lines represent the crossover of data from two separate experiments. There was an inconsistency in the range of RTs across experiments due to a different (less accurate) data collection tool employed for the middle dataset than that used for the datasets at either end of the graph (see section 2.3 Apparatus for details).

The primary focus of the individual experiment discussions has not been on significant results, and instead have centred on trends in the data. However, while not consistently backed up empirically, the trends in the functions for ITP and HTP RT data at each entrainment rate plotted over RP illustrates two important points. The position of the target in the RP cycle at the time of presentation influences whether responses to the harmonic targets are facilitated or disrupted. Presentation during or approaching the deviant pip facilitated a response (experiment 1, 4, and 5), while presentation during the baseline pips disrupted the response to the harmonic (experiment 2, 3, and 5). However, this is not consistent with the pop-out effect previously found and replicated when employing the original pip-sequence, as this occurred due to a disruption to harmonic responses presented during the deviant pip trace when presentation time was out of phase with a 6.69 Hz rhythm. Secondly, and importantly, the influence of the phase relation with 6.69 Hz at the time of target presentation increased with increased presentation rate (see results and discussion for experiment 5). Both ITP and HTP functions mapped each other perfectly when the target was presented at a 95.5° phase angle with this rhythm, while an extra 34.5° in the phase angle (at 130°) demonstrated a facilitation of harmonic responses at or approaching the deviant pip trace. Also, when the target was presented at the same position in the RP cycle, but at a phase angle of 24.5° with 6.69 Hz, a disruption of harmonic responses was demonstrated, while adjustment of presentation time by a few degrees, to a zero phase-lag, did not replicate this trend at 29 and 32 pps entrainment rates but did at 35, 38, 41/42, and 48 pps (see figure 2.13). This suggests great sensitivity to the timing of target presentation in relation to the phase of a 6.69 Hz rhythm. It is suggested that RP must be considered more closely to reconcile the move from the pop-out effect for a target presentation during the deviant pip trace when presentation was out of phase with a 6.69 Hz wave when primed with the original sequence, to a facilitation of harmonic responses under the same conditions when primed with the altered sequence, particularly in light of the observed

facilitation when the target was presented aligned with a 6.69 Hz wave, both out of phase (experiment1) and with zero phase-lag (experiment5). As discussed in the previous chapter, findings in the visual binding research using a similar priming paradigm suggest that a rhythm matching the periodicity of the four-frame prime within the premask is established by repetition and thus generates a model of the input. This model is evaluated by the backpropagation of the established response matching the premask presentation rate from neurons within the inferotemporal (IT) area of visual processing. Four frames within a 40 Hz premask display would last 100 ms which has a periodicity matching a 10 Hz rhythm. This is referred to as the local response, while the overall 'global' rhythm, in this scenario 40 Hz, depends on the rate of flicker, arising in this case from the presentation of 40 frames of equal duration (25 ms), in a one second period. Thus, the neural oscillations are considered a resonance between both stages of processing and are therefore a result of processing rather than the processing mechanism itself. By this account, the RP contains information specific to the four-pip sequence embedded in the entrainer. By moving the deviant pip, the local rhythm primes the auditory system with a 500 Hz template that reaches maximum coherence approaching the deviant pip, whereas the previous arrangement began with maximum coherence, which dropped sharply and then began to rise steadily until the end of the sequence. The difference between these two primes is the point at which maximum coherence of a 500 Hz template is reached; for the new prime this is three quarters way through, and for the old prime this was at the beginning and end of the resonant cycle.



Figure 2.14. Return Phase (RP) resonance.

Illustration of the RP resonance generated within the old prime (left) and the new prime (right).

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By this rationale, the resonance of the new prime, generated by RP, would prime the auditory system to expect a 500 Hz harmonic, while the system would be primed to expect an inharmonic from the resonance generated by the RP of the old prime (see figure 2.14). This explanation for the effects illustrated by the trends in the data over the course of these experiments, and the pop-out effect when the deviant pip is first in the sequence, emphasises RP as an effect of priming, while suggesting an interaction with a 6.69 Hz (and possibly other) theta rhythm(s) as a more general mechanism of auditory binding, particularly when the system is primed with faster gamma frequencies (> 32 Hz).

In conclusion, while these experiments lack empirically significant results, the trends in the data when the ITP and HTP RTs at each entrainment rate are plotted over RP illustrate a complex interplay between the priming effects of RP and a more general interaction with a slower endogenous theta rhythm (~ 6 Hz). It was proposed that the first baseline pip should be comparable to the first frame in the visual priming paradigm, and therefore altering the sequence was hypothesised to bring about a facilitation of responses to the inharmonic for target presentations during the deviant trace when also presented in phase with a 6.69 Hz rhythm, and during the first baseline pip trace when out of phase with this rhythm. The HR model describes a mechanism which aids perception of novel, yet related stimuli, by ensuring that the GBR evoked by a new stimulus that is either harmonically or spatially related to a pre-existing stimulus, is noticed by first abolishing the GBR to the pre-existing stimulus. An inharmonic target would be most salient as it would trigger a different neural response to that expected. The null hypothesis was not rejected by the findings of this investigation. However, important information regarding the auditory priming paradigm has been uncovered. Firstly, RP explains facilitatory effects based on resonance arising from the process, but the effect is influenced by the position of the deviant pip in the oscillatory trace of the entrainer, and therefore is largely an effect of priming. The GPAH predicts a facilitation of a primed response that is dependent on specific temporal dynamics. Presuming a constant time delay, this facilitation occurs for specific, or critical, frequencies at regular time intervals corresponding with an integer multiple of their reciprocal time periods. The inference is that a primed response is facilitated at regular intervals when there is an interaction in phase between a slower rhythm, whose period matches that of the regular interval, and specific gamma frequencies whose periods are integer multiples

of this regular interval. By extension, this requires that the response is primed via entrainment of a critical gamma-band response. In this regard, comparisons between the auditory and visual binding research using a paradigm which entrains a gammaband response can be made. In both cases, there is evidence which supports the RPH. From the results presented here, support is weak for a modulation effect of a slower endogenous rhythm of approximately 6.69 Hz, as predicted by the GPAH – grounded in the findings from the visual binding research.

There are differences in the physical properties of both paradigms, beyond the sensory modality tested by each one, which perhaps makes correspondence difficult. In the case of the visual priming paradigm, the primed target is a singular event, and it is primed or not, in one specific frame. In contrast, the auditory paradigm contains two targets, one harmonic and the other inharmonic. A further complication arises as the target absent condition exists purely to provide a discernible response for the participant, yet this target also contains a harmonic of the entrainment pips (1000 Hz). Furthermore, the target is not primed in a single pip, rather the entire sequence of pips forms the prime. Thus, the auditory priming paradigm should be treated slightly differently. Rather than considering the responses to represent a facilitation of a harmonic, or an inharmonic response based on anticipation of a specific tone, or responses that lag the priming of such a tone – it is suggested that the prime provides a gamma code which establishes a representation of a 500 Hz template, that is rhythmically desynchronised and reset. The details of the prime are coded by RP, and deviations in the response to both harmonics depend on a cross-frequency coupling of the aGBR and a modulating slower theta rhythm, as predicted by the GPAH. All such responses can be considered anticipatory, with the sequence of the pips dictating the salience of the harmonic versus the inharmonic. In real-world instances the inharmonic is more salient as it is contrary to what is expected. In fact, the inharmonic responses have been consistently faster throughout the experiments (and more accurate according to the error data analyses) using this pip arrangement as well as the previous arrangement, with the difference between the speed of these responses serving as a means of estimating empirical significance. Much-studied cortical responses in auditory and in particular music cognition are the early right anterior negativity (ERAN) and the right anterior temporal negativity (RATN) responses, which have peak latencies of around 150-350 ms, post-stimulus onset, both of which are

generated when there has been a violation of the listeners expectancies (see Rohrmeier & Koelsch, 2012, for review). In music this would mean a musical phrase ends with a dissonant⁸ rather than a consonant⁹ chord.

There is a large and growing body of research to date examining thetagamma cross-frequency coupling which supports this theory (Sauseng et al., 2009; Sauseng, Griesmayr, Freunberger, & Klimesch, 2010; Sauseng, Klimesch, Gruber, & Birbaumer, 2008; Fell & Axmacher, 2011; Friese et al., 2013; Mormann et al., 2005). Within the research to date examining theta-gamma cross-frequency coupling, two types of coupling have been identified; phase-amplitude (PAC) and phase-phase (PPC) coupling. The former has been implicated in working memory storage (Belluscio, Mizuseki, Schmidt, Kempter, & Buzsáki, 2012). Lisman and Idiart (1995) presented a neural network model exhibiting nested oscillations which emerge when neural action potentials become concentrated at specific phases of both the high and low frequencies of the coupled oscillations. This model predicts that successive high-frequency oscillations code individual items to be maintained in memory, and in this way all items are stored within subcycles of the slower rhythm. The latter is a much more temporally precise form of coupling and involves phaselocking between single cycles of the higher frequency and a specific phase of the slower frequency. Thus, PAC involves the entire cycle of both frequencies, whereas PPC is confined to extremely precise temporal windows. Both are complimentary phase-based mechanisms which are considered to be independent processes, with different underlying mechanisms and functions (Fell & Axmacher, 2011). PAC results in synchronisation of higher frequencies to the amplitude of the slower rhythm, and is important for working memory storage. However PPC results in phase-locking of the high frequency with a specific phase of the slow frequency, and has been found to increase with load in a working memory task, and even predicts the working memory capacity of an individual (Sauseng et al., 2009). The research findings stemming from the auditory and visual binding experiments discussed so far support the idea that RP is described by PAC, while the GPAH is described by PPC. Given the complexity of the interactions involved and the factors that impact on the

⁸ Dissonance refers to sounds with partials that are not harmonic.

⁽Note: A complex tone is a combination of simple periodic waves (i.e., sine waves). In music these are referred to as partials. Each has its own frequency, amplitude, and phase. Inharmonicity describes the deviation of a partial from the nearest ideal harmonic.)

⁹ Consonance refers to sounds with harmonic partials (integer multiples).

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interpretation of the results, such as the position of the deviant pip and time of target presentation, this line of research is extremely time-consuming, and a more complete picture will require many more iterations and manipulations. Future research should consider the implications of priming on cross-frequency coupling and take care to separate priming effects from process effects.

3 A Temporal Model to Guide Auditory Binding Research

3.1 Introduction

The findings discussed in the previous chapter illustrate the sensitivity of a reaction time (RT) advantage to the target presentation time. By extension, this emphasises the importance of the precision of phase-phase coupling (PPC) with a slower endogenous rhythm, and the effect of return phase (RP) described by phaseamplitude coupling (PAC). However, due to the harmonic structure of the auditory prime it is difficult to separate the effects of priming from the effects of the binding process. Also, a theta frequency as singular as the 6.69 Hertz (Hz) rhythm implicated in a facilitation of synchronous prime responses in visual binding has not been evidenced in the auditory modality. The psychophysical goal of these experiments has been to find the specific temporal and phase conditions required for an invariant response to harmonically primed relations, as the goal of psychophysics, in general, is to establish laws based on invariant properties of the perceptual system. Invariance in perceptual experience reflects invariance in the process that underlies the experience (Stevens, 2017). Therefore, to achieve this goal psychophysical experiments aim to uncover the stimulus conditions required to produce an invariant response. Building on ground-breaking work in this field, and including psychophysical principles such as 'Weber's fraction' (sometimes referred to as Ekman's constant), 'Steven's power law', and 'Teghtsoonian's range of acceptable stimulus intensities' (RAISINs – a subjective dynamic range), Hans-Georg Geißler (1988; 1985) has developed the Time Quantum Model (TQM) based on a taxonomy of the basic units in the structure of mental timing (Geißler, 2009; Stevens, 1957, 2017; Teghtsoonian, 1971; Teghtsoonian & Teghtsoonian, 1997). This taxonomy relates to diverse types of mental timing such as perceived durations, processing epochs, and temporal thresholds. Like Quantum Wave Theory, TQM asserts that mental activity such as perception and cognition are the product of undisturbed superposition and selective amplification of the wave-like information carriers. More specifically, TQM describes an oscillatory mechanism within which are nested oscillations with time periods (T) that are related to a smallest quantal time unit (Q_0 = 4.57). The superposition of these cyclic carriers of different, yet related, periods consequently reaches a coherence limit (M = 30), related to the range of frequency

durations in the nested oscillations. Therefore, each processing epoch is dynamically flexible depending on the task, as *M* is determined by the oscillation with the shortest period duration within an oscillatory mechanism (Geißler, Schebera, & Kompass, 1999).

There are four main hypotheses (H*n*) upon which this taxonomy is based (Geißler, Vangas, Svegzda, Bliumas, Stanikunas, & Vaitkevicius, 2012; Geißler, 2009). A short description of each is as follows:

H1: The range hypothesis ($M \cong 30$): Internal representations of time form ranges, such that the ratio of the largest to the smallest possible value within a given range is a constant $M \cong 30$. Each range represents a quantal structure.

H2: Ekman's constant ($c \approx 1/30$) – The dispersion-progression hypothesis: For judged magnitudes of internal representations along a full quantal range, the Weber fraction has a constant value $c \approx 1/30$.

H3: Coherence limit $N \ (1 \le N)$: Greatest common denominators (GCDs) increase in linear progression with range size, according to H1. This hypothesis assumes a modular property of internal representations, whereby the possible periods are integer multiples (N) of modular units (Q_q) which in turn are integer multiples (q) of an elementary smallest unit (Q_0 – the value of which is 4.57milliseconds (ms) such that $Q_0 \le Q_q$, ($1 \le N$).

H4: The Double Constraints hypothesis $(1 \le N \le M)$: Admissible processing cycles are both integer multiples of the respective operative modular cycles, and integer fractions of larger multiples, if there are any.

The Principle of Progressive Constraining extending from these hypotheses, asserts that hierarchic phase coupling requires a production rule that grants uniformity, is recursive (each term is determined by applying a formula to preceding terms) and produces results that are maximally dense. The requirements of recursive generation and maximum density reduces the possible set of ranges to R_1 , R_2 , R_4 , R_8 , R_{16} , ... R_x (for R_1 the range is Q_0 to 30 x Q_0 , for R_8 the range is $8Q_0$ to 30 x $8Q_0$, and so forth). These quantal ranges are referred to as "generator sets" (G_1 , G_2 , G_4 , G_8 , G_{16} , ... G_x), with G_1 as the universal generator, as all larger sets represent integer magnifications of G_1 .

Quantal boundaries have been demonstrated to remain stable when applied to RT data acquired through simple stimulus-response, and synchrony priming,

paradigms (Geißler, 2009). The relation between the latter datasets and TQM pertain to the findings for anticipatory coding only, and agreement with statistical analyses rely on the following criteria; (i) priming frequencies involved in facilitating an anticipatory response have a period duration that is a multiple of Q_0 having a value in the range of 4.5-4.65, (ii) the relations between frequencies at different scales (i.e. frequency bands) which interact to provide a facilitatory effect, is not necessarily hierarchical, and (iii) a limit cycle of $32*Q_0$ is assumed (M = 32) (Elliott & du Bois, 2017). According to the findings of this synchrony priming research, the critical frequencies involved in anticipatory coding are 32.25-33.5 Hz, 38-40 Hz, 45.75-46.5 Hz, 53.25-53.75 Hz, 59-60.75 Hz, and 65.75-67.5 Hz. The corresponding period durations are 29.85-31 ms, 25-26.32 ms, 21.5-21.86 ms, 18.6-18.8 ms, 16.46-17 ms, and 14.8-15.2 ms. All frequencies are separated by \cong 7 Hz. When the spectral density of the data was analysed for periodicity, a clear peak was found at 6.69 Hz, thus implying a facilitation of anticipatory coding due to a gamma-theta interaction when the frequencies involved have period durations that fit into a quantal range (R_1) assuming a value of $Q_0 = 4.53$, and M = 32. By this rationale a proposed $Q_0 = 4.53$, due to undisturbed superposition, will reach maximum coherence at $33*Q_0$ presuming systematic coherence decay over 32 cycles (4.53*33 = 144.96), 1000/144.96 = 6.69). The 33 pips per second (pps) pop-out effect found to facilitate a response to an inharmonic in auditory priming closely fits the model also, as a 33 Hz wave has a period duration of 30.3 ms which is close to seven times $Q_0(7*4.53 =$ 31.71). Due to the extremely time-consuming nature of the psychophysical method, this chapter discusses two experiments that investigated the utility of TQM as a guide to the temporal and phase parameters that are optimal for an invariant response to a primed harmonic relation.

For experiments measuring thresholds of stable perceptions of motion, where stimuli are presented with alternating exposure duration (ED), and inter-stimulus interval (ISI) is adjusted downwards, there is a period referred to as the zone of transition during which the perception of motion is meta-stable. During this period there are competing time-slots for motion breakdown and given the constant speed of adjustment of the ISI, there is only one factor affecting uniformity – that is the number of alternative realisations of the options, i.e., the prominence values ($\Pi(N)$). According to the Principle of Progressive Constraining all realisations are of equal right across time slots, and thus the time slots are accessed in proportion to their

prominence along the entire range of ISIs. Guided by these principles and hypotheses, TQM describes beta motion in a time-free form, using the following equation: $cISI/Q_0 \ge D/2Q_0 = 30$, a capacity sharing relation whereby the limit M = 30 defines the maximum number of available units that ISI and ED can occupy together (Geißler, 2009). The experiments in this chapter aimed to adapt this equation as a guide to the optimal temporal parameters required to facilitate an anticipatory response to a tone that is inharmonically related to a primed harmonic representation.

3.2 Stimuli

Stimulus generation is as described in the previous chapter. Physically piptrains resemble amplitude modulated (AM) tones, with the number of pips dictating the AM frequency. Unlike the entrainer described in chapter two, the embedded harmonic relations were consistent with the original auditory priming paradigm designed by Aksentijevic, Barber, and Elliott (Aksentijevic et al., 2011), which was a repeated four-pip sequence comprising a deviant 1000 Hz pip followed by three 500 Hz baseline pips. To recap, the target absent (TA) and both the target present (TP) conditions, i.e., the harmonic target present (HTP) and the inharmonic target present (ITP), consisted of a repeated baseline-deviant pip sequence (BDBD; Aksentijevic, Smith, & Elliott, 2014), consistent with the description given in chapter two. The pip-train in the HTP condition repeated between a baseline pip carrying 1000 Hz and a deviant pip carrying 2000 Hz and was therefore harmonically related to the entrainer (the target deviant frequency was an octave higher in pitch compared to the primed deviant frequency and the fourth harmonic of the primed baseline frequency). The ITP target pip-train alternated between a baseline pip carrying 1000 Hz and a deviant carrying 2400 Hz and was thus inharmonically related to the entrainer carrier tones (the target deviant frequency was an octave plus a minor third higher in pitch compared to the primed deviant frequency).

3.3 Apparatus

Experimental trial and stimulus generation were controlled by a Dell Latitude E5450, Intel Core i7-6700HQ 2.60 GHz laptop. Sound stimuli were presented electronically via Chronos PST-101600, a multifunctional response and stimulus device, which also measured RT, offering an RT resolution of <1 ms, achieved by

preloading the sounds onto the Chronos box. Experiments were programmed in E-Prime 2.0 (Professional, SP2, build 2.0.10.356) (Schneider, W., Eschman, A., & Zuccolotto, 2002).

3.4 General methods

For a full description of the procedure for both experiments, please read section 2.4 General Methods in chapter two. Importantly, both experiments were conducted in a sound-attenuated chamber, with a background noise level < 30 dB SPL, located in the School of Psychology building at the National University of Ireland, Galway. Ambient lighting was kept at a constant low level. The stimuli were presented diotically via Sennheiser HD 25 headphones. Stimulus intensity, measured using a Gold Line sound level meter (model SPL120), was kept at an average 50 dB sound pressure level (SPL); A-weighting; average error 3 dB SPL, to achieve a stable steady state response (SSR) and yet avoid aural harmonics (Aksentijevic et al., 2011). Experimental sessions began with a practice block of 20 trials which were randomly selected from a list of all possible condition combinations, with no repeat allowed following the list-reset after each trial. Sessions were run on different days and lasted between 40 minutes and one hour. Ethical approval was obtained for this study from the National University of Ireland Galway Research Ethics Committee. A repeated measures design was used. The factor target was again asymmetrical with two levels – target absent (TA) and target present (TP), and within this latter condition were two levels of harmony – harmonic target present (HTP) and inharmonic target present (ITP). Therefore, trials were proportioned in the ratio: TA = 50%, TP = 50% (HTP = 25%, ITP = 25%).

3.4.1 Statistical Analyses. RT data were corrected and analysed as described in chapter two, and error reports for each experiment are included in the results section.

3.5 Experiment 1

3.5.1 Research question. Geißler (2009) developed the equation $ISI/Q_0 + ED/2Q_0 = 30$ as a TQM-related description generalising breakdown of Beta and Gamma motion. Taking account of the pop-out effect found to occur for responses to inharmonic tones at an entrainment rate of 33 pps and, based on the doubling cascade – it is proposed to extend the capacity sharing relation to 30 x 4Q₀, R₄. Thus,

the maximum number of available units that ISI and ED together can occupy is extended to 120; (ISI/Q₀ + ED/2Q₀ = 120) = (ISI/4Q₀ + ED/2*4Q₀ = 30). The popout effect at 33 Hz occurs at an ISI of 100 ms following a constant entrainment period of 1000 ms – taking Q₀ to equal 5 ms fits the equation 100(ISI)/4*5(4Q₀) + 1000(ED)/2*4*5(2*4Q₀) = 30. Thus, this research question hypothesises that the equation ISI/Q₀ + ED/2Q₀ = 30 can be adapted for 30 x 4Q₀ (R₄) based on the doubling cascade. It is expected that this ratio of entrainment and ISI will facilitate a speeded response to inharmonic targets at critical frequencies. Therefore, the effects of target presentation will be examined when presented in phase with the beginning of the 7th oscillation of a 7.29 Hz frequency (which has an oscillatory duration of 30 times Q₀ = 4.57 ms (137.1 ms). For Q₀ = 4.57, according to ISI/4Q₀ + ED/2(4Q₀) = 30, if ISI = 137 and ED = 822, then (137/4(4.57)) + (822/2(4(4.57))) = 7.5 + 22.5 = 30.

3.5.2 Sample and design. Sixteen participants recruited in the Galway area took part in this study. Four were left-handed (male n = 7, female n = 9, age M = 21.25 years, SD = 2.29). Seven participants did not have any experience playing an instrument. Nine had varying levels of training, ranging from 5 - 14 years in duration (M = 8.8 years), and all but two had not played an instrument in the last two years. All participants reported normal hearing and provided informed consent.

A repeated measures design was used with two factors, rate (11 levels; 28 - 38 pps) and target (asymmetrical as described for all previous experiments). The entrainer pip-train stimulus was presented for a constant period of 822 ms, referred to as exposure duration, and ISI was kept constant at 137 ms. Participants were presented with 30 trials per condition which resulted in 1320 trials per participant, ($11 \ge 2(2) \ge 30 = 1320$). As described for experiments 4 and 5 in chapter two, at the end of each block, the experimental programme presented the first two trials, any error trials, and the trial directly proceeding an error trial, again. Thus, the number of repetitions were reduced. These trials were presented over two sessions, on separate days, in blocks of ~ 44 trials (each session was approximately 50 minutes in duration and covered 660 trials). Individual sessions began with a 15 – trial practice block. Experimental conditions were completely randomised within and between blocks. The dependent variable was RT.

3.5.3 Results. An 11 x 2(2) repeated measures ANOVA was conducted on the exponents of the means of log-transformed RT data (corrected RT data) to evaluate the effect of presentation rate (28, 29,...38 pps), and harmonic relations (TA and TP (including HTP and ITP targets) on RT responses, when the timing of exposure duration of the entrainer, and the timing of target presentation were determined according to a capacity sharing relation derived from Hans Geißler's TQM (Geißler, 2009). Significant main effects were found for target, and rate; $F_{(1,1)}$. $_{16.649} = 4.38, p = .049, \eta_p^2 = .23, F_{(10, 150)} = 6.09, p < .001, \eta_p^2 = .29$ respectively. The main effect for target was due to slower RTs to HTP targets compared to both ITP and TA targets (HTP-TA difference; MD = 27.67, SE = 11.27, p = .027, and HTP-ITP difference; MD = 12.14, SE = 3.03, p = .001), while the effect for rate was due to generally faster overall response times as entrainment rate increases. A second ANOVA (11 x 2 repeated measures) was conducted on the TP data only to evaluate the effect of presentation rate (frequency), and harmonic relations (ITP and HTP targets) on RT responses, to test the principle hypothesis that faster responses to inharmonic targets at specific frequencies would be evidenced following a combined entrainer exposure and ISI duration, when the ratio relation is calculated according to the equation $ISI/4*Q_0 + ED/4*2Q_0 = 30$. Significant main effects were found for harmony, and rate; $F_{(1,15)} = 16.05$, p = .001, $\eta_p^2 = .52$, $F_{(4.9,73.55)} = 4.75$, p = .001, η_p^2 = .24 respectively. The main effect for harmony was due to faster RTs to ITP targets (MD = 12.14, SE = 3.03, p = .001), while the effect for rate was again due to slower response times at lower entrainment frequencies, i.e. RTs at 28 pps were significantly slower than those at 33 and 34 pps (p = .013, and p = .035 respectively), RTs at 29 pps were significantly slower than those at 34 pps (p = .003), and at 30 pps RTs were significantly slower than those at 36, 37, and 38 pps (p = .013, p = .011, and p = .034 respectively).

Rate	Harmony		Mean Difference (2-1)	Std. Error	Sig. ^b	95% Confidence Interva for Difference ^b	
pps	2 = HTP, 1 = ITP		× ,			Lower Bound	Upper Bound
28	2	1	.168	8.960	.985	-18.930	19.266
29	2	1	9.581	7.337	.211	-6.056	25.219
30	2	1	12.467	8.007	.140	-4.598	29.533
31	2	1	7.730	8.001	.349	-9.323	24.783
32	2	1	20.696*	8.416	.027	2.758	38.634
33	2	1	17.737	9.251	.074	-1.980	37.454
34	2	1	13.602*	5.749	.032	1.348	25.856
35	2	1	20.613*	7.091	.011	5.500	35.726
36	2	1	14.063	7.159	.068	-1.197	29.323
37	2	1	16.534*	7.363	.040	.841	32.228
38	2	1	.306	8.655	.972	-18.141	18.753

Table 3.1. Study 2, Experiment 1, Pairwise Comparisons: Rate by Harmony.

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

2 = HTP; harmonic target present.

1 = ITP; inharmonic target present.

A pairwise comparison revealed that ITP RTs were significantly faster than HTP RTs at 32, 34, 35, and 37 pps (p = 0.027, p = .032, p = .011, and p = .04 respectively). The results, therefore, do not allow the null hypothesis to be rejected conclusively owing to the absence of an interaction effect highlighting one or more entrainment rate(s) facilitating a faster ITP response found to be significant compared to all other rates.

3.5.4 Error analysis. The percentage error reported was 6.1%. The arcsine of the square root of the proportion of errors for each condition were analysed and a significant main effect of target was found due to fewer ITP errors compared to HTP errors (p = .006); $F_{(2, 30)} = 6.34$, p = .005, $\eta_p^2 = .3$. This higher rate of accuracy in ITP response suggests speed-accuracy is not a likely factor in the ITP advantage found in the harmony analysis.

3.5.4 Discussion. While a facilitation of inharmonic responses was found generally rather than at specific rates of entrainment, it is only at 32 pps that the trend in the data for ITP and HTP RTs as a function of rate deviates, illustrating a pop-out effect (see figure 3.1). Of interest also is the near identical response times for both harmonic and inharmonic targets at 28 and 38 pps (p = .985, and p = .972 respectively), especially given that the period durations for both these frequencies,

and 32 Hz, shares an almost identical relation to Q0 ((1000/28 = 26.85)/4.57 = 7[.81]; (1000/38 = 36.44)/4.57 = 5[.76]; (1000/32 = 30.69)/4.57 = 6[.84]). The entrainment rates 31 and 36 pps shared the closest relation to Q0 (-0.3 off 7Q0 and - 0.09 ms off 6Q0 respectively), and yet an effect was not elicited under these entrainment conditions.



Figure 3.1. TQM 1; graphed harmony RT data.

Illustration of the RT responses to both harmonic (circle legend) and inharmonic (diamond legend) targets (*y*-axis), mapped over the entrainer at the time of target presentation, when aligned with the beginning of a 7.29 Hz wave cycle (i.e. zero phase-lag). The top *x*-axis represents the position of the target in the oscillatory trace of the entrainer, while the bottom *x*-axis illustrates the number of oscillatory cycles completed.



Figure 3.2. TQM 1; priming as a function of return phase.

Illustration of the strength of the effect of the prime – calculated as the difference between the RTs (y-axis = HTP-ITP RTs) for each level of harmony at the same level of entrainment (legend labels) as a function of the RP for the pip sequence (bottom x-axis), given target presentation aligned in phase with a 7.29 Hz rhythm, with zero phase-lag. The middle x-axis defines the last fully presented pip (LFPP). The top x-axis is a measure of the completion of the pip represented on the bottom axis (CNP; completion of next pip).

The magnitude, or strength, of the priming effect, is measured as the difference between HTP and ITP RTs; the greater the difference, the greater the strength of priming. When this difference measure is graphed over the RP of the prime clear peaks can be seen in the data at 30, 32, 33, 34, 35, and 37 pps, as illustrated in figure 3.2.



Figure 3.3. TQM 1: Illustration of phase relations.

Illustration of the phase relation between the entrainment frequencies which produced a significant effect of priming, i.e., 32, 34, 35, and 37 pps, and a 7.29 Hz theta wave, at target presentation time (959 ms: ISI (137 ms) + ED (1822 ms) = Total 959 ms). The time of target presentation is illustrated in seconds on the *x*-axis and the frequency amplitude on the *y*-axis.

At the time of target presentation, all these frequencies align in phase very close to an angle of 270°, particularly 32 Hz. Of these entrainment rates, ITP RTs were found to be significantly faster at 32, 34, 35, and 37 pps. The phase relation between these entrainment frequencies and a 7.29 Hz wave at target presentation time is illustrated in figure 3.3. Interestingly there does not appear to be any effect attributable to RP (see figure 3.2). It is tentatively suggested that temporal constraints imposed by the capacity sharing relation has an effect on responses to inharmonic tones that is independent of the prime.

3.6 Experiment 2

3.6.1 Research question. Given the results of the previous experiment demonstrating greater magnitudes of priming when targets were presented with a phase-lag of between 180° and 270° in relation to the entrained oscillatory activity (see figure 3.3), this experiment further extended the capacity sharing relation to 8x $30Q_0$ to examine the effect of target presentation at the negative peak of a 7.29 Hz wave, whose period duration matches 30Q = 137 ms. Thus, the parameters for entrainment and target presentation time are based on ISI/8Q₀ + ED/2(8Q₀) = 30

coinciding with target presentation at the negative peak $(270^{\circ} \text{ phase angle})$ of a 7.29 Hz wave; therefore ISI = 171 ms and exposure duration for the entrainer = 1852 ms; (171/(8(4.57)) + (1852/(2(8(4.57)))) = 4.67 + 25.33 = 30. This places the target at a time point when all phases between 30 and 37 Hz also align at a phase angle $\cong 270^{\circ}$. It is hypothesised this ratio of entrainment and ISI will facilitate a speeded response to inharmonic targets at critical frequencies.

3.6.2 Sample and design. Fifteen participants recruited in the Galway area took part in this study. Two were left-handed (male n = 6, female n = 9, age M = 30 years, SD = 7.71). Twelve participants did not have any experience playing an instrument. Three had varying levels of training (M = 10.66 years duration), however, all three had not played an instrument in the last ten plus years. All participants reported normal hearing and provided informed consent.

A repeated measures design was used with two factors, rate (16 levels; 30 - 45 pps) and target (asymmetrical as described for all previous experiments). The entrainer pip-train stimulus was presented for a constant period of 1852 ms, referred to as exposure duration, and ISI was kept constant at 171 ms. Participants were presented with 30 trials per condition which resulted in 1920 trials per participant, ($16 \ge 2(2) \ge 30 = 1920$). As described for experiments 4 and 5 in chapter two, at the end of each block, the experimental programme presented the first two trials, any error trials, and the trial directly proceeding an error trial, again. Thus, the number of repetitions were reduced. These trials were presented over three sessions, on separate days, in blocks of ~ 32 trials (each session was approximately 50 minutes in duration and covered 640 trials). Individual sessions began with a 20 - trial practice block. Experimental conditions were completely randomised within and between blocks. The dependent variable was corrected RT.

3.6.3 Results. A 16 x 2(2) repeated measures ANOVA was conducted on corrected RT data to evaluate the effect of presentation rate (30, 31, 32, ...45 pps), and harmonic relation (target) on RT responses, when the timing of exposure duration of the entrainer, and the timing of target presentation were determined according to a capacity sharing relation derived from Hans Geißler's TQM (Geißler, 2009). Significant main effects were found for target, and rate; $F_{(1.4, 19.56)} = 6.41$, p = .013, $\eta_p^2 = .31$, $F_{(15, 210)} = 5.43$, p < .001, $\eta_p^2 = .28$ respectively. The main effect for target was due to slower RTs to HTP targets compared to ITP targets only

(HTP-ITP difference; MD = 16.14, SE = 3.5, p = .001, and HTP-TA difference; MD= 14.95, SE = 6.37, p = .1), while the effect for rate was due to a general decrease in overall response times as entrainment rate increases. The interaction effect between target and rate was significant; $F_{(30, 420)} = 1.89$, p = .004, $\eta_p^2 = .12$, due to TA responses that were similar to ITP responses at all levels of rate, except 34 and 41 pps, when responses were much slower, and closer to HTP RTs at the same rate of entrainment. A second ANOVA was performed on the TP data only to test the main hypothesis that faster responses to inharmonic targets at specific frequencies would follow when the ratio relation between entrainer exposure and ISI duration is calculated according to the equation $ISI/8Q_0 + ED/2*8Q_0 = 30$, at which point there is a phase-lag of 270° with a 7.29 Hz theta rhythm at target presentation time. Significant main effects were found for harmony, and rate; $F_{(1, 14)} = 21.31$, p < .001, $\eta_p^2 = .6$, $F_{(15, 210)} = 4.57$, p < .001, $\eta_p^2 = .25$ respectively. The main effect for harmony was due to faster RTs to ITP targets (MD = 16.14, SE = 3.5, p < .001), while the effect for rate was due to slower response times at 30 pps, compared to 38 and 39 pps (p = 0.013 and p = 0.017, respectively), at 31 pps compared to 37, 41, and 44 pps (p = 0.023, p = 0.036, and p = 0.007, respectively), and at 33 pps compared to 40 pps (p = 0.014), again reflecting a general decrease in overall response times as entrainment rate increases.

Rate (pps)	Harmony		Mean Difference (2-1)	Std. Error	Sig. ^b	95% Confidence Interval for Difference ^b	
	2 = HTP, 1 = ITP					Lower	Upper
						Bound	Bound
30	2	1	2.789	7.375	.711	-13.029	18.607
31	2	1	19.629*	8.432	.035	1.544	37.713
32	2	1	4.244	4.764	.388	-5.973	14.461
33	2	1	23.109*	7.741	.010	6.506	39.711
34	2	1	8.438	6.235	.197	-4.935	21.811
35	2	1	24.051*	6.016	.001	11.148	36.953
36	2	1	23.257*	6.612	.003	9.075	37.438
37	2	1	17.981*	7.671	.034	1.528	34.433
38	2	1	17.175*	7.540	.039	1.005	33.346
39	2	1	20.511*	9.310	.045	.544	40.479
40	2	1	12.039	10.068	.252	-9.554	33.631
41	2	1	18.783*	6.173	.009	5.544	32.022
42	2	1	13.423	6.363	.053	225	27.070
43	2	1	10.968	6.708	.124	-3.420	25.356
44	2	1	24.997*	5.777	.001	12.606	37.387
45	2	1	16.789*	7.462	.041	.784	32.794

Table 3.2. Study 2, Experiment 2, Pairwise Comparisons: Rate by Harmony.

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

2 = HTP; harmonic target present.

1 = ITP; inharmonic target present.

A pairwise comparison revealed that ITP RTs were significantly faster than HTP RTs at 31, 33, 35, 36, 37, 38, 39, 41, 44, and 45 pps (p = 0.035, p = .01, p = .001, p = .003, p = .034, p = .039, p = .045, p = .009, p = .001, and p = .041, respectively). Again, the absence of an interaction effect highlighting a significantly faster ITP response at one or more entrainment rates compared to all other rates, does not allow the null hypothesis to be rejected.

3.6.4 Error analysis. The percentage error reported was 5.64%. Again, the arcsine of the square root of the proportion of errors for each condition were analysed. A significant main effect of target was found due to a higher error rate for HTP targets compared to both the TA and ITP error rate (HTP-TA p = .007, HTP-ITP p = .001); $F_{(2, 28)} = 15.33$, p < .001, $\eta_p^2 = .52$. A significant interaction effect revealed an overall higher error rate in responses to HTP targets, with fewer ITP errors occurring at lower entrainment rates and fewer TA errors occurring at higher entrainment frequencies ($F_{(30, 420)} = 1.57$, p = .03, $\eta_p^2 = .1$). This interaction effect was driven by the error rate for TA responses and did not remain when the arcsine-transformed TP (ITP and HTP) error means were analysed ($F_{(15, 210)} = .91$, p = .55,

 $\eta_p^2 = .06$). Again, greater accuracy in ITP responses argues against a speed-accuracy trade-off as an explanation for the ITP advantage in the harmony analysis.

3.6.4 Discussion. The expected interaction effect for an ITP advantage at one or more entrainment rate(s) having a phase angle of ~ $270^{\circ}(248^{\circ} - 306^{\circ})$ at target presentation time, compared to the other entrainment frequencies was not found. However, overall there were sixteen rates of entrainment employed, across ten of which there was a significant difference between ITP and HTP RTs, with a borderline significant difference at 42 pps also (p = .053). This suggests that the deviations in the trend of ITP and HTP data as a function of entrainment rate occur when the difference is not significant.





Illustration of the strength of the effect of the prime – calculated as the difference between the RTs (y-axis = HTP-ITP RTs) for each level of harmony at the same level of entrainment (legend labels) as a function of the RP for the pip sequence (bottom x-axis), given target presentation aligned in phase with a 7.29 Hz rhythm, at the negative peak (phase angle of 270°). The middle x-axis defines the last fully presented pip (LFPP). The top x-axis is a measure of the completion of the pip represented on the bottom axis (CNP; completion of next pip).

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At 30, 32, 34, 40 and 43 pps entrainment the responses do not differ statistically (p = .71, p = .39, p = .2, p = .25, and p = .12 respectively). Across all the other entrainment conditions the responses to both harmonics decreased with increasing entrainment rate, with responses to inharmonics consistently maintaining a 17 to 25 ms advantage (figure 3.4).



Figure 3.5. TQM 2; graphed harmony RT data.

Illustration of the RT responses to both harmonic (circle legend) and inharmonic (diamond legend) targets (y-axis), mapped over the entrainer at the time of target presentation, when aligned in phase with a 7.29 Hz wave cycle at the negative peak (phase angle of 270°). The top x-axis represents the position of the target in the oscillatory trace of the entrainer, while the bottom x-axis illustrates the number of oscillatory cycles completed.

Visual inspection of the data in figure 3.5 suggests that this is due to faster HTP responses at 30, 32, and 34 pps, while the absence of a significant difference at 40 and 43 pps appears to be due to slower ITP responses. Again, these deviations in trends do not appear to be explained by RP (figure 3.4), thus supporting the suggestion that the constraints imposed by TQM's capacity sharing relation

influence auditory binding. When the gamma-theta oscillator is phase-aligned at the negative peaks during the 30, 32, and 34 pps conditions, an anticipatory response to a harmonic tone is facilitated. However, target presentation aligned at the negative peak of the 7.29 Hz theta wave when the participating gamma frequencies during the 40 and the 43 pps entrainment conditions are not aligned, results in a reduced saliency of the unexpected inharmonic tone. Thus, it is suggested that phase alignment between primed gamma frequencies and a 7.29 Hz theta wave at the negative peak facilitates a harmonic response, and when the primed gamma frequencies are not aligned at the negative 7.29 Hz peak, responses to the unexpected inharmonic tones are disturbed.

3.7 General Discussion

Previous research has manipulated target presentation time to coincide with a specific point in the phase of an endogenous theta rhythm to examine a facilitation effect that is dependent on this phase interaction, presupposing a zero phase-lag between this rhythm and entrainer onset. The rationale for this assertion is that theta oscillations undergo phase-reset, thus facilitating synchronisation between gamma and theta activity. Furthermore, gamma-theta oscillators thus generated are considered the neural mechanism involved in matching an expected representation to an external visual stimulus (Sauseng et al., 2008). When there is an effect of priming that is also dependent on this phase relation it is inferred that interactions between the entrained gamma frequencies and the theta rhythm enhance binding mechanisms by providing a code in advance. Thus, corresponding presentation rates are considered critical frequencies in the binding process. The second experiment reported represents the first examination of an effect of target presentation time when the oscillatory cycles of both the auditory gamma-band response (aGBR) and an endogenous theta wave were mutually aligned in phase (at a phase angle of 270°) – interestingly this has led to results which rely less on RP and more on general gamma-theta interaction.

The inferences suggested by the findings presented here, again, are derived from the deviations in RT trends rather than significant differences in responses to target sounds on the basis of their harmonic relation to the primed representation. The results from the first experiment indicate that the critical influence on responses was the phase angle of the entrained gamma frequency at the time of target

presentation, whereby there was a significant difference between HTP and ITP RTs, highlighting faster ITP responses for targets at entrainments aligned in phase between 180° and 270°. Subsequently, a 270° phase-lag between target presentation and a 7.29 Hz theta rhythm (based on a period duration equal to 30Q₀) demonstrated a facilitation of HTP responses when the entrainment frequencies were also phasealigned at the negative 7.29 Hz peak, while there was a disruption to the usually more salient ITP responses when the entrainment frequencies were not phase-aligned to the negative peak. There are a couple of interesting points to be made based on the analysis of this experiment. Firstly, it is usually the case that TA RTs are either faster overall, or at least close to ITP RTs, even though the carrier frequency is 1000 Hz for all pips in the TA condition and is thus harmonically related to the prime. This efficiency of TA responses is due to the flat pitch of the amplitude modulated tones in the TA pip-train making it the easiest target to discriminate. In this experiment however, there was an unusual interaction effect due to TA responses that were much slower (and thus closer to HTP RT times) at 34 and 41 pps entrainment rates (separated by 7 Hz), suggesting a modulation due to a phase-amplitude coupling (PAC) that provides a consistent representation of the harmonic structure. Secondly, consistent across both experiments, the graphed data illustrating the HTP-ITP RT differences as a function of the targets position in the RP of the four-pip prime, highlights the lack of an influence of RP (see figures 3.2, and in particular 3.4). However, there appears to be a common factor for both the facilitated HTP RTs and the disrupted ITP RTs which has not previously been observed – entrainment frequencies eliciting the effect in both cases are separated by 2 to 3 Hz. This could imply an interaction with delta band frequencies.

Recent research supports the theory that superimposed theta and delta oscillatory activity trigger ERP components associated with many tasks (Harper, Malone, & Bernat, 2014). Memory-related changes in theta and delta induced band power (IBP) and an increase in the positive ERP known as the P300, associated with remembered items (as opposed to new distractor items), have been demonstrated to be functionally related. Importantly the P300 ERP elicited during this memory task was found to be generated by sub-delta oscillatory activity (Klimesch, Doppelmayr, Schwaiger, Winkler, & Gruber, 2000). This relation can be explained when it is considered that delta contributes a sustained positive response which boosts the polarity shift from the negative N200 deflection to the positive P300 deflection

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caused by a rapid rise and fall in theta oscillatory activity (Harper et al., 2014). Regarding the current paradigm and auditory task, enhanced theta activity has been demonstrated to be associated with prediction, i.e., when a prime accurately predicts a response, whereas delta activity increases when there is uncertainty - and it is a sustained oscillatory response, reflecting increased attention (Dikker & Pylkkänen, 2013). Kirmizi-Alsan et al. (2006) examined the involvement of theta and delta activity on two frontal executive tasks, one requiring inhibition of a response on some trials (Go/NoGo, (GNG)) and the other requiring a response on every trial (a continuous performance task, (CPT)). The findings highlight the involvement of theta in response inhibition and delta with sustained attention (Kirmizi-Alsan et al., 2006). The task undertaken in the experiments discussed here demanded both sustained attention, as a response was required following every trial, and prediction based on a primed harmonic representation. Therefore, perhaps the predicted harmonic response is facilitated when the entrained gamma frequencies and a theta oscillation of 7.29 Hz are phase-aligned at the negative peak, while the inharmonic response is disrupted if these frequencies are not phase-aligned.





Illustration of the phase position, when target presentation time is aligned at a 270° phase angle for a 7.29 Hz theta rhythm, for frequencies corresponding to the entrainment conditions which resulted in an advantage for HTP responses, i.e., 30, 32, and 34 pps, and a disruption of ITP responses, i.e., 40 and 43 pps. Gamma frequencies 30, 32, and 34 Hz were mutually aligned at a 270° phase angle (red, blue,

and green legends), while target presentation coincides with a 0° phase angle with 40 and 43 Hz (cyan and magenta legends). Target presentation time was 2023 ms post entrainer onset: ISI (171 ms) + ED (1852 ms) = Total 2023 ms. Also illustrated is a 2.43 Hz delta wave; delta is considered to be functionally associated with sustained attention, and in this capacity, it is hypothesised here to interact with theta and gamma, thus selecting between gamma frequencies approximately separated by this period duration as feedforward servers carrying stimulus input and prediction errors. The time of target presentation is illustrated in seconds on the *x*-axis (time, in seconds), and the frequency amplitude on the *y*-axis.

At the same time, a dissociated delta band oscillatory process could be responsible for a ~ 2 Hz shift between the gamma frequencies expediting the effect. If the theta oscillation is presumed to have a period duration equal to $30Q_0$ (137.1 ms => 7.29 Hz), then a related but separable delta oscillation could have a period duration of 90Q₀ (411.3 ms), corresponding to 2.43 Hz, which would match the frequency separation illustrating the harmonic facilitation and inharmonic disruption when the ITP and HTP RT data is mapped as a function of entrainment rate (figure 3.5). When these entrained gamma frequencies, a 7.29 Hz theta frequency, and a 2.43 Hz delta frequency, are all graphed at target presentation time, the delta wave is also in the negative peak period. While 30, 32, and 34 Hz are mutually phase-aligned with the theta wave at a 270° phase angle, 40 and 43 Hz are phase-aligned at an angle of 0° (see figure 3.6). It is suggested that based on the trends in the data, a PAC between the entrained gamma frequencies and a sustained 2.43 Hz delta oscillation, with a period duration three times that of the 7.29 Hz theta oscillation, maintains a representation of the harmonic structure, thus predicting a harmonic target. This gamma-delta PAC also provides the focused attention required to make a quick response under uncertain conditions. In conjunction with this activity, a superimposed PPC between the gamma frequencies and a 7.29 Hz theta rhythm determines the strength of inhibition of responses to targets that do not meet these expectancies (deviant inharmonics). When the gamma frequencies selected via the gamma-delta PAC, and a 7.29 Hz theta wave, are phase-aligned at the negative peak, response inhibition is improved.

The findings illustrate auditory binding related events that are independent of the primed harmonic sequence itself, i.e., the trace of the prime does not seem to

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affect the facilitation or disruption of the RT responses, rather the frequency related phase interactions appear to be the contributors of these effects. Thus, it is suggested that TQM provides a temporal guide by which the parameters of the dynamics involved in auditory binding can be further investigated. Future research should explore these frequency and phase relations further, using TQM as a temporal guide. Importantly convergence between these behavioural findings and activity at the cortical level should be examined.
4 Functional Differences in the Neural Substrates of Auditory Cognition as a Consequence of Music Training.

4.1 Introduction

Music perception relies on several cognitive processes, including auditory scene and acoustic analyses to decode the acoustic information, auditory memory, processing of musical syntax and semantics, and extends to stimulating pre-motor representations of action (Koelsch, 2011). Additionally, multimodal integration and action are necessary for musicians when playing, while performing in a group further requires social cognition. In cognitive psychology, music cognition is the area of research involved in determining the cortical processes underlying music perception (Justus & Bharucha, 2002). The first chapter of this thesis focused on the importance of anticipatory/predictive coding for cognitive processes in general – the temporal dynamics of the interactions between fast gamma carriers of stimulus information and slower endogenous rhythms sub-serving top-down stimulus representations generates the anticipatory code necessary to predict change, and guide behaviour. Music performance requires the precise timing of several hierarchically organised actions, and exact control over pitch interval production, realised through a diverse network of effectors (efferent neurons) determined by the instrument being played (Zatorre et al., 2007). A corollary of this is that expectation and prediction (reliant upon temporally accurate anticipatory coding) are necessary for music perception (Rohrmeier & Koelsch, 2012). In fact, it has been demonstrated that interactions between posterior auditory cortices and premotor cortices mediate the cognitive representations required for feedforward and feedback information during music performance and perception, specifically through the emergence of metricality (higher-order temporal organisation) from the temporal predictions this system facilitates (Zatorre, Chen, & Penhune, 2007). Consequently, there is a privileged link between the auditory and motor systems in the cortex that is not present between the visual and motor systems. Thus, music has the ability to drive metrically organised, rhythmic, motor behaviour which visually rhythmic information does not. People tap their feet to a musical beat, but they do not tap their feet to a bouncing ball (Zatorre et al., 2007). Music and music-related behaviour, including dance, is considered to have involved, and simultaneously supported, the evolution of important social

behaviours, such as communication, social cohesion and cooperation (Cross & Morley, 2008; Koelsch, 2011). These auditory-motor interactions are not confined to musicians; however, highly trained musicians turn this natural ability into a skill of the highest order, performing complex movements with absolute temporal precision (Chen, Penhune, & Zatorre, 2008).

Auditory-motor feedforward interactions relay information from the auditory system to the motor system to influence motor behaviour. It has been demonstrated experimentally that these feedforward prediction errors provide information to correct behaviour. For example, rhythmic auditory stimuli have been demonstrated to improve the ability to walk in patients with Parkinson's disease, and acute stroke victims (Mcintosh, Brown, Rice, & Thaut, 1997; Thaut, Mcintosh, & Rice, 1997). Auditory-motor feedback interactions are particularly important for music production, as the performer must continuously update predictions. To convey the metrical structure and to create the appropriate musical expectations essential in music performance, temporal precision is critical, and so also is the ability to correct errors via real-time auditory feedback (meaning at the same rate and time as the event is unfolding). For instance, the variability of pitch on a violin requires continuous control, involving precise appropriately timed motor adjustments, and therefore performance relies on auditory feedback. When this feedback is blocked through experimental manipulation using sound delays and distortions, performance is significantly affected. Asynchronous feedback disrupts the timing of events, but pitch distortion affects the selection of appropriate actions but not the timing of those actions (Pfordresher, & Palmer, 2006). These findings suggest that both movement in music production and the perception of music depend on the feedforwardfeedback predictive coding required to continually update mental auditory representations. Thus auditory-motor system connectivity can be considered the neural substrate of these representations.

Auditory scene decoding begins in the superior olivary complex and the inferior colliculus. At the earliest stages, projections from the dorsal cochlear nucleus to the reticular formation elicit a startle-reaction in response to loud noises with a sudden on-set, and furthermore, before any acoustic information reaches the auditory cortex (AC), hyperarousal (fight-or-flight response) is initiated within the inferior colliculus. Additionally, the brains sensory and motor signal relay centre, the thalamus, in particular the medial geniculate nucleus (auditory thalamus) while

projecting auditory signals mainly to the auditory cortex, also sends the information to the amygdala and medial orbito-frontal cortex. Importantly, the dorsal nucleus of the inferior colliculus is believed to receive more descending than ascending projections from diverse auditory cortical areas (Koelsch, 2011). Despite earlier encoding of specific acoustic attributes, the processing of fine-grained information of complex sounds is conducted in the primary auditory cortex (A1). Thus, the transformation of acoustic features into auditory objects mainly occurs in A1, in preparation for higher order conscious abstract processing.

Regarding functional hemispheric differences, the left AC has a higher temporal resolution while the right AC has a higher spectral resolution, which results in right hemispheric weighting for tonal processing (Koelsch, 2011; Zatorre et al., 2007). Anatomically the auditory cortex comprises a hierarchical system emerging from the primary auditory cortex (A1). Ventral pathways extend from A1 within the temporal neocortex, and possibly a second ventral stream projects anteriorly along the superior temporal gyrus (STG). It is considered these pathways are involved in time-independent, invariant auditory object properties, such as timbre, thus less related to motor systems. The dorsal pathway is more posterior, extends to parietal areas, and is thought to track changes in spectral energy across time (Zatorre et al., 2007). This pathway is therefore relevant for time-dependent events such as spatial processing and understandably projects to motor areas. Auditory-motor interactions have been examined in non-musicians using electroencephalography (EEG), and when there is a direct learned mapping between action and sound, i.e. when the nonmusicians subsequently listened to trained melodies, significant activation in the ventral premotor cortex (vPMC) was observed. Activation was also found to be sensitive to the degree of mapping. Thus, intermediate activation of vPMC is evident when listening to melodies that contain the same notes as the trained melody, but in a different sequence. The vPMC is also activated in response to melodic discrimination and listening to consonant melodies (Brown & Martinez, 2007; Koelsch, Fritz, Yves Cramon, Müller, & Friederici, 2006). Research has shown that musicians have specific anatomical adaptations that correlate with their level of training. For example, a greater volume of auditory cortex is positively correlated with pitch perception ability, and a larger corpus callosum has been found to be negatively correlated with age of commencement of music training (larger volume decreasing as age music training began increases), (Gaser & Schlaug, 2003; Schlaug,

Jäncke, Huang, Staiger, & Steinmetz, 1995). Furthermore, musicians present with greater grey matter concentration in motor cortices, with expert string musicians found to have a larger cortical representation of the digits of the left hand which is negatively correlated with the age of commencement of musical training (larger representations the lower the age training began) (Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995). Activation of motor regions is similar for both musicians and non-musicians, with the exception that musicians show more engagement of frontal cortical areas, possibly due to top-down strategies (Chen et al., 2008). Musicians also demonstrate a more efficient pattern of neural recruitment for simple motor tasks, illustrated by lower levels of activity in motor areas for musically relevant tasks (Hund-Georgiadis & Yves von Cramon, 1999). Research contrasting cortical activity in musicians and non-musicians during listening and performance tasks has evidenced a tight coupling between auditory and motor systems, which is stronger in trained musicians - specifically PMC, supplementary motor area (SMA), and planum temporale (PT), located in the posterior superior temporal plane, involved in the analysis of complex sounds (for review see Zatorre et al., 2007).

Regarding harmonic and melodic prediction, neurophysiological music research has demonstrated that syntactically irregular chords elicit event-related potentials (ERPs) with negative polarity and peak latencies of around 150-350 milliseconds (ms) post-stimulus onset (Rohrmeier & Koelsch, 2012). The early right anterior negativity (ERAN), and the right anterior temporal negativity (RATN) responses are passively evoked responses, elicited by music-syntax violations. The former arises ~150 ms post-stimulus onset in electroencephalography (EEG) recordings and ~ 200 ms in magnetoencephalography (MEG) recordings, while the latter arises ~ 300 ms post-stimulus onset in electroencephalography (EEG) recordings and ~ 350 ms in magnetoencephalography (MEG) recordings, (Maess, Koelsch, Gunter, & Friederici, 2001; Rohrmeier & Koelsch, 2012). Both the ERAN and RATN response are measured as the difference in cortical activation in response to deviant tones compared to a standard tone. The former is elicited by violations in musical syntax, while the latter occurs when the position of an irregular tone structure within a sequence is unknown, or unpredictable. The RATN response is associated with applying syntactical rules (Koelsch & Mulder, 2002). By age five, children demonstrate the ERAN response, and a negative voltage response known as the N5 (~ 500 ms after the stimulus onset), both of which occur in response to

violations to musical expectations consistent with their culture (Jentschke, Koelsch, Sallat, & Friederici, 2008). Thus it is suggested that humans are born with the ability to acquire musical syntax in much the same way as they are born with the ability to acquire language. However, there is a large body of research documenting structural and functional differences in musicians' brains compared to their non-musician peers (Angulo-Perkins et al., 2014; Gaser & Schlaug, 2003; Schlaug et al., 1995; Schneider et al., 2005; Zatorre et al., 2007). Therefore, music perceptual processes provide an excellent means to examine the interactions underlying predictive coding.

4.2 Magnetoencephalography (MEG) Experiment

The current research study aims to apply what has been learned so far about the temporal dynamics involved in low-level auditory binding to a magnetoencephalography (MEG) examination of the effects of priming on responses to violations of these expectancies, and how they differ as a consequence of musical experience. Previous research has found that while musicians respond faster to inharmonic tones, compared to non-musicians, they respond faster to both harmonics (harmonic and inharmonic tones) overall, and unlike their musically naïve peers, they do not demonstrate slower responses to harmonic target tones when the auditory system has been primed with a 33 Hertz (Hz) entrainment frequency (Aksentijevic et al., 2014). In addition to the neural recruitment involved in the auditory binding process, the behavioural evidence strongly suggests an interaction between the evoked auditory gamma-band responses (aGBRs) and a 6.69 Hz theta rhythm possibly others (Aksentijevic et al., 2011; 2013). Given the findings of the experiments presented in the previous chapter, using the Time Quantum Model (TQM) as a guide for the optimal temporal parameters required for stimulus entrainment to facilitate an anticipatory response, 7.29 Hz has been identified as an example of further theta interactions. Therefore, this research aims to establish convergence between the behavioural evidence and neural activity apropos the involvement of neural networks in pitch processing and interactions in phase between emergent oscillatory systems and endogenous brain rhythms.

4.2.1 Research question. It is hypothesised there will be differences in the neural networks recruited by musicians and non-musicians during pitch processing. Specifically, the ERAN and RATN response will be influenced by music training, resulting in stronger event-related field (ERF) activity overall in the musician group.

However, among the non-musicians, as a consequence of priming, it is expected that the strength of these responses will be increased during the 33Hz priming condition, perhaps resulting in a response strength similar to that of a musician, as behavioural evidence suggests that priming at this rate facilitates auditory binding. The strength of activations of the planum polare (anterior portion of the superior temporal gyrus (aSTG)) is increased in response to music stimuli compared to vocal stimuli. However, more left hemispherical activation is observed for non-musicians, while activations are bilateral for musicians. Also, activation of the planum temporale, located posterior to planum polare (in pSTG) is strong in response to vocal stimuli for non-musicians, while musicians demonstrate strong activations in response to both vocal and musical stimuli, suggesting recruitment of language associated cortical resources in musicians (Angulo-Perkins et al., 2014). Therefore, it is expected there will be similar functional differences in the sources of responses to the target stimuli in the current study dependent on music training. The auditory priming paradigm uses pip-train stimuli to entrain a response in the auditory cortex that is phase-locked to the amplitude modulation (AM) frequency, of the tone bursts (pips). The AM frequencies used are in the gamma range (30-100 Hz), and the response is referred to as an evoked aGBR. Finally, this experiment will examine the strength of entrainment in both groups at each entrainment frequency in the range 31 - 39 Hz in 2 Hz intervals. It is hypothesised that at each level of entrainment, there will be an increase in the amplitude of the frequency corresponding to entrainment rate, during the 100 ms inter-stimulus interval (ISI) between entrainer and target presentation.

4.3 Methods

Experimental sessions (1 per participant, ~ 50 minutes duration) were conducted at the Northern Ireland Functional Brain Mapping (NIFBM) facility, at the Intelligent Systems Research Centre, Magee Campus, Ulster University, Derry, Northern Ireland. Following consent, participants were prepared for the MEG recording outside the magnetically shielded chamber. Once the set-up phase was complete participants were seated inside the chamber, with their back supported by in the upright position, and their legs on rests. Participants were assisted as they fitted the ear inserts for the audio feed, to ensure that they were fully inserted. The response pads were placed on a table which was fitted to the arms of the chair and

adjusted so that participants could rest their arms on the table with their left and right index fingers on the corresponding response pad. The chair was then elevated so that the top of their head touched the top surface of the MEG helmet. A screen was placed in front of the participant to provide response feedback on their accuracy during the practice block, and to provide instructions throughout the experiment. Sessions lasted between 60 and 80 minutes and consisted of a practice block (20 trials randomly selected from a list of all possible condition combinations, with no repeat allowed following the list-reset after each trial), followed by six blocks of 200 trials, with a break half-way through (for 30 seconds) and at the end of each block (until they were happy to continue). As before the experimental exercise was a forced choice response task based on the target stimulus properties. Each trial was cued by a fixation cross and following a one-second entrainer and 100 ms interstimulus interval (ISI) the target was presented. If the overall pitch of the sound was flat, the target was absent, and the response was 'No' – press the left response pad. If the sound alternated in pitch, the target was present, and the response was 'Yes' press the right response pad. Approval was obtained for this study from both the National University of Ireland Galway Research Ethics Committee and the Ulster University, Magee Campus, Research Governance department.

4.3.1 Sample. Twenty-two participants recruited in the Derry area took part in this study. Two of the non-musician group were excluded from analyses due to insufficient data resulting in the number of trials for these participants presenting as outliers. Therefore, the sample consisted of two groups: Musicians with grade 3+ or an international equivalent (n = 11, six male, M age 32.55 years, SD 14.16), and non-musicians with no music experience (n = 11, nine male, M age 37.44 years, SD 9.71). Of the musician group, all played at least one instrument, and nine played regularly. Grades achieved were as follows – four grade 8+, three grade 6 or 7, and four grade 3 or 4. All participants were right-handed, reported normal hearing and provided informed consent.

4.3.2 Stimuli. The parameters of the auditory pip-train stimuli were designed to replicate the stimuli in the paradigm which produced the previous 'pop-out' effect at 33 pips per second (pps) entrainment rate – that is slowing of reaction time (RT) responses to harmonic responses at a 33 pps entrainment rate, resulting in a deviation in the trend (see Aksentijevic et al. 2011, 2014, for details). This original experiment used a rate range of 30 to 39 pps and each trial condition was repeated 40 times.

MEG experiments repeat trial conditions 60 times on average, as several trials are lost due to movement artifacts. A further consideration was the length of time it takes to prepare a participant for MEG. Most experiments take 40- 60 minutes to complete, and longer than this may affect the quality of responses due to fatigue. To ensure a sufficient number of trials per participant while avoiding fatigue, the range for this experiment was 31 to 39 pps in 2 Hz intervals. Experimental trial plus stimulus and trigger generation were coded in-house using the Cogent toolbox for Matlab (Matlab R2016b (9.1.0.441655) and Cogent, www.vislab.ucl.ac.uk/Cogent/; The Mathworks, Inc, Natick, Massachusetts, United States).

4.3.3 MEG recording: Acquisition parameters and apparatus. The continuous raw MEG was recorded per participant, per block (200 trials) using the superconducting quantum interference device (SQUID) based 306-channel whole head MEG Elekta Neuromag TRIUX system (Helsinki, Finland), comprising 204 gradiometers and 102 magnetometers. Head shape was obtained by using a threedimensional Fastrak digitiser (Polhemus) by acquiring three fiducial (or cardinal) points (nasion and left and right preauricular points) and at least 300 points of the surface of the scalp. In addition, four head position indication (HPI) coils were placed on the subjects' head: two on the mastoids and two on the forehead. The positions of the HPI coils were acquired using the Fastrak device to provide continuous head position estimation during the recording. Ocular movements and cardiac activity were measured for cleaning purposes using four electro-oculography (EOG) electrodes (two horizontal, and two vertical), and one cardiac muscle electrode. Signals were digitised with a bandwidth of 0.1 Hz to 300 Hz and a sampling rate of 1000 Hz. Sound stimuli were presented binaurally via ER-3A ABR Insert Earphones, and the decibel level was attenuated to 50 SPL, as measured by a Precision Gold (IEC 651 TYPE II) sound level meter (model #: N05CC). A zerojitter 3-DLP video projector and lens were used to project instructions and a cross to cue the start of each trial onto a non-magnetic 44" back-projection screen, placed 120 centimetres (cm) from the participant. A bilateral finger response system was used to collect participants RT responses.

4.4 Statistical analyses

Statistical analyses included testing for significant within and between group (mixed) differences in the behavioural RT data and the event-related field (ERF)

data, at the sensor and source level. Analyses also included a frequency power analysis to examine differences in entrained aGBRs between groups.

4.4.1 Analysis of reaction time (RT) data. Error trials were removed from the analysis and RT data were transformed as described in chapter two. A mixed design was used with group as the between factor (musicians and non-musicians), and two within factors; rate (5 levels; 31, 33, 35, 37, and 39 pps) and target (asymmetrical as described for all previous RT experiments). Levene's test for equality of variance was applied to the analysis, as was Greenhouse-Geisser estimates of sphericity, and degrees of freedom were corrected when a violation to an assumption was indicated. Bonferroni correction was applied to all pairwise comparisons. The entrainer pip-train stimulus was presented for a constant period of 1000 ms, and ISI was kept constant at 100 ms. Participants were presented with 60 trials per condition which resulted in 1200 trials per participant, (5 x 2(2) x 60 = 1200).

4.4.3 Analysis of MEG data. Data cleaning and analyses were performed using in-house scripts in the Fieldtrip toolbox for Matlab (Matlab R2016b (9.1.0.441655); The Mathworks, Inc, Natick, Massachusetts, United States, and Fieldtrip; Oostenveld, Fries, Maris, & Schoffelen, 2011).

4.4.3.1 Preprocessing. The continuous raw data were filtered off-line using Max Filter temporal signal space separation (tSSS). Data for each participant were then epoched and preprocessed, removing target absent trials and offsetting the samples to account for the delay in sound stimuli presentation. A bandpass filter was used to filter out frequencies above 150 Hz, and a discrete Fourier transform was used to filter out line noise. Separate blocks for each participant were concatenated and resampled from 1000 to 500 samples per second. Trials were manually inspected to remove noisy segments, and the data were checked for trials and channels that were outliers. Squid jump detection was used to identify jumpy channels (a cut-off zscore of 25 was used). Following removal of bad channels, the remaining bad trials detected were removed. Muscle artifacts were removed (using a cut-off z score of 12), and a final visual inspection was performed. Finally, an independent component analysis (ICA) was performed to identify and remove electro-ocular and electrocardiac components. The clean data were interpolated to repair bad channels. Data were then averaged across trial conditions, i.e., inharmonic target present (ITP) by rate and harmonic target present (HTP) by rate, for each participant.

4.4.3.2 Event-related field (ERF) analysis. Two cluster-based permutation tests were performed using 50 ms time windows overlapping the ERAN and RATN response times, between 190 and 240 ms and 340 to 390 ms respectively. According to the literature the ERAN is typically maximal between 150 and 250 ms (~200 ms for MEG, Maess et al., 2001), while the much less studied RATN response has been found to have a post-stimulus latency of approximately 350 ms (Koelsch, 2005; Koelsch & Siebel, 2005; Patel, Gibson, Ratner, Besson, & Holcomb, 1998). The ERFs of interest were calculated by subtracting the ERFs elicited by harmonic targets from the ERFs of inharmonic targets, in the time windows corresponding with the ERAN and RATN responses. The design was within subjects, in which differences between (planar gradient) ERFs over all subjects, grouped as musicians and non-musicians, were compared. The Monte Carlo Method was used to calculate the significance probability using the dependent samples t-statistic as a measure to evaluate the effect at the sample level (samples refer to (channel, frequency, time)triplets obtained from the raw spatiotemporal data). These data were not averaged over time.

4.4.3.3 Between-group analysis of the difference wave peak amplitudes. Based on the topographies of significant ERAN and RATN ERFs, channel 0731 (temporo-parietal scalp area) was selected for an examination of the difference wave refers to the difference in the time-frequency response to the harmonic and inharmonic targets and is calculated by subtracting the averaged time-frequency response to harmonic targets from the response to inharmonic targets (ITP-HTP), in each entrainment condition, for each participant. The peak amplitudes of the difference waves, during each entrainment condition across both the ERAN and RATN time windows (190 - 240 ms, and 340 - 390 ms, respectively), were calculated at this sensor site. A Mann-Whitney U test was performed on the data to compare group differences in each entrainment condition dependent on music training.

4.4.3.4 Source analysis. A source reconstruction analysis was performed using a linearly constrained minimum variance (LCMV) beamformer (Van Veen, Van Drongelen, Yuchtman, & Suzuki, 1997). In the absence of a T1 MRI for the participants, a 1-millimetre (mm) resolution template MRI was used to create the headmodel and 3D sourcemodel. The template MRI was co-registered to the MEG coordinates using the three fiducial points (i.e., nasion, left preauricular, and right

preauricular point). The registered images were normalised to the MNI template using a nonlinear registration algorithm (Ashburner, 2007) and then used to define a homogeneous grid of 2 mm resolution. A single shell volume conduction model was created based on the segmentation of the head tissues. Lead fields were defined using the single shell headmodel to fit the head shape of each subject in the vicinity of each sensor. Spatial filter coefficients were estimated for each participant using the computed lead field and an average of the covariance matrix for all the epochs (both harmonic and inharmonic). Thereafter, this filter was used to compute the sources for each harmonic and inharmonic condition separately. This method results in independent scaling factors for all three spatial dimensions, thus enabling source localization with an accuracy close to that achieved with individual MR-based models. The source activity elicited by harmonic and inharmonic targets, in the time windows corresponding with the ERAN and RATN responses, were averaged over trials within each condition and the Monte Carlo Method was used to calculate the significance probability of variability using the dependent samples t-statistic. The following four analyses were performed in this way, on the source data in both the ERAN and the RATN time windows (a total of eight permutation tests).

- Analysis to examine variance between the source activations elicited by the inharmonic compared to the harmonic, at each level of entrainment in the non-musician group.
- Analysis to examine variance between the source activations elicited by the inharmonic compared to the harmonic, at each level of entrainment in the musician group.
- Analysis to examine variance between the source activations elicited by the inharmonic compared to the harmonic, at each level of entrainment for the combined sample.
- 4. Analysis to examine variance in inharmonic-harmonic source activity differences, i.e., the source activity elicited by the harmonic subtracted from the inharmonic source activity, at each entrainment rate, dependent on music group.

The design matrix for each analysis was for a within-subject manipulation – therefore, number of participants was the unit of observation, and the harmonic condition (harmonic or inharmonic) was the independent variable. In order to have equal units of observation for the musicians versus non-musicians matrix (analysis

number four), two musicians were randomly selected, in Matlab, to be excluded from the musician sample.

4.4.3.5 Frequency power analysis during the 100 ms interval between entrainer and target presentation. The grandaverage for the time-frequency data at each rate of entrainment during the entrainment period (-1000 to 0 ms) was calculated for each group. These data were used to perform a multi-taper method fast Fourier transform (mtmfft) using a discrete prolate spheroidal sequences (dpss) multi-taper, to calculate the average frequency-content, within the range 28 to 45 Hz, during the 100 ms ISI between the entrainer and target presentation, as measured at all channels covering both temporal lobes, at each rate of entrainment, and for each group. The results were then plotted for each group. Three participants from the musician group displayed extremely high gamma activity (10⁻²⁷ microvolt (μ V) measurements), one exhibited high amplitude gamma activity in general, while two displayed low frequency (28 – 31 Hz) spikes. These participants were considered outliers and were removed from this analysis. The remaining musicians (*n* = 8) displayed gamma activity similar in amplitude to that of the non-musicians (*n* = 9), with a maximum amplitude of 14 x 10⁻²⁷ μ V.

4.5 Results

4.5.1 Behavioural results. A mixed ANOVA was conducted on the exponents of the means of log transformed RT data to evaluate the effect of presentation rate (31, 33, 35, 37, and 39 pps), and harmonic relation (TA and TP (including HTP and ITP targets) on RT responses, as a function of music experience (group being the between factor; musicians and non-musicians). Significant main effects were found for target, and rate; $F_{(2, 38)} = 4.6 p = .016$, $\eta_p^2 = .2$, $F_{(4, 76)} = 3.81$, p = .007, $\eta_p^2 = .17$ respectively. Responses to HTP targets were slower compared to both TA and ITP targets (HTP-TA difference; MD = 23.07, SE = 8.4, and HTP-ITP difference; MD = 15.32, SE = 6.19), however the main effect for target was due to a significant result for the former difference (HTP-TA difference, p = .039), not the latter (HTP-ITP difference, p = .069). The effect for rate was due to faster overall response times at 35 and 39 pps entrainment rates compared to RTs during the 31 pps entrainment condition (p = .008 and p = .025, respectively). It was hypothesised that the rate specific 33 Hz pop-out effect would be observed for the non-musician group only, consistent with previous findings (Aksentijevic et al., 2014). Therefore,

a second mixed ANOVA was conducted on the TP data only to evaluate the effect of presentation rate (pps), and harmonic relation (ITP and HTP targets) on RT responses, dependent on music training to later examine correspondence between trends in the RT data and group differences at the neural level. Significant main effects were found for harmony, and rate; $F_{(1, 19)} = 6.13 \ p = .023, \ \eta_p^2 = .24, \ F_{(4, 76)} =$ 2.79, p = .032, $\eta_p^2 = .13$ respectively. The effect of group was not found to be significant ($F_{(1, 19)} = .004$, p = .97). The main effect for harmony was due to slower responses to harmonic compared to inharmonic targets (MD = 15.32, SE = 6.19, p =.023). However, a pairwise comparison revealed that the HTP-ITP difference was not significant for either group alone, although the difference in the non-musician's responses approached significance (musicians -MD = 13.43, SE = 8.54, p = .13, and non-musicians -MD = 17.21, SE = 8.96, p = .07). The main effect for rate was due to faster RTs to targets presented at 35 pps compared to 31 pps (MD = 11.9, SE =3.25, p = .016). While the interaction between harmony and rate was not significant (p = .76), a pairwise comparison revealed significant RT differences between harmonic targets at 33, 37, and 39 pps entrainment rates (MD = 18.31, SE = 6.68, p =.013, *MD* = 15.58, *SE* = 7.14, *p* = .042, and *MD* = 19.08, *SE* = 7.59, *p* = .021, respectively). Again, while the three-way interaction between group, harmony and rate did not reach significance (p = .54), a pairwise comparison found this harmony by rate effect held at entrainment rates 33 and 39 pps, but for non-musicians only (*MD* = 21.22, *SE* = 9.66, *p* = .041, and *MD* = 25.14, *SE* = 10.99, *p* = .034, respectively).



Figure 4.1. MEG; graphed harmony RT data (a & b) and priming as a function of return phase (c).

(a) Illustration of musicians' RT responses to harmonic (unfilled legend) and inharmonic targets (filled legend) (*y*-axis in ms), at each entrainment rate (legend labels), mapped over return phase (top *x*-axis, four-pip sequence, and the bottom *x*-axis, number of completed entrained oscillatory cycles). (b) Illustrates the same function except for non-musicians. (c) the scale of the difference in response times to both targets (y-axis, HTP-ITP RTs in ms) for each group (musicians filled legend, and non-musicians unfilled legend) mapped over the oscillatory trace of the entrained pip-sequence (bottom *x*-axis, while the top *x*-axis illustrates the completion of the pip at target presentation time – completion of next pip (CNP)).

Figure 4.1 depicts the trends in the RT data. The results suggest that while the 33 Hz pop-out effect does occur among the non-musician group, as hypothesised, there is evidence for a similar effect at 39 pps entrainment. Furthermore, at 35 pps entrainment the musicians in the Aksentijevic et al. (2014) sample responded at approximately the same speed to both harmonic and inharmonic targets. In this study, the main difference in the trend of the RT data for both groups can be observed at a 35 pps rate of entrainment. Non-musicians responded much faster to harmonic targets during this condition, and responses to the inharmonic at this rate were faster compared to the other entrainment conditions. While inharmonic RTs at 35 pps entrainment were not faster for musicians compared to other entrainment rates, similarly to their non-musician counterparts, and to the Aksentijevic et al. musician sample, responses to the harmonic were faster.

4.5.1.1 Error Analysis. The percentage error reported was 8.21%. The arcsine of the square root of the proportion of errors for each condition were analysed, and a significant main effect of target was found due to a lower rate for TA errors compared to the HTP error rate; $F_{(2, 38)} = 7.98$, p = .001, $\eta_p^2 = .3$. Analysis of the arcsine-transformed ITP and HTP error means did not reveal a significant difference in error rate for either of the TP conditions, suggesting that the effects found in the analysis of the corrected RT means were not affected by a speed-accuracy trade-off.

4.5.2 ERAN and RATN: ERFs

4.5.2.1 Analysis of ERAN responses. Musicians tend to demonstrate stronger ERAN responses compared to non-musicians, considered to be connected to an increased ability to detect regularities in music-syntax due to music training (Koelsch, Schmidt, & Kansok, 2002). It was hypothesised that the strength of the ERAN response during the 33 pps condition would be similar between groups due to the rate specific effect of priming evident for non-musicians following 33 pps entrainment.



Figure 4.2. Graphed sensor level ERF differences between groups.

The column on the far left illustrates the sensor recording the greatest ERF difference, circled in red on a neuromag306 sensor template. To the right of this are the entrainment rates followed by the topographies of these ERF differences during the time windows displayed on the far right (non-musician topographies on the left, and musician topographies on the right).



Figure 4.3. Graphed difference waves for each group, and statistical results. Again, the column on the far left illustrates the sensor recording the greatest ERF difference, circled in red on a neuromag306 sensor template. To the right of this are the entrainment rates. Next to the right are the difference wave graphs as recorded at channel 0731. The y-axis displays amplitude (μ V) and the x-axis time (ms) post-

target presentation. On the far right are the significant statistical results for the preceding depictions.

Within the specified ERAN response time window of 190 to 240 ms, when the ERF elicited by harmonic targets was subtracted from the inharmonic ERF a significant early magnetic field effect, negative in polarity, remained in the cortical activity of musicians only during the 31, 33, and 35 pps entrainment conditions; 31 pps, time window (t) = [204 - 236 ms (post-target presentation)], p = .002, 33 pps, t= [202 - 240], p = .001, 35 pps, t = [220 - 240], p = .012. The topographies of these negative ERF differences are illustrated in figure 4.2. For the 31 and 35 pps entrainment conditions, the topographies are very similar to the ERAN response (see Maess, Koelsch, Gunter, & Friederici, (2001) for an example of the ERAN topography). An examination of the difference ERF activity within the specified RATN response window of 340 to 390 ms revealed a later magnetic field effect, negative in polarity, in the cortical activity of non-musicians only during the 39 pps entrainment condition; t = [380 - 390 ms], p = .039. However, unlike the RATN response topography, this ERF difference was left-hemisphere weighted. Thus, it cannot be concluded that the ERAN response is similar in strength for both groups at a 33 pps entrainment rate, as hypothesised. However, there is weak evidence that the pop-out at 39 pps observed in the RT analysis for non-musicians may be supported by a later magnetic field effect (~ 385 ms post-target onset) which is negative in polarity and generated in the left hemisphere.

4.5.3 Peak amplitude values for the difference waves. To further test for statistically significant differences in cortical responses dependent on entrainment rate between groups, a common sensor was selected from the ERF topographies in the previous analysis. The peak amplitude values for the HTP-ITP difference waves recorded at this sensor were averaged for each condition within each group and compared for group differences – during the ERAN and RATN time windows, at each entrainment rate. The sensor at which the largest ERF difference was recorded for the 31 and 33 pps conditions was channel 0731 (with neighbouring channel 0721 registering the highest amplitude for the 35 pps ERF difference), and therefore this channel was selected for the between groups analysis. Statistical analysis revealed a significant difference in the peak amplitude of the difference wave for musicians compared to non-musicians at a 33 pps rate of entrainment (U = 21, p = .03). This

difference was due to a higher peak amplitude for musicians (musicians, MR = 7.91, and non-musicians, MR = 13.67, lower MR implies greater negative peak amplitude value). The early ERF difference at an entrainment rate of 39 pps was not found to be significant for either group, and the later ERF difference was found to be significant for the non-musician group. Contrary to this, the peak amplitude analysis of the difference waves found that the difference wave for musicians at this sensor site had a significantly greater amplitude compared to non-musicians during the ERAN time window, while a group difference was not found during the RATN time window (U = 22, p = .037; musicians, MR = 8, and non-musicians occurred over the posterior temporal region of the left hemisphere, at sensor 1841. However, further analysis of the peak amplitude values of the group difference waves at this site, during the RATN time window, did not reveal a significant difference.

4.5.4 Entrainment period time-frequency spectral power at temporal lobe sensor sites. The purpose of this analysis was to establish the persistence of an evoked aGBR of the same frequency as the rate of entrainment in the 100 ms ISI prior to target presentation. It was anticipated that the amplitude of the frequency corresponding to the rate of entrainment would be higher during each entrainment condition. As the evoked response is auditory, the analysis was concentrated on the left and right temporal lobe sensor channels.



Figure 4.4. Spectrograms.

Graphed frequency power analysis on (a) the non-musician and (b) the musician time-frequency data, during the 100 ms interval between entrainer offset and target onset, bandpass filtered between 28 and 45 Hz. Each line (legend) represents a different entrainment condition, with amplitude (μ V) on the *y*-axis and frequency (Hz) on the *x*-axis.

The graphs in figure 4.3 illustrate the power spectrum of gamma frequencies in the range 28 – 45 Hz under each entrainment condition during this 100 ms period, in the time-frequency data for each group. Non-musicians exhibited higher amplitude gamma activity following 31 pps entrainment, specifically 31, 36, and 41 Hz activity. It is possible that this pattern is a result of phase-phase coupling (PPC) with a 5 Hz theta rhythm (31, 36, and 41 Hz being separated by 5 Hz), strengthened by the 31 pps entrainment. Also, of interest, 33 and 38/39 Hz were reduced in amplitude across all conditions, which could infer general inhibition due to a modulation between gamma and a 5-6 Hz theta wave. For musicians, following entrainment at 31, 33, and 35 pps, there is a peak in 31 Hz, presenting as a dominant spike during the 33 pps condition, inferring a phase-amplitude coupling (PAC), perhaps due to a 2 Hz delta wave modulation, associated with uncertainty and attentional processes (Dikker & Pylkkänen, 2013; Kirmizi-Alsan et al., 2006). While following entrainment at 33 and 39 pps the matching frequencies are completely attenuated, suggesting a tight inhibitory PPC with a 6 Hz theta rhythm, similar to that observed in the non-musician spectrum except for musicians the coupling is specifically between the theta rhythm and the corresponding entrained (33 and 39 Hz) gamma frequency – it does not occur under all entrainment conditions. Musicians demonstrate low amplitudes in 35 and 39 Hz activity across all conditions, and following 39 pps entrainment, in conjunction with the attenuation of 39 Hz observed, a peak in 34 Hz amplitude is observed – perhaps due to a PAC with a 5 Hz theta rhythm. One similarity between both spectrums is the pattern following entrainment at 35 pps. Although much higher in amplitude at the peaks in the musician group spectrum, the pattern shows a peak in 30 Hz in the non-musician spectrum and 31 Hz in the musician spectrum (also in 32 and 33 Hz respectively, perhaps due to an interaction with delta), attenuation of 34 and 35 Hz - similar in amplitude for both groups, and a second peak in 36 Hz for the non-musician, and 37 Hz for the musician group. This pattern is suggestive of a PPC between 35 Hz and 5-6 Hz which is again more finely tuned in the cortical processing of tones in musicians.

While the results of this analysis do not reveal the hypothesised amplitudefrequency pattern in either group, it is suggested that the evoked aGBR is modulated by endogenous brain rhythms, even at this early stage, presumably due to expectancies generated by the carrier tones in the pip-trains of the entrainer. However, modulation is differentially affected by music ability.

4.5.5 Source. To assess functional differences in the sources of responses to the target stimuli dependent on music training, a source analysis was conducted, focused on the early ERAN response time window, and the later RATN response time window. As already stated, four analyses were conducted at the source level. A statistically significant functional or anatomical difference in the source ERF generators dependent on music ability was not found at an alpha level of .05, i.e., in

separate analyses for musicians and non-musicians, the source activity elicited by the harmonic subtracted from the inharmonic source activity, at each entrainment rate did not meet the statistical criteria.



Figure 4.5. Image of ERAN source activation following 39 pps entrainment. Mean image for the variance between musicians and non-musicians in the early (ERAN time window) source difference between ERF activation elicited by harmonic and inharmonic stimuli, under the 39 pps entrainment condition. The difference is calculated by subtracting the harmonically elicited ERF from the activity elicited by the inharmonic (ITP-HTP difference), at 39 pps entrainment during the ERAN time window, for both groups and then comparing the variance in ITP-HTP differences for each group.

An analysis of variance in inharmonic-harmonic source activity differences, at each entrainment rate, dependent on music group, i.e., inharmonic-harmonic source activity differences for non-musicians subtracted from inharmonic-harmonic source activity differences for musicians, was also not significant at an alpha level of p < .05. However, it is possible this is because the inharmonic-harmonic source activity does not differ significantly between groups at this alpha level, while lowering the statistical threshold might reveal a difference if the source strength is greater for one group compared to the other (for details see Gaab & Schlaug, 2003). The statistical threshold was therefore lowered to p < .01. Under these statistical parameters a significant early source ERF difference was revealed (ERAN, p =.038), following entrainment at 39 pps, positive in polarity and located in the right Rolandic operculum and right insula (see figure 4.4). Although positive in polarity, according to the Montreal Neurological Institute (MNI) standard brain coordinates, the mean coordinates for this source are close to the mean coordinates for the location of the ERAN response reported by Maess et al., (2001); mean x, y, z coordinates for this source are [44 4 12], and for the ERAN response [50 6 14] (see figure 4.4 above).

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The third source analysis examined the difference in ERF activity elicited by harmonic and inharmonic targets at source level across the combined sample of musicians and non-musicians, at each entrainment rate and during the ERAN and RATN time windows separately. The results yielded a significant early source ERF difference (ERAN, p = .006), following entrainment at 31 pps, negative in polarity and located in the right supramarginal gyrus (SMG) (see figure 4.5).

4.6 Discussion

This research thesis has so far discussed the temporal dynamics involved in low level visual, and auditory, scene analysis, using the psychophysical method, i.e., providing a manipulable temporal code (embedded in the premask for visual, and the entrainer for auditory, experiments) and analysing the corrected RT output to extract

information about the frequency interactions in the brain that facilitate the integration of visual, or auditory, information. The aim of this study was to apply the accumulated knowledge to an MEG paradigm examining the effect of priming the system with a temporal code on responses to target stimuli which deviate from the expected harmonic representation, and how, or if, the effect differs as a consequence of music ability. The temporal code refers to the aGBR presumed to be evoked by, and phase-locked to, the entrainer stimulus, while the harmonic relations, also embedded in the entrainer stimulus, generate the listeners' expectancies regarding the next event. The harmonic target is related to the 1000 Hz tones in the entrainer by an octave, while the inharmonic is related by an octave and a minor third. Thus, the harmonic target is an expected harmonic (consonant), and the inharmonic is considered a deviant (dissonant). It was hypothesised that using a brain-imaging technique would provide support for the behavioural findings regarding the temporal and phase relations of the oscillatory mechanisms underlying the integration of pitch information. MEG provides very high temporal and spatial resolution, and offers the best solution to the inverse problem, i.e., the relations between current sources and electromagnetic fields (Hansen, Kringelbach, & Salmelin, 2010). Furthermore, in the case of the auditory cortex, it can be difficult to discern activity as the scalp recordings originate directly below the electrode sites, and not perpendicular to them. Therefore, MEG emerges as the best technique for the required investigation. The auditory priming paradigm underlying each of the experiments discussed so far has been used previously to examine differences in musicians' and non-musicians' responses to the harmonic structure of a sound, when the auditory system has been primed both with a specific temporal code (the evoked aGBR), and to expect a harmonic tone. Musicians responded faster overall to both harmonic types, and unlike non-musicians, they did not exhibit a pop-out effect when primed at 33 pps rate of entrainment, i.e., musicians' responses to harmonic targets were not significantly slower than their responses to inharmonic targets at this rate of entrainment (Aksentijevic et al., 2013, 2014). The analysis of the RT data for this study revealed a 33 pps rate specific pop-out effect for non-musicians only, consistent with the previous research. Additionally, the results from these data also found the effect was present following a 39 pps entrainment rate, again for nonmusicians only (see figure 4.1). Following an entrainment rate of 35 pps, musicians exhibited a dip in HTP RTs (faster responses to harmonic targets), while non-

musicians responded faster to both harmonics, markedly so to HTP targets at this entrainment rate (see figure 4.1). Overall target responses were slower, and HTP-ITP differences were larger, for the musician group, compared to the sample examined by Aksentijevic et al. (2014). These inconsistencies may be due to the fact the musicians in this study were classically trained, whereas the Aksentijevic et al. sample were contemporary musicians. This latter style of music relies more on training by ear than sight reading sheet music, as is the case for classical music training, and this may result in faster overall responding among contemporary musicians.

The time-frequency analysis revealed early negative ERF activity, for musicians only, in response to the deviant inharmonic stimuli, following entrainment at 31, 33, and 35 pps. A later, left hemispheric, negative ERF was detected for nonmusicians following 39 pps entrainment, perhaps contributing to the pop-out effect observed in the corrected RT analysis for this group. The topographies of the early ERF activity during the 31 and 35 pps conditions resemble the ERAN response reported by Maess et al. (2001), (see figure 4.2). However, it is the early negative ERF during the 33 pps condition that is qualified by a significant difference in the amplitude of the difference waves (the difference in the time-frequency response to the harmonic and inharmonic targets at the selected sensor site) – revealing a larger deflection in amplitude for musicians compared to non-musicians. During this earlier (ERAN) time-window, musicians again exhibited a larger peak amplitude for the difference wave at this site for the time-frequency data during 39 pps, even though a significant ERF was not elicited. However, at this rate of entrainment (39 pps) when the inharmonic-harmonic source activity differences for non-musicians were subtracted from inharmonic-harmonic source activity differences for musicians an early source ERF difference was revealed – located in the right Rolandic operculum and right insula. Although positive in polarity, the generators of this response are located close to those of the ERAN response reported by Maess et al. (2001), approximately 6 cm to the right, 2 cm posterior, and 2 cm inferior, in comparison. While a significant source generator was not detected for responses to inharmonic compared to harmonic stimuli for either group separately, when analysed for the combined sample, an early negative source generator was located in the right SMG following 31 pps entrainment. The SMG is part of the somatosensory associative cortex, involved in multisensory integration, body ownership, and proprioception

(Vaquero et al., 2016). A reported case of damage to the SMG resulted in a deficit in the comprehension of the emotional component of music, and musical appreciation or what is termed gestalt type perception, while leaving analytical perception intact. The patient, an accomplished musician, reported the loss of aesthetic pleasure when listening to music (Mazzoni, Moretti, Pardossi, Vista, Muratorio, & Puglioli, 1993). In a sample of non-musicians, analysis of the activation pattern over time epochs, while performing a pitch discrimination task, found the left SMG and the dorsolateral cerebellum play a critical role in pitch discrimination processing and short-term pitch information storage, with increased activation of the left SMG positively correlating with improved performance accuracy (Gaab, Gaser, Zaehle, Jancke, & Schlaug, 2003). Expanding on these findings, a recent study using a nonmusician sample, has revealed a different hemispheric involvement of the SMG that is dependent on the type of auditory information being processed, specifically, the left SMG is involved in maintenance of pitch information while the right SMG retains the rhythmic structure (Schaal, Pollok, & Banissy, 2017). However, the left SMG is typically associated with linguistic syntax processing, yet when highly trained jazz drummers are presented with a rhythm that deviates from temporal expectancies generated by a rule-based rhythmically structured sequence of beats, they exhibit additional activity in the left SMG, compared to non-musicians (Herdener et al., 2014). Again, both the complexity of processing mechanisms in the brain and the plasticity effects of music training resulting in this type of functional recruitment, are revealed. Regarding pitch maintenance strategies, both musicians and non-musicians demonstrate bilateral activation of the superior temporal gyrus, SMG, as well as posterior (middle and inferior) frontal gyrus, and superior parietal lobe. However, non-musicians rely more on pitch discrimination processing (Helsch's gyrus) and general short-term memory strategies (hippocampal gyrus), while musicians activate an auditory short-term memory network involving more bilateral, yet with more right hemispheric weighting, activation of the SMG, as well as the superior parietal cortex, also implicated in visual-spatial processing (Gaab & Schlaug, 2003). Beyond the functional differences in pitch perceptual and maintenance processes, there are also differences in the brains response to expectancy violations involving the SMG. An fMRI study investigating the neural correlates of music-syntax processing revealed a complicated fronto-temporoparietal network of auditory attention, including increased right SMG activation in

response to violations of music syntax, perhaps due to a mismatch between the stimulus and the representation in short-term memory (Tillmann et al., 2006). Thus, the source generator revealed in this analysis suggests that entrainment at a rate of 31 pps facilitates auditory attention.

Stimulus entrainment entails driving brain oscillations using an external periodic force and is characterised by the adjustment of phase to the external stimulus (phase-locking) and an increase in amplitude among participating neurons (Thut, 2011). The auditory priming paradigm uses stimulus entrainment to evoke an aGBR which has been demonstrated to persist for up to 400 ms (Aksentijevic et al., 2013). The frequency power analysis aimed to examine the amplitude of the frequency matching the entrained frequency during each entrainment rate condition in the 100 ms ISI prior to target presentation. It was hypothesised peaks (increases) in the amplitude of the frequency corresponding to the rate of entrainment would be observed. The findings did not support this hypothesis. Instead, a complicated interplay between the entrained frequencies and slower endogenous brain rhythms was suggested, which altered between groups (as a function of music training). The pattern for non-musicians suggested a PPC with a 5-6 Hz theta wave during the 31 pps entrainment condition, while the low amplitude 33 and 38/39 Hz under all entrainment conditions also indicates a 5-6 Hz modulation. For musicians, entrainment at 31, 33, and 35 pps appeared to amplify 31 Hz presumably due to attentional processes driven by a PAC with a 2 Hz delta wave. Musicians exhibit a PPC between a 6 Hz theta rhythm and gamma frequencies, similar to the inhibitory effect observed in the spectrogram for non-musicians. However, for musicians the interaction is only observed following 33 and 39 pps entrainment and is marked by a complete attenuation of the entrained frequencies – thus, indicating a tight PPC between these specific gamma frequencies and a 6 Hz theta rhythm, which is strengthened by their entrainment. There is also a suggested PAC with a 5 Hz theta rhythm following 39 pps entrainment. A more general inhibition occurs for frequencies 35 and 39 Hz. It is further suggested that the general modulation effect of 5-6 Hz theta on 33 and 38/39 Hz gamma, observed in the non-musicians' spectrogram, could be responsible for the pop-out effect evidenced for musicians when these gamma frequencies have been entrained. Following entrainment at 35 pps, the spectrograms for both musicians and non-musicians exhibit a PPC between a 5-6 Hz rhythm and the entrained 35 Hz gamma wave that is increased in amplitude

and is shifted forward by 1 Hz for musicians and is accompanied by a PPC with a 2 Hz delta wave also. Superimposed theta and delta oscillatory activity has been demonstrated to elicit ERP components associated with many tasks – enhanced theta activity is associated with prediction and underlies response inhibition, while delta activity is a sustained oscillatory response shown to increase where there is uncertainty, indicating heightened attentional processes (Dikker & Pylkkänen, 2013; Harper et al., 2014; Kirmizi-Alsan et al., 2006). Interestingly the corrected RT data illustrates faster responses to harmonics for musicians, and faster responses to both harmonics and inharmonics for non-musicians following 35 pps entrainment.

While these amplifications do not allow the null hypothesis to be rejected, they do emphasise the increased range of interactions between gamma and theta/delta in musician's brains presumably due to the plasticity effects of music training, as these slower endogenous frequencies are relied upon to feedback predictions, manipulate information (theta), and sustain attention (delta) (Dikker & Pylkkänen, 2013; Kirmizi-Alsan et al., 2006; Sauseng, Griesmayr, Freunberger, & Klimesch, 2010). It is also suggested that the general inhibitory effect of 5-6 Hz theta on 33 and 38/39 Hz gamma, observed in the non-musicians' spectrogram, could be responsible for the pop-out effect evidenced for musicians when these gamma frequencies have been entrained. The late ERF following 39 pps entrainment evidenced for non-musicians further supports this finding. Musicians demonstrated increased cortical activity generally compared to musically naïve participants, both during the entrainment and response periods. To recap early negative ITP-HTP ERF activity was evidenced following entrainment at 31, 33, and 35 pps, while musicians had a larger deflection in the difference wave at the selected temporo-parietal site following entrainment at 33 and 39 pps during this earlier time window, and again the difference in the strength of the source generator following entrainment at 39 pps, also in the earlier time-window, was greater for musicians.

It was hypothesised there would be differences in the neural networks recruited by musicians and non-musicians during pitch processing. Functional differences were evidenced in response to a music-syntax violation (deviant, or inharmonic tone) between groups, indicating the range and strength of cortical responses were greater for musicians across all priming conditions, except at an entrainment rate of 37 pps. Additionally, entrainment at a rate of 39 pps evidenced a source activation, positive in polarity, yet similar in its topography and time course

to the ERAN response, in the cortical response to a deviant tone in musicians only. While the strength of entrainment was expected to be evident in the amplitude of the entrained frequencies during the 100 ms ISI, instead, a much more complicated pattern of gamma interactions with slower endogenous rhythms was revealed. It was also expected there would be an effect of priming which would enhance the cortical response for non-musicians following entrainment at 33 pps. While this was not obvious in the cortical responses following target presentation, the analysis of the average frequency content, in the range 28-45 Hz, for each entrainment condition during the 100 ms window between entrainment and target presentation, suggests a general inhibitory effect of 5-6 Hz theta on 33 and 38/39 Hz, which perhaps enhanced responses to the inharmonic when these specific frequencies were entrained. Interestingly, the spectrograms for both musicians and non-musicians revealed differential effects following entrainment at 31 pps – the pattern for nonmusicians suggested a PPC with a 5-6 Hz theta wave, while the pattern for musicians indicated a PAC with a 2 Hz delta oscillation. Coincidentally, an early source ERF generator was found following 31 pps entrainment in both groups, located in the right SMG. The implication is that following entrainment at 31 pps, the difference in source activity in response to the inharmonic minus that of the harmonic, reveals additional activity in the right SMG, perhaps improving auditory attention. While entrainment at 31 pps seems to amplify responses to the deviant tone in both groups, the frequency power analysis suggests different interactions produce the result depending on music ability, perhaps suggesting a differential effect of priming at 31 pps as a function of music training. Thus, spectrograms for each group indicate differences in the patterns of interactions, and in the case of the 35 pps entrainment condition, the strength of the interaction. Coupled with the overall increased cortical activation in response to a deviant tone evidenced for musicians, it is concluded that musicians integrate pitch information much more efficiently – their response to the harmonic structure of a sound depends more on top-down processing (greater range of interactions with slower brain rhythms) than the bottom-up processing enhancement provided by the entrained prime.

4.7 Future Research

The current analysis provides motivating information regarding the differences in low level auditory binding processes dependent on musical ability.

However, further analysis is recommended. While the frequency power analysis illustrated a very complex interplay between gamma and slower endogenous oscillatory mechanisms, which increased in complexity and variety among the musician group, the suggested basis of these interactions, i.e., theta and delta modulations, have not been substantiated. A cross-frequency coupling analysis should be performed to clarify. Secondly, the source analysis conducted used a generic 3D lattice of voxels as a grid, confined to a mask of the grey matter. Thus, the source amplitudes were analysed across thousands of points in the entire volume of the brain. By reducing the area using regions of interest (ROI) it is possible functional differences in cortical responses to deviant stimuli, under each priming condition, dependent on music ability, may be revealed.

5 Differences in the Effect of Priming on Auditory Cognition Dependent on Musical Ability.

5.1 Introduction

Music, and music making behaviour, is fundamental to human social cognition, playing a vital phylogenetic role in functions such as communication, and group cohesion and co-ordination (Koelsch & Siebel, 2005). Ontogenetically, language is initially based on prosodic information, and there is evidence to support the role of music in the social, cognitive, and emotional, development of children (Trehub, 2003). Therefore, while music cognition does not involve processes that are unique to musicians, due to the complexity of the cognitive demands required to master music production, learning to play a musical instrument results in structural and functional plastic changes, as described in chapter four. Thus, the study of auditory cognitive processes in musicians and non-musicians provides an excellent means with which to investigate the underlying neural mechanisms.

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Spectrograms from the magnetoencephalography (MEG) described in chapter four – illustrating the frequency power analysis on the time-frequency data for (a) nonmusicians and (b) musicians, during the 100 milliseconds (ms) interval between entrainer offset and target onset, bandpass filtered between 28 and 45 Hertz (Hz). Each line (legend) represents a different entrainment condition, with amplitude (μ V) on the *y*-axis and frequency (Hz) on the *x*-axis.

The findings of the magnetoencephalography (MEG) experiment presented in the previous chapter suggest auditory priming differentially affects auditory processing, depending on musical ability. To recap, on each trial non-musicians and musicians were primed with pip-train stimuli (1000 milliseconds (ms) in duration), designed to entrain an auditory gamma-band response (aGBR) phase-locked to the amplitude modulation (AM) frequency of the pips which is determined by the

number of pips per second (pps). Following a short inter-stimulus interval (ISI) of 100 ms they were presented with a target pip-train stimulus, to which they made a forced choice response – the target is absent when the pip-train is monotone, and present when it alternates in tone. On half the trials, the deviant in the target pip-train was either harmonically related to (an octave higher in pitch than), or inharmonically related to (an octave plus a minor third higher in pitch than), the deviant 1000 Hertz (Hz) carrier tone within the entrainer four-pip sequence. A frequency power analysis of the time-frequency data for each group (musician and non-musician) during the ISI, examining the spectral power of gamma frequencies ranging from 28 to 45 Hz, which overlapped the entrainment range of 31 to 39 Hz in 2 Hz intervals, revealed very different amplitude-frequency patterns depending on musical ability. To summarise, 31 Hz was high in amplitude for the musician group during 31, 33, and 35 pps entrainment conditions, suggesting a phase-amplitude coupling (PAC) with a 2 Hz delta wave due to attentional processes, while entraining a 31 Hz aGBR in nonmusicians indicated a phase-phase coupling (PPC) with a 5-6 Hz theta rhythm. Also, a 6 Hz inhibitory modulation was suggested, for both groups, however, for nonmusicians this modulation was manifest as a general reduction in 33 and 38/39 Hz, while for musicians the interaction occurred only during 33 and 39 pps entrainment and was evident as a complete attenuation of the corresponding entrainment frequency. Finally, a 6 Hz theta PPC was suggested, again for both groups, during 35 pps entrainment conditions, slightly shifted in phase between groups, and more amplified in the musicians' spectrogram. Interestingly, entrainment at a rate of 35 pps also resulted in the smallest difference in reaction time (RT) responses to harmonic and inharmonic targets in both groups, while the theta modulation resulting in reduced 33 and 38/39 Hz observed in the non-musician spectrogram possibly influenced the pop-out effect revealed in the RT responses for this group. The findings suggest that the effects of auditory priming on the temporal dynamics involved in auditory binding processes differ as a consequence of music training. Thus, the question is raised – what are the differences in the dynamic-systems structure of auditory cognition dependent on music training, when the effect of auditory priming is removed?

The focus of this chapter is on examining the differences in musicians' and non-musicians' responses to harmonic and inharmonic tones when the auditory system has been primed with an entrained aGBR compared to when the entrainment

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is disrupted. To achieve this, musicians and non-musicians participated in two counterbalanced experimental sessions, one replicating the paradigm used during the MEG experiment, i.e., the no-mask condition, and another which presented white Gaussian noise as a simultaneous mask during the 1000 ms entrainment period, i.e., the mask condition. A simultaneous white Gaussian noise masker was chosen as the aim of using a masker was to completely disrupt any priming effect due to entrainment. White Gaussian noise is a random signal of broadband frequencies, i.e., it covers a wide audible range as opposed to a narrow range of frequencies, with all frequencies present at the same average intensity, and a normal (Gaussian) distribution of amplitude fluctuations, i.e., probability is greater for amplitudes closest to zero. The frequencies present in the entrainer include the carrier frequencies of 500 and 1000 Hz, and the AM gamma frequency ranging from 31 to 39 Hz depending on entrainment rate. Masking frequencies that are close in range to the signal frequency, or frequencies, increase detection threshold levels, and therefore a broadband spectrum of frequencies is considered most appropriate for this study due to the wide variation in the range of frequencies present in the entrainer stimulus. Most masking experiments examine detection thresholds, however, in this case the aim is to present the mask at an intensity which is above the detection threshold of the entrainer. Therefore, the signal to noise ratio (SNR) was kept in line with the recommended SNR of less than 5 dB (Yost, 2007).

The deleterious effects of noise on neural synchrony have been well documented (Billings, Tremblay, Stecker, & Tolin, 2009; Russo, Zecker, Trommer, Chen, & Kraus, 2009; Warrier, Johnson, Hayes, Nicol, & Kraus, 2004), including degradation in the processing of temporal information required for speech onset response and formant transition processing, at the brainstem level (Burkard & Sims, 2002; Cunningham, Nicol, Zecker, Bradlow, & Kraus, 2001). Neural responses to auditory stimuli are delayed and reduced in children with specific language impairment (SLI) (Banai et al., 2009; Hornickel, Skoe, Nicol, Zecker, & Kraus, 2009), while these same responses are enhanced among musicians (Kraus, Skoe, Parbery-Clark, & Ashley, 2009; Parbery-Clark, Skoe, Lam, & Kraus, 2009). These neural enhancements have also been associated with years of musical experience (Kraus et al., 2009; Musacchia, G., Strait, D., & Kraus, 2008). Notably, Norton et al. (2005) evidenced neural, cognitive and musical ability enhancements among children following just 18 months of musical training compared to an age-matched sample, with whom there were no measurable differences prior to training. Auditoryspecific effects of musical training have been demonstrated to generalise to language processing benefits associated with the neural plasticity effects of musical training (Moreno et al., 2009; Parbery-Clark et al., 2009; Schön, Magne, & Besson, 2004). Furthermore, temporal processing deficits found among children with specific language impairment (SLI), dyslexia, and auditory processing disorder, are related to the backward masking effect during the formant transition period, produced by the vowel on the preceding consonant (Johnson, Nicol, Zecker, & Kraus, 2007; Rosen & Manganari, 2001). Based on these findings, by masking the entrainer with noise, as described above, any effect of entrainment on the responses of musicians and nonmusicians will be removed, thus allowing for a comparison to be made between responses following entrainment versus no entrainment.

5.2 Research question.

According to Musacchia et al. (2007), musicians demonstrate practice-related changes as training leads to reciprocal efferent and afferent plasticity which strengthens subcortical and cortical centres (Musacchia, Sams, Skoe, Kraus, & Merzenich, 2007). Thus, it is suggested that musicians depend less on early auditory binding processes and by extension, the effect of priming is possibly reduced in this population. Therefore, it is considered that by disrupting the entrainer with a noise masker, the difference in RTs to harmonically related stimuli, as a function of music training, can be compared when the auditory system is primed with gamma-band frequencies and when it is not primed. It is hypothesised that musician's performances do not benefit from entrainment. Therefore, the musicians' responses will not differ significantly across the mask and no-mask conditions, while non-musicians' responses will.

5.3 Methods

5.3.1 Sample. Thirty-two participants recruited in the Galway area took part in this study. The sample consisted of two groups: Musicians with grade 4+ or an international equivalent (n = 16, 3 male, 2 left-handed, M age 26.69 years, SD 10.1), and non-musicians with no music experience (n = 16, 9 male, 3 left-handed, M age 31.19 years, SD 8.3). Of the musician group, all played at least one instrument regularly (four played two, and one played three, instruments regularly). Grades
achieved were as follows – ten grade 8+ (including two degrees and one Masters Level) in at least one instrument, one grade 7, four grade 6, and one grade 4. All participants reported normal hearing and provided informed consent.

5.3.2 Apparatus and stimuli. As for the TQM based experiments, experimental trial and stimulus generation were controlled by a Dell Latitude E5450, Intel Core i7-6700HQ 2.60 GHz laptop. Sound stimuli were generated electronically via Chronos PST-101600, which also measured RT (with a resolution of <1 ms). Experiments were programmed in E-Prime 2.0 (Professional, SP2, build 2.0.10.356) (Schneider, Eschman, & Zuccolotto, 2002). The pip-train stimuli were identical to the stimuli used in the magnetoencephalography experiment, which were in the range originally tested by the developers of the auditory priming paradigm, Aksentijevic, Barber, and Elliott (2011), and were created in audacity (for details see section 2.2 Stimuli, in chapter 2). Sound stimuli were presented diotically, and stimulus intensity was kept at an average 40 dB sound pressure level (SPL; Aweighting). Participants were instructed to respond as rapidly and accurately as possible to the presence or absence of the target tone in the second sound stimulus. During the masked session, the entrainer on each trial was simultaneously masked with broadband white Gaussian noise, with an increased stimulus intensity of 15 dB compared to the entrainer and target stimuli, i.e. measuring an average 65 dB sound pressure level (SPL; A weighting). Stimulus intensity during the mask condition was controlled using an application available on the Chronos response device, allowing the sound level intensity of a selected sound stimulus to be attenuated – in this case the entrainer was attenuated by 15 dB. Calculated in Matlab, the SNR for the entrainer and broadband white Gaussian noise measured 2.5 dB, which is below the recommended SNR for signal thresholds (between 5 and 15 dB; (Yost, 2007).

5.3.3 Design and statistical analyses. Error trials were removed from the analysis and RT data were corrected as described in chapter two. A mixed design was used with group as the between factor, with two levels (musician, and non-musician), and three within factors, mask, with two levels (mask, and no-mask), rate (pps: five levels; 31 - 39 Hz) and target (asymmetrical as described for experiment one, chapter two). Levene's test for equality of variance was applied to the analysis, as was Greenhouse-Geisser estimates of sphericity, and degrees of freedom were corrected when a violation to an assumption was indicated. Bonferroni correction was applied to all pairwise comparisons. The entrainer and ISI were again kept

constant at 1000 ms and 100 ms, respectively. Participants were presented with 30 trials per condition which resulted in 1200 trials per participant, $(2 \times 5 \times 2(2) \times 30 = 1200)$. At the end of each block, the experimental programme presented the first two trials, any error trials, and the trial directly proceeding an error trial, again. Thus, the number of repetitions were reduced. These trials were removed during the analysis, and the repeated trials were retained. RTs are often delayed at the start of a block and following an error, and for this reason the design was changed. There were two experimental sessions, one which presented the usual entrainer-ISI-target sequence on each trial, and one which presented this sequence with a simultaneous white Gaussian noise mask during presentation of the entrainer. Experimental sessions were counterbalanced and took place on separate days (approximately 40 minutes in duration each). Individual sessions began with a 15-trial practice block, followed by 600 trials presented in blocks of 40. Experimental conditions were completely randomised within and between blocks. The dependent variable was corrected reaction time (RT).

5.4 Results

A mixed ANOVA with group as the between factor, and mask (two levels; mask and no-mask), rate (pps: five levels; 31, 33, 35, 37, and 39 pps), and target (three levels; TA, ITP, and HTP) as within factors, was conducted on the exponents of the means of log-transformed RT data. The effect for group was not significant $(F_{(1,30)} = .28, p = .6, \eta_p^2 = .01)$. There was a significant main effect for target $(F_{(1,24,1)})$ $_{37.31} = 4.57$, p = .032, $\eta_p^2 = .13$), due to faster ITP RTs compared to HTP RTs (MD =14.56, SD = 2.46, p < .001), and rate ($F_{(4, 120)} = 6.19$, p < .001, $\eta_p^2 = .17$), due to significantly slower RTs to targets presented at 31 pps entrainment compared to targets presented at 35, 37 and 39 pps rates of entrainment. A significant four-way group by mask, by rate, by target interaction was revealed ($F_{(8, 240)} = 2.03, p = .044$, $\eta_p^2 = .06$). Under normal entrainment conditions (no-mask), musicians demonstrated faster ITP RTs compared to HTP RTs (p = .02, to p < .001), (TA RTs were also faster than HTP RTs at 31 (p = .045), and 37 pps (p = .023)), while RTs to both ITP and HTP targets did not differ significantly at 35 and 39 pps entrainment rates when the entrainer was disrupted by the noise masker (p = .068, and p = .087, respectively) (again TA RTs were faster than HTP RTs at 37 pps (p = .021)). While for nonmusicians, ITP RTs were significantly faster compared to HTP RTs when

entrainment was disrupted by a noise mask at entrainments of 31 and 37 pps (p = .027, and p = .017, respectively), and when entrainment occurred, i.e., without masking, this ITP advantage switched to targets presented at 33 pps (p = .005).

To examine this interaction effect more closely, and the overall effect of priming on RT responses to a harmonic relation as a function of music training, a mixed ANOVA was conducted for the between and within factors on corrected RT responses. While the effect of group was not significant ($F_{(1, 30)} = .6$, p = .44, $\eta_p^2 = .02$), significant main effects were found for harmony, and rate; $F_{(1, 30)} = 35.1$, p < .001, $\eta_p^2 = .54$, and $F_{(4, 120)} = 3.38$, p = .012, $\eta_p^2 = .1$, respectively. Also, there were significant interaction effects between group and harmony ($F_{(1, 30)} = 6.8$, p = .014, $\eta_p^2 = .19$), and between group, mask, harmony and rate ($F_{(4, 120)} = 2.93$, p = .024, $\eta_p^2 = .1$). The main effect for harmony was due to overall faster RTs to ITP targets (MD = 14.56, SE = 2.46, p < .001), while the effect for rate was due to RTs during the 35 pps condition that were significantly faster compared to RTs during the 31 and 33 pps conditions (MD compared to 31 pps RTs = 5.15, SE = 1.59, p = .029, and MD compared to 33 pps RTs = 5.69, SE = 1.59, p = .046,).

Gr.	Mask	Rate	Harmony		Mean	Std.	Sig. ^b	95% Co	nfidence
					Diff.	Error	•	Interval for	
					(2-1)			Differ	rence ^b
	1=Mask		2 = HT	P,1 = ITP				Lower	Upper
	2=No-							Bound	Bound
	Mask								
Mus	1	31	2	1	16.235*	6.131	.013	3.715	28.755
		33	2	1	16.500*	5.573	.006	5.119	27.881
		35	2	1	16.893*	7.039	.023	2.517	31.269
		37	2	1	14.738*	5.143	.008	4.234	25.242
		39	2	1	17.434*	7.598	.029	1.916	32.951
	2	31	2	1	31.741*	7.995	.000	15.413	48.070
		33	2	1	16.111*	5.407	.006	5.068	27.154
		35	2	1	26.024*	6.153	.000	13.458	38.589
		37	2	1	23.069*	7.899	.007	6.938	39.200
		39	2	1	31.053*	6.240	.000	18.310	43.797
nMus	1	31	2	1	17.118*	6.131	.009	4.598	29.638
		33	2	1	8.819	5.573	.124	-2.562	20.200
		35	2	1	1.349	7.039	.849	-13.027	15.726
		37	2	1	15.374*	5.143	.006	4.870	25.878
		39	2	1	6.399	7.598	.406	-9.119	21.916
	2	31	2	1	-12.750	7.995	.121	-29.079	3.579
		33	2	1	18.507*	5.407	.002	7.464	29.551
		35	2	1	2.561	6.153	.680	-10.005	15.126
		37	2	1	9.494	7.899	.239	-6.637	25.625
		39	2	1	14.548*	6.240	.027	1.805	27.292

Table 5.1. Study 4, Pairwise Comparisons: Group by Mask by Rate by Harmony.

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

2 = HTP; harmonic target present.

1 = ITP; inharmonic target present.

Gr; Group: Mus (musicians), and nMus (non-musicians).

Bonferroni adjusted pairwise comparisons revealed that the four-way interaction was due to the differential effects of music ability dependent on entrainment. HTP-ITP RT differences were significant for musicians at all rates and independent of the mask, i.e., both when entrainment was masked and when it was not (p = .029, to p < .001). However, the difference in HTP RTs during the 31 pps condition, between the mask and no-mask conditions, was found to be significant, i.e., HTP responses following entrainment at 31 pps (no-mask condition) were significantly slower compared to HTP responses during this condition when the entrainer was disrupted by noise (mask condition), (MD = 22.7, SD = 10.2, p = .033). For non-musicians, the entrainment rates which yielded a significant HTP-ITP difference altered depending on the mask. Under normal entrainment conditions, i.e., no-mask, faster ITP compared to HTP RTs were found at entrainment rates 33 and 39 pps (p = .002, and p = .027, respectively), while masking the entrainer with noise resulted in faster ITP responses during the 31 and 37 pps conditions (p = .009, and p = .006, respectively) (see table 5.1).





Graph of the RT responses (*y*-axis) to both harmonic (unfilled) and inharmonic (filled) targets, for both musicians (red-diamond) and non-musicians (blue-square), during (a) the no-mask (normal entrainment) condition, and (b) the mask (disrupted entrainment) condition, mapped over the oscillatory trace of the entrainer pip-sequence (top *x*-axis, bottom *x*-axis represents the number of oscillatory cycles completed by the four-pip prime at target presentation time).

Given the four-way interaction effect, to examine the effect of entrainment versus no entrainment more closely the alpha level was adjusted to .025, and a further ANOVA was carried out on the data for each mask condition separately. When the entrainer was not masked, i.e. under normal entrainment conditions, there was a significant effect of harmony, and rate ($F_{(1,30)} = 23.8$, p < .001, $\eta_p^2 = .44$, and $F_{(4, 120)} = 3.4$, p = .011, $\eta_p^2 = .1$, respectively), a significant interaction effect between harmony and group ($F_{(1,30)} = 8.49$, p = .007, $\eta_p^2 = .22$), and a significant three-way interaction between group, harmony and rate ($F_{(4, 120)} = 4.67$, p = .002, $\eta_p^2 = .14$). The effect of harmony was due to faster ITP RTs overall (MD = 16, SE = 3.28, p < .001), while the harmony by group interaction was due to the main effect of harmony holding for musicians only (musicians HTP-ITP RTs; MD = 25.6, SE = 4.64, p < .001, non-musicians HTP-ITP RTs; MD = 6.42, SE = 4.64, p = .173). The effect of rate was due to faster overall RTs as rate increased. While ITP RTs were faster at all entrainment rates for the musician group (MD = 25.6, SE = 4.64, p < .001), the

interaction effect was due to ITP RTs that were significantly faster compared to HTP RTs for the non-musician group at 33 pps entrainment only (MD = 18.51, SE = 5.41, p = .002) – evidence of a pop-out effect which is consistent with the previous literature (see figure 5.2). The difference for this group at 39 pps approaches significance (p = .027), which is consistent with the MEG RT results.



Figure 5.3. Masking experiment; priming as a function of return phase.

The above illustration graphs the HTP-ITP difference (*y*-axis) at each rate of entrainment (legend labels) for musicians (red filled diamonds) and non-musicians (blue unfilled squares) during (a) the no-mask (normal entrainment) condition, and (b) the mask (disrupted entrainment) condition, mapped over the oscillatory trace of the entrained pip-sequence (bottom *x*-axis). The middle *x*-axis defines the last fully presented pip (LFPP), while the top *x*-axis is a measure of the completion of the pip represented on the bottom axis (CNP; completion of next pip).

The results were decidedly different when the entrainer was masked by noise. The only main effect was for harmony ($F_{(1, 30)} = 26.63$, p < .001, $\eta_p^2 = .47$), due to faster ITP RTs for both groups (musicians; MD = 16.1, SE = 3.59, p < .001, and non-musicians; MD = 9.8, SE = 359, p = .01).

Group	Rate	Harmony		Mean Difference	Std. Error	Sig. ^b	97.5% Confidence Interval for	
				(2-1)			Difference ^b	
		2 = HTP, 1 = ITP					Lower	Upper
							Bound	Bound
Musician	31	2	1	16.235*	6.131	.013	1.770	30.700
	33	2	1	16.500*	5.573	.006	3.351	29.649
	35	2	1	16.893*	7.039	.023	.283	33.503
	37	2	1	14.738*	5.143	.008	2.602	26.874
	39	2	1	17.434	7.598	.029	495	35.362
nMusician	31	2	1	17.118*	6.131	.009	2.653	31.583
	33	2	1	8.819	5.573	.124	-4.330	21.968
	35	2	1	1.349	7.039	.849	-15.260	17.959
	37	2	1	15.374*	5.143	.006	3.238	27.510
	39	2	1	6.399	7.598	.406	-11.530	24.327

Table 5.2. *Study 4, Pairwise Comparisons, Mask Condition: Group by Rate by Harmony.*

Based on estimated marginal means

*. The mean difference is significant at the .025 level.

b. Adjustment for multiple comparisons: Bonferroni.

2 = HTP; harmonic target present.

1 = ITP; inharmonic target present.

Bonferroni adjusted pairwise comparisons revealed the HTP-ITP difference was significant at rates 31, 33, 35, and 37 pps for the musician group, and marginally significant at 39 pps entrainment (p = .029, to p = .006), while the difference only remained significant for the non-musician group at entrainment rates 31, and 37 pps (p = .009, and p = .006, respectively, see table 5.2). From figure 5.2 (b), it can be observed that RTs did not decrease with increasing rate for either group. The results support the hypothesis that entrainment does not facilitate an enhancement of musician's responses to the harmonic structure of a sound. Furthermore, the evidence suggests that the effect of priming on the response of non-musicians to harmonic structure does not so much facilitate a response dependent on the gamma frequency entrained, as shunt the normally occurring gamma oscillators by approximately 2 Hz.

5.4.1 Error Analysis. Musicians made fewer errors overall, with an average 4.38% error rate compared to 7% for non-musicians. The arcsine of the square root of the proportion of errors for each condition were analysed to examine error rate depending on music ability (group; musicians and non-musicians) and the disruption of entrainment (mask condition; mask and no-mask). There was a significant main effect for target ($F_{(1.66, 49.9)} = 20.03$, p < .001, $\eta_p^2 = .4$), due to a higher error rate in response to HTP targets (HTP-TA error rate difference; MD = .057, SD = .016, p =

.003, and HTP-ITP error rate difference; MD = .087, SD = .015, p < .001), while the error rate in response to ITP targets was lowest (TA-ITP error rate difference; MD = .029, SD = .01, p = .025, and HTP-ITP error rate difference; MD = -.087, SD = .015, p < .001). Therefore, it can be concluded that the facilitation of ITP responses, and related effects, in the statistical analyses of the corrected RT means, were due to the effect of entrainment on performance in both groups, and not a speed-accuracy trade-off.

5.5 Discussion

In summary, the findings suggest that entrainment does not benefit the oscillatory mechanism involved in binding pitch information in musicians and may even slow responses to harmonically consonant targets – particularly following a 31 pps entrainment, given the significant difference between the mask and no-mask conditions for HTP RTs following this entrainment rate. By comparison, when participants do not have any music training, entrainment at a specific rate of 33 pps (and to a lesser extent at 39 pps) facilitates a response to inharmonically related tones, which supports the interaction between 33 and 39 Hz gamma and a slower ~ 6 Hz theta rhythm implied by the frequency power analysis conducted on the MEG data for non-musicians. Interestingly when the system is not primed with these gamma frequencies, the non-musician group demonstrate a shift in the ~6 Hz interaction from 33 and 39 Hz to 31 and 37 Hz (see figures 5.2 and 5.3). There are two differences in the findings of this experiment compared to previous findings under normal entrainment conditions that should also be noted. One is that HTP responses at an entrainment rate of 31 pps were faster than ITP RTs at this rate for the non-musicians (ITP responses in all other studies have been consistently faster than HTP responses). Second, previously the HTP-ITP difference has not been found to be significant for musicians, at any rate. This response time difference has been used as a measure of the strength of the prime, and therefore it was suggested that the prime did not influence musician's responses, while the magnitude of this difference in the non-musician population was taken as an indication of the strength of the priming effect dependent on the entrained frequency. Based on the findings here, coupled with the findings from the MEG experiment, it is suggested that priming may interfere with the oscillatory mechanism involved in auditory binding, and the auditory system overcomes this hindrance more efficiently when it has been

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musically trained – due to an increase in theta activity (top-down processing). The graphed data in figure 5.3 highlights this interference to responses to the harmonic structure of a sound dependent on musical ability. When the entrainment process is disrupted, i.e., a stimulus code is not provided in advance (figure 5.3 (b)), musicians and non-musicians respond more rapidly to inharmonic tones. This pattern is expected as an inharmonic tone contradicts the listeners anticipation of a consonant tone. However, for musicians this HTP-ITP RT difference is not affected by entrainment, except following entrainment at a rate of 31 pps – in which case responses to the harmonic are slower. By comparison, non-musicians display differences in this HTP-ITP RT difference dependent on entrainment. It should be noted that regardless of whether the entrainer is disrupted or not (masked versus normal entrainment), the target is presented at the corresponding rate, i.e., during the 33 pps condition, in both the mask and no-mask conditions, the target is presented at a rate of 33 pps. When a non-musician's auditory system is primed with either 33 or 39 Hz, the HTP-ITP difference increases, and when it is not primed, and targets are presented at 31 or 37 pps, the HTP-ITP difference increases. In fact, when entrainment is disrupted, and targets are presented at 31 or 37 pps, the HTP-ITP RT difference is the same for both musicians and non-musicians (see figure 5.3(b)). When correspondence is drawn between these findings and the information from the spectrogram for musicians and non-musicians in the previous chapter, it is considered that 31 Hz has a critical role in auditory binding. When musicians are primed with this gamma frequency, responses to a consonant harmonic are interrupted. Also, the amplitude of 31 Hz was large among musicians following entrainment at 31, 33, and 35 pps in the MEG data, indicating a PAC with delta. Therefore, it is suggested that entraining a 31 Hz wave may impact negatively on normal 31 Hz activity. Priming the auditory system of a non-musically trained brain with a 31 Hz frequency promotes a PPC with a 5-6 Hz theta wave, according to the MEG spectrogram for non-musicians, possibly enhancing responses to harmonic targets presented at the same rate. However, when the auditory system is not primed, the HTP-ITP RT difference for targets presented at 31, or 37 pps, are the same for musicians and non-musicians. Under this no-mask condition, the trend of the data in figure 5.3 (b) suggests that the difference in responses to harmonically dissonant (inharmonic) compared to consonant (harmonic) tones, is consistent for musicians, regardless of the presentation frequency, and it is greatly reduced for targets

presented at 31 and 37 pps among non-musicians – to the extent that the difference is in-line with musician's responses. Interestingly, the HTP-ITP RT differences are somewhat reversed among non-musicians when entrainment is disrupted compared to when primed. Following entrainment, a pop-out occurs during the 33 and 39 pps conditions while the HTP-ITP RT difference during the 31 and 37 pps conditions is not significant, however, the pop-out shifts to targets presented at 31 and 37 pps when a corresponding prime is not provided, and the HTP-ITP RT difference is reduced during the 33 and 39 pps conditions (see figure 5.2). The findings of the source analysis on the MEG data found increased activation in the right supramarginal gyrus (SMG) in the cortical responses of both musicians and nonmusicians to a deviant tone (the inharmonic), following a 31 pps rate of entrainment. Yet when targets are presented at 35 pps, regardless of a prime, the HTP-ITP RT difference in non-musicians' responses is very small (non-musicians; no-mask, MD = 2.56, SD = 6.15, p = .68, versus mask, MD = 1.35, SD = 7.04, p = .849). Coupled with the PPC theta modulation observed in the spectrogram for both musicians and non-musicians following 35 pps entrainment, it is further suggested that 35 Hz is instrumental in auditory binding mechanisms. However, the question is raised as to why target presentation at 35 pps closes the gap in RT responses to both consonant and dissonant tones in non-musicians, while remaining consistent with other presentation rates for musicians. Target presentation time in both the mask and nomask condition remained constant at 1100 ms. Presuming the important influence during the 35 pps condition is a PPC modulation with a 6 Hz theta wave (given peaks in the spectrogram, illustrated in chapter four, for both musicians and nonmusicians following 35 pps entrainment occurred at a distance of 6 Hz), at 1100 ms a 6 Hz wave emerging in response to the stimulus onset (entrainer or masked entrainer) would have completed 6.6 oscillatory cycles, which is close to the negative peak. However, it should also be noted at 1100 ms stimulus onset, a target would be presented at the positive peak (90° phase angle) of 6.6 Hz theta wave, which is very close to the 6.69 Hz interaction evidenced in previous behavioural findings in both the auditory and visual binding research. Perhaps it is a theta phase relation such as this, that underlies the consistent HTP-ITP RT difference in nonmusicians' responses to targets presented at a rate of 35 pps.

Music training induces practice-related changes in cortical processing, presumed to underlie pitch perception. It has been suggested that this is due to a

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combination of top down and bottom up influence. The former is the result of modified neural architecture required for performance, due to music training, beginning with higher processing areas and gradually enhancing lower sensory areas. The latter is a consequence of Hebbian learning, which arises from the simultaneous activation of pre- and post-synaptic auditory brainstem neurons, strengthening the efficacy of the brainstem responses encoding sound (Musacchia et al., 2007) – the difference in harmonic responses under normal stimulus entrainment compared to when masked at 31 pps reflects this influence. Altogether, the findings of this experiment support this practice-induced change in cortical processing hypothesis. Effects of entrainment occur at an early stage of processing, which influences the feedforward gamma oscillators that carry the stimulus information generating predictions, thus influencing a response to a harmonic relation. The effect is greatly reduced for musicians, presumably due to top-down influence resulting from music training. While the responses of non-musicians to harmonic structure are more affected by the feedforward gamma oscillators, the evidence suggests that a 6-6.6 Hz theta rhythm does play an important role in the auditory binding process when the brain is not musically trained.

5.6 Future research

It would be advisable to test the findings of this experiment using MEG. While the data suggest the entrainer disrupts the normal binding mechanisms in the musician's brain, convergence with brain imaging data is required for further investigation. Analyses examining the exact cross-frequency couplings involved in pitch processing is also recommended. The results from this study, combined with the MEG findings, have provided new insight into the differences in pitch processing mechanisms dependent on music training, and the auditory paradigm its-self has proven to be a very useful tool in this regard. Presuming entrainment disrupts the normal pitch processing mechanisms in the musically trained brain, future research could use this to examine the effects of the dissociation in processing when entrainment is disrupted.

It is evident from the findings of this experiment that the white Gaussian noise masker used was sufficient to disrupt the entrainment of an aGBR. However, the low amplitude modulation frequency was vaguely audible. According to Yost (2007), the signal to noise ratio (E/N_0) must be ~5 to 15 dB for signal detection,

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however, the ratio is closer to the lower extreme, i.e., closer to 5 dB, for lowfrequency signals. The signal to noise ratio for this experiment was 2.5 dB which was sufficient according to the literature, and for the purposes of this experiment the results concur. However, it is also the case that maskers with frequencies near the signal frequencies are the most effective – once the signal is less than 200 ms in duration to avoid beating. Beating occurs when the difference frequency between the mask and the signal is between 3 and 5 Hz, which implies a period duration of 333 ms and 200 ms respectively. Therefore, restricting the duration of the signal to below one period duration of a 5 Hz (200 ms) frequency will eliminate beating. It is possible that the use of three simultaneous narrowband noise maskers, each with frequencies centred on 500 Hz, 1000 Hz, and the gamma frequency for the corresponding condition, would act as a more efficient mask, eliminating the detection of either carrier frequency and the AM (gamma) frequency. The use of three different narrow bands of noise should also eliminate the effect of beating by increasing the number of frequencies in the overall mask.

6 Conclusion

6.1 Introduction

The current doctoral research built upon visual and auditory binding studies which have employed stimulus entrainment as a psychophysical method to investigate the temporal dynamics involved in low-level object feature integration (Aksentijevic et al., 2011, 2013, 2014; Elliott, 2014; Elliott & Müller, 1998; 2004). These paradigms manipulate the rate of an entrainment stimulus, i.e., the number of frames per second in vision, resulting in a corresponding rate of flicker, and the number of on- and off- set ramped pure tone-bursts (pips) per second in audition, resulting in a corresponding amplitude modulation frequency – to prime the cortex with a temporal code matching the frequency of entrainment (always in the gamma range, 30-70 Hz). To investigate a possible interaction in phase between these evoked gamma frequencies and an endogenous brain rhythm, the target presentation time is calculated to place the target in a specific phase relation with the slower rhythm. Participants in the auditory task make a response regarding the harmonic structure of the target. Analysis of the corrected reaction time (RT) data allows for an examination of the frequency interactions that invariably facilitate these responses.

The purpose of this dissertation was to investigate the parameters of the oscillatory temporal dynamics involved in auditory binding. The aim of the experiments presented in this volume was two-fold. Firstly, correspondence in the oscillatory mechanisms involved in this low-level feature binding across the visual and auditory modalities was investigated. Two theories deduced from the findings of the visual binding research were tested in the auditory domain, using the auditory stimulus entrainment paradigm designed by Aksentijevic et al. (2011), to assess similarities. One, the General Phase Angle Hypothesis (GPAH), explains an anticipatory response to a primed stimulus dependent on the phase relation, at target presentation time, of evoked frequency oscillations and a specific theta brain rhythm whose periods regularly align in phase. Two, the Return Phase Hypothesis (RPH), predicts an anticipatory response that lags the prime in the oscillatory trace of the entrainer when out of phase with this rhythm. Secondly, differences in the dynamic

systems structure of auditory binding mechanisms as a function of music training were examined using a combined behavioural experiment (as for the previous experiments – an RT study) and brain imaging approach. The final study disrupted the entrainment process to investigate differences in the effects of priming the auditory system with a temporal code dependent on music training.

The first line of investigation focused on an examination of similarities in the temporal dynamics of visual and auditory binding mechanisms, and the second line on differences in the system structure of the auditory binding dynamics dependent on music training. Increasing our knowledge of mental timing systems that cross modalities develops our understanding of global communication systems within the brain, while examining differences in how such a system operates when optimised compared to a standard level, i.e., through the plasticity effects of music training, provides insight into the microstructure of the underlying mechanism. Finally, combining psychophysical and neuroimaging methods uncovers converging findings, promoting increased confidence in the interpretation of the underlying mental events.

6.2 Summary of findings

Chapter 2 discussed the findings of five experiments assessing generalisation of the temporal and phase dynamics of low-level visual feature binding mechanisms to the equivalent auditory mechanisms, based on similar frequency-specific priming effects found using theoretically similar stimulus entrainment priming paradigms. The findings from the visual stimulus entrainment research suggest that gamma frequencies which regularly converge in phase with a 6.69 Hz rhythm (whose periods share integer relations) promote an anticipatory response, as predicted by the GPAH, while according to the RPH, target presentations in phase with this rhythm facilitate an anticipatory response, however, when presented out of phase with this rhythm a response that lags the prime in the oscillatory trace of the entrainer is facilitated. Table 6.1. Predicted Effects and the Main Outcome for Each Experiment in StudyOne.

Column one details the study and the experiment number, while column two indicates both the theta wave presumed to modulate the entrained auditory gammaband response (aGBR), and the phase of this wave at target presentation time. The predicted effects are listed in column three and the main findings in column four.

Exp.	θ phase	Hypotheses	Outcomes		
Study 1	6.69 Hz	Examine auditory priming effects			
Exp 1	130°	A facilitation of responses to inharmonic targets will depend on presentation during the deviant pip trace.	H0 rejected: However, the effect presents as a facilitation of harmonic, not inharmonic, responses.		
Exp 2	(a) 95.5°	(a) Target presentation during the deviant pip trace will result in faster HTP RTs	(a) H0 not rejected: ITP and HTP RT data trends are the same.		
	(b) 24.5°	(b) Target presentation early in the theta cycle will influence a facilitatory response	(b) H0 rejected: Disruption of the harmonic salience/ facilitation of inharmonic responses.		
Exp 3	0°	Target presentation at zero phase lag with theta will disrupt harmonic salience	H0 rejected: Pop-out half way through the oscillatory trace of the prime.		
Exp 4	0°	Frequency range precedes range in Exp. 3 - target presentation at zero phase lag with theta will disrupt harmonic salience	H0 not rejected: It is suggested that the deviant pip trace is a stronger determinant of a priming effect at slower gamma frequencies, than theta phase.		
Exp 5	0°	Frequency range proceeds range in Exp. 3 - target presentation at zero phase lag with theta will disrupt harmonic salience	H0 rejected: Pop-out half way through the oscillatory trace of the prime.		

Table 6.2. Predicted Effects and the Main Outcome for Each Experiment in StudiesTwo to Four.

As for Table 6.1, column one provides the study and experiment numbers. Column two specifies both the theta wave presumed to modulate the entrained auditory gamma-band response (aGBR), and the phase of this wave at target presentation time. The predicted effects are listed in column three and the main findings in column four.

Exp.	θ phase	Hypotheses	Outcomes		
Study 2	7.29 Hz	TQM as a guide			
Exp 1	0°	Guided by TQM parameters, target presentation at zero phase lag with theta will disrupt harmonic salience	H0 not rejected: However, evidence of harmonic disruption due to a 270° entrainer frequency relation at target presentation time.		
Exp 2	270°	Guided by TQM parameters, target presentation at a 270° phase lag with theta will disrupt harmonic salience	H0 not rejected: However, gamma-theta phase alignment at the negative peak facilitates a harmonic response, while non-alignment disrupts the unexpected inharmonic tones.		
Study 3	6.69 Hz	Magnetoencephalography (MEG) study			
	130°	There will be differences in priming effects dependent on music ability	H0 rejected: Musicians exhibit stronger cortical responses to inharmonic deviant tones, and a greater range of gamma- theta/delta cross-frequency coupling.		
Study 4	6.69 Hz	Auditory Masking Study			
	130°	Priming the auditory system with a gamma-band frequency does not facilitate musicians' responses to a harmonic	H0 rejected: Priming does not facilitate musicians' responses. Priming non-musicians shifts the facilitation of a response by 2 Hz, from 31 and a 37 Hz when not primed, to 33 and 39 Hz when primed, with the corresponding gamma-band response.		

The findings of these five experiments were complicated and often contrary to expectations (see table 6.1). It is posited the reason for this is that while the

hypotheses were based on priming effects that have been evidenced in the visual priming research, and theories grounded in these findings, the prime in each paradigm is unique and therefore does not allow for a direct comparison of effects. The visual paradigm has two conditions – either the target is primed at the correct location in the first frame of each four-frame sequence of the premask (intraphase), or the crosses marking the location of each of the four corners of the Kanizsa square (target) are located across the frame sequence (interphase). Following premask termination, the target is presented at the correct location (present), or it is not (absent). In contrast the auditory prime is a repeated four-pip sequence, comprising a 1000 Hz tone pip, and three 500 Hz pips. The response is based on the harmonic relation between the target and the prime. Participants are instructed to report the target as present if it alternates in pitch. Target present stimuli are either harmonically related, i.e., the deviant pip (second in a repeated two pip sequence) shares an integer relation with the deviant (1000 Hz) pip in the prime (deviant prime: deviant harmonic as 1:2), or it is inharmonically related, i.e., the target deviant shares a semitone relation with the prime's deviant (deviant prime: deviant inharmonic as 5:12). The target absent stimulus is a repetition of a single 1000 Hz pip. Therefore, it is also harmonically related to the prime – the first harmonic of the 500 Hz pips, and serves merely to provide the participant, particularly the musically naïve participant, with a discernible response. Importantly, unlike the visual prime, the auditory prime is not confined to one pip, as the deviant pip in the prime sequence is the first harmonic of the baseline 500 Hz pips, and therefore, target absent stimuli, harmonic target present stimuli, and inharmonic target baseline pips, are all harmonically related to the primed baseline pips also. Thus, responses to the primed visual target can be discerned as anticipatory, or lagging the primed event, while responses to the primed auditory target can be considered anticipatory, based on the coherence of the 500 Hz primed template, and therefore the salience of the expected harmonic/inharmonic.

The overall conclusion based on the results of these five experiments is as follows. A gamma-code is initiated through stimulus entrainment, establishing a 500 Hz representation that waxes and wanes periodically. RP encodes the details of the four-pip prime, while a cross-frequency coupling of the aGBR with a modulating (~6 Hz) theta wave facilitates an anticipatory response to the harmonic structure, i.e., targets presented phase aligned with a modulating theta rhythm facilitate an

anticipatory response that is based on a violation of expectancies, established by RP. Responses are faster to inharmonics when the target coincides with a 500 Hz template that is maximally coherent (thus a harmonically consonant tone is expected), and faster to a harmonic when presentation occurs closer to the reset of the 500 Hz template, which requires the inhibition of odd harmonics. Overall, the results of these experiments suggest that while the findings from both the auditory and visual binding (stimulus entrainment) paradigms support the GPAH and the RPH, procedural differences between both paradigms do not allow for a test of equivalence.

Chapter 3 presented the results of two experiments which used the Time Quantum Model (TQM), a taxonomy of the fundamental temporal building blocks (epochs, thresholds and perceived durations) of mental timing, as a guide to the exact temporal and phase conditions required for an invariant response to the harmonic structure of a sound. The findings support the utility of this capacity sharing relation as a guide to the optimal temporal characteristics of the oscillatory mechanisms involved in auditory binding; cISI/Q₀ x ED/2Q₀ = 30, whereby the limit M = 30defines the maximum number of available units that ISI and ED together can occupy (Geißler, 2009). The second of these experiments manipulated target presentation time to examine the effect on RT responses when some, but not all, of the entrained aGBRs where mutually aligned in phase with a 7.29 Hz theta wave, (7.29 Hz has a period duration equal to 30 times Q_0). This target presentation time was then divided into an entrainment period and an ISI that satisfied the TQM capacity sharing relation. The findings demonstrate that while the inharmonic is consistently more salient, thus eliciting faster responses compared to harmonically consonant targets, using this guide, target presentation coincident with a phase alignment of a 7.29 Hz wave and critical gamma frequencies at an angle of 270° (the negative peak of an established theta-gamma oscillator), facilitates faster responses to the harmonic targets (compared to the overall trend). When target presentation is aligned at the negative peak of this theta rhythm and at a 0° phase angle in the oscillatory trace of entrainment frequencies, responses to the inharmonic are disrupted (again compared to the overall trend). Unlike previous experiments, target presentation time was manipulated to examine gamma-theta interactions when some of the entrained aGBRs and a theta rhythm were mutually aligned in phase, resulting in a priming effect that does not rely on RP. Furthermore, the results of these experiments

introduced the first evidence for superimposed delta and theta oscillatory activity associated with memory tasks (Harper et al., 2014). This was further supported by the magnetoencephalography (MEG) study findings.

Using a combination of the auditory priming paradigm and MEG brainimaging techniques, chapter 4 highlighted differences in the dynamic systems structure of the oscillatory mechanism involved in auditory binding as a consequence of music training, through an examination of differences in the priming effect on RT and cortical responses in musicians and non-musicians. The right supramarginal gyrus (SMG) was identified as a common source of activity in response to the discrimination of a deviant tone, regardless of musical ability, during 31 pps entrainment conditions. A response similar in topography to the ERAN response, but positive in polarity, was evident among musicians following 39 pps entrainment. Also, the spectral power of the time-frequency data during the 100 ms prior to target presentation revealed differential frequency modulation effects involving 31 Hz depending on music ability, suggesting a PPC modulated by a 5-6 Hz rhythm in nonmusicians and a PAC modulation of a 2 Hz delta rhythm in musicians. While a 5-6 Hz PPC theta modulation was evident in the spectrograms for both musicians and non-musicians (in conjunction with implied superimposed delta modulation), the strength and pervasiveness of theta modulation was greater for musicians. Thus, it was concluded that musicians rely more on top-down oscillatory mechanisms and therefore the effect of priming is reduced in this population, as priming enhances early bottom-up (gamma) carrier frequencies.

Chapter 5 communicated differences in the priming effect on responses to the harmonic structure of a sound, dependent on music training, by examining differences in musicians' and non-musicians' RT responses when primed with a harmonic sequence embedded in a stimulus entrainer, compared to when this entrainment process was disrupted by a noise masker. As hypothesised pitch discrimination processes in musicians did not benefit from entrainment, presumably due to a greater reliance on top-down processing. Furthermore, among musicians, entrainment at 31 pps may disrupt the normal oscillatory mechanism involved in this process, suggested by slower responses to the harmonic target (not in step with the overall trend) under normal stimulus entrainment at this rate, compared to responses when entrainment is disrupted with a noise masker. During the 35 pps presentation rate, the HTP-ITP difference was very small in non-musicians' responses regardless

of stimulus entrainment, i.e., under normal entrainment conditions and when this process was masked. Correspondence between the results of this experiment and the MEG experiment suggests that 31 Hz and 35 Hz are uniquely involved in oscillatory auditory binding mechanisms. Regarding top-down theta modulation, the main evidence is derived from the RT responses of non-musicians. It is speculated that the invariance in HTP-ITP RT differences for non-musicians at 35 pps presentation rates, is due to an alignment of target presentation either at the positive peak of a 6.6 Hz theta wave, or the negative peak of a 6 Hz theta rhythm, due to target presentation at 1100 ms (1100/(1000/6.6) = 7[.26]), and .26 of 360° equals a phase angle of 94°, or 1100/(1000/6) = 6[.6], with .6 of 360° equal to a phase angle of 216°). Furthermore, under normal entrainment conditions, a pop-out is revealed following 33 and 39 pps entrainment, suggestive of a 6 Hz theta modulation consistent with the MEG data for this group. However, when stimulus entrainment is disrupted with a noise masker, this pop-out effect is shifted to target responses presented at 31 and 37 pps. It is suggested that this 2 Hz difference could be a consequence of superimposed theta and delta activity under stimulus entrainment conditions due to memory related processes (Harper et al., 2014). Thus, the ~6 Hz theta modulation remains constant, while for non-musicians the gamma oscillators involved are dependent on the presence or absence of an entrained aGBR. It is therefore concluded that the effect of stimulus entrainment on the oscillatory mechanisms involved in auditory binding differs depending on music ability, and, is reduced as a consequence of music training.

6.3 Implications of the Experimental Results

Four key inferences can be drawn from the overall findings of this dissertation. Firstly, when stimulus entrainment is used to elicit a primed response, frequency-specific priming effects evidenced in both the visual and auditory binding research support an anticipatory response as predicted by the GPAH and the RPH, while a response that lags a primed event due to RP is only evident in the visual binding research findings. Procedural differences between the stimulus entrainment paradigms do not allow for direct correspondence to be made. Notably, the evidence suggests gamma-theta oscillators are involved in visual and auditory binding. Furthermore, stimulus entrainment in the auditory domain prompts an anticipatory response dependent on the harmonic relation established by the RP, and violations to

this expectancy elicit faster responses. Importantly, as in visual binding mechanisms, phase alignment with a theoretical theta rhythm facilitates a response to an anticipated event. Secondly, Hans-Georg Geißler's TQM, and more specifically a capacity sharing relation derived from this model (Geissler, 2009), provides an effective temporal framework upon which an investigation of the frequency and phase interactions within the oscillatory mechanisms that bring about auditory binding (and possibly visual binding) can be examined more efficiently and transparently. Thirdly, combining psychophysical and brain imaging methods provides a more wholistic approach to the investigation of the temporal dynamics involved in fundamental perceptual binding processes. The data from the MEG experiment provided a wealth of information that could not have been deduced from the RT data alone, allowing connections and associations to be made that would have otherwise remained under-supported, and in some cases invisible. An example of the former case is the implied gamma-theta and gamma-delta phase couplings observed in the spectrograms for both music groups, while the latter case can be highlighted by the effect of 31 pps entrainment on a cortical response to a deviant stimulus that surpasses the plasticity effects of music training, and the increased activation of a response to a deviant tone following 39 pps entrainment in the musically trained brain, despite any indication of an effect in the RT data for this group – in fact, contrary to this finding, a pop-out effect is observed in the RT responses of nonmusicians following entrainment at 39 pps. Finally, the value of comparing the system structure of the construct under investigation when it is at baseline, and when it has been enhanced, has been emphasised by the analysis of differences in the priming effect, and the effect of priming, on musicians and non-musicians. Music cognition is not unique to musicians (Koelsch, Gunter, & Friederici, 2000). However, music training strengthens cortical and sub-cortical centres due to reciprocal efferent and afferent plasticity effects, resulting in a corticofugal system that allows for more efficient feedback from higher cortical areas to the inferior colliculus, whilst at the same time enhancing pitch information relayed from the subcortical structures to the neocortex (Musacchia et al., 2007). The evidence from the masking experiment suggests that the effect of stimulus entrainment on the auditory system is to disrupt the oscillatory mechanisms involved in auditory binding. Yet this interference is less effectual in musicians, presumably due to their reduced reliance on bottom-up processing. However, the impact on the gamma-

information carriers involved in early bottom-up processing in the non-musician's brain, results in a shift in frequencies by 2 Hz (possibly due to the influence of delta modulation under entrainment conditions). Taken together, the implication is that this mask vs no-mask paradigm provides a unique method by which the dissociation in processing under entrainment and no-entrainment conditions can be examined, both when the auditory system is enhanced through music training and when it is not – thus allowing for a more complete examination of these complex oscillatory mechanisms.

Temporal cues are fundamental to auditory perception. In the early stages these cues are important for auditory stream segregation, as temporal coherence between responses encoding features of a sound source are necessary for stream formation (Shamma, Elhilali, & Micheyl, 2011). The neural responses encoding the time-varying features of complex sounds such as music and speech depend on temporal cues which provide necessary information. For example, in speech, timing information is required to encode stimulus onset and formant transitions; the resonance accompanying the transition from a stop consonant to a vowel (Skoe & Kraus, 2010). Furthermore, the temporal dynamics of the oscillatory mechanisms integrating music stimuli dictate the perception of these sounds. For example, auditory evoked potentials (AEPs) in response to dissonant chords, such as a minor third, are phase-locked to the predicted difference frequencies. The difference frequency is the difference between the frequency (or fundamentals of complex stimuli) of two sounds which gives rise to our perception of beats, in accordance with Helmholtz's psychoacoustic theory of consonance and dissonance. However, the AEP responses to consonant sounds, such as perfect fifths, do not demonstrate phase locked activity (Fishman et al., 2001). The auditory brainstem response (ABR) is an evoked response to auditory stimulation that occurs within 10 milliseconds of stimulus onset and results in a familiar pattern of activity representative of normal auditory perception (Johnson et al., 2007). The morphology of this response can be separated into two components; the transient onset response (OR), and the sustained frequency following response (FFR). Both components convey important acoustic information. Temporal and spectral precision is paramount when delivering the neural code for the relevant acoustic cues to the auditory cortex. The transient OR signals the onset of the sound, while the FFR synchronises to the periodicity of the sound and therefore represents the temporal structure precisely. This sustained

response reflects neural phase-locking and has an upper limit of ~1000Hz (Anderson, Skoe, Chandrasekaran, & Kraus, 2010). Pitch contour is a function (curve) that tracks the perceived pitch across time. The FFR encodes this information. Thus, the auditory brainstem response (ABR) represents the pitch contour and filter elements; such as onset, formant transitions (transition from one sound segment to another), and offset. Auditory processing deficits can be comorbid with Autism Spectrum Disorder (ASD), and underlies dyslexia and specific language impairment (SLI) (Hämäläinen, Salminen, & Leppänen, 2013; Kargas, López, Reddy, & Morris, 2015; Krishnan, Watkins, & Bishop, 2016). A sub-group of these populations have difficulty interpreting prosody-related sound features, including rise times (the time from sound onset to peak amplitude), and perception of amplitude modulation (AM - changes in sound intensity), and frequency modulation (FM – changes in the frequency of the sound) (Hämäläinen et al., 2013; Paul, Augustyn, Klin, & Volkmar, 2005). Given the importance of timing in auditory perception on so many different levels, and additionally, to remediate the effects of an auditory system failure, it is essential to understand the temporal relations underlying the oscillatory dynamics of auditory binding. The research described in this contribution lays the foundation for future work in this area.

6.4 Future Research

The research findings presented in this dissertation barely scratch the surface on the temporal dynamics underlying auditory binding oscillatory mechanisms. However, they do provide a roadmap for future investigation. Optimal phase alignments, entrainment durations and inter-stimulus intervals should be calculated using Hans-Georg Geißler's capacity sharing relation (Geissler, 2009), while a combination of psychophysical and brain imaging methods is advisable, allowing for a more in-depth analysis and highlighting of convergent evidence. Finally, an examination of the differences in the system structure and the effects of stimulus entrainment dependent on music ability will provide a comprehensive perspective. Cross-frequency coupling analyses should be included in the examination of timefrequency brain imaging data, given the importance of substantiating inferences regarding frequency-specific phase interactions – this remains a limitation of the current dissertation. Further consideration should also be given to the statistical

methods employed. Bonferroni adjustment can be overly conservative. An alternative method to control for multiple comparisons would be the Tukey's test considered to detect a more realistic significant difference by comparing each pair of means separately (Day & Quinn, 1989). However, future research should consider using Linear mixed effects models (LMEM) to analyse the RT data, as it is increasingly preferred by researchers over the repeated measures ANOVA, due to nonindependence in the data as each participant provides multiple data points, in each condition - resulting in some data points being more similar to each other, i.e., data from a single participant in one condition. The maximal random effects structure of the LMEM is determined based on the experimental design and includes all random effects due to variation in the independent variable (each condition) within and between participants. Thus, a LMEM accounts for nonindependence in the data. In this way, imbalance in the number of data points per participant (due to variation in error responses across participants), and variation in the range of RTs for each participant, across conditions, are accommodated (Brauer et al., 2018). Furthermore, a LMEM approach would allow for an examination of individual differences. Elliott (2014) examined Individual differences in entrainment frequencies that facilitate a response to a primed visual target, i.e., tested whether the frequencies (when entrained) that facilitate a response to a primed visual target, vary across participants. This hypothesis was not supported by the results of the investigation. However, due to differences in the auditory prime highlighted by the findings of this thesis, and also considering the amplitude differences in the spectrographs of the four musicians removed from the frequency power analysis (for that reason) in the MEG study – future research should consider examining individual differences in the effects auditory priming.

Two roadblocks to this line of research remain however – and they are time and expense. The time that the researcher and the participant must give to the data collection phase restricts the range of stimulus entrainment frequencies that can be included in each experiment – slowing down investigation procedures. To avoid fatigue effects, an experimental session is kept to within one hour. For each entrainment condition, 40 repetitions at each target presentation level are required to achieve a reliable average. This results in 4 conditions per each entrainment rate, as ITP (25% of trials) and HTP targets (25% of trials) must be balanced with TA targets (50% of trials). Therefore, in an experiment using ten entrainment rates, there are

1600 trials – 10 (rate) x 4 (target) x 40 (repetitions), and that is if a constant ISI is used. When a brain imaging technique is applied, the number of repetitions required is 60, due to movement artifacts contaminating data, resulting in several trials being lost. Hence the second roadblock – expense. The cost of an experiment soars using traditional MEG procedures due to the cost of liquid helium which is required to keep the system cooled. Magnetometers are sensors that measure magnetism, and the most commonly used magnetometers are made up of an array of superconducting quantum interference devices (SQUIDs) which require a temperature of -183°C to operate. MEG remains the most effective technique with which to investigate temporal lobe activity (see chapter 4 for details). New technologies are advancing however. Optically pumped magnetometers (OPMs) offer the best solution – they are non-cryogenic (sensitive at room temperature) and can be attached to a helmet in much the same way as electroencephalography (EEG) electrodes attach to a cap, greatly reducing the sensitivity to movement. Thus, OPM technology offers the same temporal and spatial resolution as current MEG technologies, with the added benefit of reduced movement artifacts, thereby reducing the number of repetitions required. Lowering the costs in time and money, this new MEG system will pave the way for future research.

6.5 Concluding Remarks

The assertion that the principals governing perception are inherent in oscillatory carrier processes, emergent within the central nervous system, is rooted in the beginnings of psychophysics (Geissler, Vangas, Svegzda, Bliumas, Stanikunas, & Vaitkevicius, 2012). Gustav Theodore Fechner, known as the father of psychophysics, proposed a general law based on a relation between outer and inner psychophysics would likely possess "that simplicity which we are accustomed to finding in the fundamental laws of nature", (Fechner, p.564, 1860, translated by Langfeld, H. S., 1912).

Psychological processes, while complex and unique to a specific process, are considered to emerge from simpler system states (Fusella, 2013). If it is considered that every dynamic system, therefore including auditory binding oscillatory mechanisms, is based on a fundamental simple relation, investigating the invariant properties of such a system is the key to unlocking this code. It is hoped that the research findings described here will move this quest one step closer.

CHAPTER SIX: CONCLUSION

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Appendix 1: Tables of RT means

Chapter one

Experiment 1: Table of means

Descriptive Statistics							
Mean Std. Deviation N							
a300	521.4336	69.40738	14				
a310	523.9536	67.35539	14				
a320	519.4664	64.23342	14				
a330	515.6900	65.58972	14				
a340	514.2321	65.18230	14				
a350	516.1143	64.17046	14				
a360	515.3586	65.49625	14				
a370	511.9757	60.08992	14				
a380	512.6086	63.58533	14				
a390	519.4857	65.26753	14				
a301	517.9157	70.64254	14				
a311	512.3729	67.30931	14				
a321	520.1671	82.61630	14				
a331	522.8764	71.13282	14				
a341	509.4286	66.70546	14				
a351	518.7629	89.93202	14				
a361	525.1036	82.65743	14				
a371	514.3986	70.83363	14				
a381	511.6071	80.17779	14				
a391	512.7036	72.42955	14				
a302	548.8464	88.60135	14				
a312	534.9379	74.72569	14				
a322	534.3386	76.24918	14				
a332	548.0686	94.05244	14				
a342	536.1886	109.73625	14				
a352	535.7050	84.73308	14				
a362	534.0821	92.61635	14				
a372	531.3564	94.26212	14				
a382	528.0479	85.82982	14				
a392	530.5050	85.84974	14				

Experiment 2: Table of means

Descriptive Statistics

	Mean	Std. Deviation	N
a28086	429.6319	90.51472	16
a280206	399.8056	82.92165	16
a29086	422.9863	83.26142	16
a290206	402.7213	74.77433	16
a30086	430.2456	88.32449	16
a300206	406.7713	75.28072	16
a31086	423.1344	80.39467	16
a310206	405.0869	81.41136	16
a32086	416.3400	77.00418	16
a320206	397.4563	72.47180	16
a28186	430.7250	93.99413	16
a281206	418.8906	87.86218	16
a29186	422.2625	91.31999	16
a291206	407.1325	83.43381	16
a30186	418.8750	94.61073	16
a301206	412.3294	91.70792	16
a31186	430.1525	98.12859	16
a311206	414.1281	87.95024	16
a32186	421.0106	103.29430	16
a321206	406.5900	89.08873	16
a28286	455.3494	95.62541	16
a282206	428.8888	103.01137	16
a29286	449.1969	102.94999	16
a292206	427.5250	93.45425	16
a30286	446.6081	102.22069	16
a302206	428.5975	97.89876	16
a31286	455.6838	110.32825	16
a312206	431.0919	101.47017	16
a32286	446.1238	98.26299	16
a322206	436.4638	100.22184	16

APPENDICES

Experiment 3: Table of means

Descriptive Statistics							
	Mean	Std. Deviation	N				
a300	470.5156	46.19104	16				
a310	469.1156	45.45389	16				
a320	461.4794	45.92031	16				
a330	466.5088	44.92511	16				
a340	467.1413	40.38483	16				
a350	467.6119	42.88404	16				
a360	458.5656	44.66478	16				
a370	465.2900	41.32089	16				
a380	463.4131	37.45579	16				
a390	466.9012	40.17623	16				
a301	471.2694	38.80885	16				
a311	466.8488	40.96447	16				
a321	470.9956	44.37537	16				
a331	464.2844	42.09411	16				
a341	465.0481	40.71387	16				
a351	462.7194	42.28661	16				
a361	462.4637	45.50710	16				
a371	458.6719	40.77135	16				
a381	455.6513	41.99212	16				
a391	458.4100	47.83785	16				
a302	484.5619	47.49723	16				
a312	478.3631	50.57840	16				
a322	481.3325	49.38551	16				
a332	475.1388	39.02327	16				
a342	476.5494	49.30880	16				
a352	482.1262	49.35056	16				
a362	478.3513	50.70720	16				
a372	472.9831	41.36773	16				
a382	474.5194	45.73861	16				
a392	478.3931	45.84639	16				

Descriptive Statistics

Experiment 4: Table of means

Descriptive Statistics							
	Mean	Std. Deviation	N				
a260	360.8488	58.46421	16				
a270	354.1594	49.18790	16				
a280	355.5294	58.10737	16				
a290	351.6656	56.52380	16				
a300	353.0025	56.11497	16				
a261	359.3300	60.87215	16				
a271	365.3163	64.64246	16				
a281	358.4225	59.25708	16				
a291	353.7731	61.49259	16				
a301	353.7119	63.70047	16				
a262	380.9350	60.71619	16				
a272	374.7469	61.24431	16				
a282	382.5987	81.50691	16				
a292	377.0838	67.04388	16				
a302	375.9931	71.70132	16				

Descriptive Statistics

Experiment 5: Table of means

	Descrip	otive Statistics						
	Mean	Std. Deviation	N	{	a441	327.0881	85.61891	16
a300	325 6044	71 15433	16	1	a451	318.9625	80.94661	16
2400	323.0044	72 10922	16	2	a461	329.2256	86.49786	16
a400	222.1034	72.15055	16	1	a471	329.2519	87.96396	16
a410	222.1900	72.03033	16	1	a481	317.5869	84.28373	16
a420	323.2234	70.19491	16		a491	324.2288	85.66907	16
a430	220.2007	72.09400	10		a392	346.5944	96.41047	16
a440 9450	222.4909	60 92762	16		a402	340.4250	84.95156	16
a450	322.1413	60 56206	16		a412	352.8794	96.02004	16
a400	327.4331	71 40990	10	,	a422	345 0613	87 59906	16
a470	220.0013	71.49009	10	Ľ	a432	342 0413	88 13097	16
a4ou	327.3000	74.09907	10		2442	345 0444	92 25071	16
a490	320.2100	74.55199	10	Ľ	a442	224.0607	07.27665	10
a391	333.2500	82.61442	16		452	334.9087	87.37005	10
a401	329.2506	81.54440	16	1	a462	337.3044	81.80935	16
a411	326.2138	86.70145	16	1	a472	344.3469	94.12398	16
a421	324.4694	88.52301	16	1	a482	345.8762	93.61105	16
a431	325.7837	86.98939	16	ł	a492	337.6031	85.43245	16

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Chapter three: Tables of means

Experiment 1: Table of means

Descriptive Statistics									
Mean Std. Deviation N									
a280	386.5700	95.71411	16						
a290	383.0750	107.40125	16						
a300	371.6550	103.27774	16						
a310	370.3013	98.80382	16						
a320	374.5875	108.30313	16						
a330	378.2438	104.15414	16						
a340	371.1519	95.16261	16						
a350	369.2906	98.98153	16						
a360	368.4213	95.30364	16						
a370	369.2506	100.01663	16						
a380	375.5469	110.49581	16						
a281	412.4300	129.23926	16						
a291	397.9619	117.45286	16						
a301	401.1181	120.99524	16						
a311	395.0225	117.67697	16						
a321	383.5906	119.35335	16						
a331	384.3206	118.02671	16						
a341	378.7463	110.95283	16						
a351	384.3825	108.34349	16						
a361	380.1019	115.33997	16						
a371	383.2769	109.91441	16						
a381	388.0050	121.55414	16						
a282	412.5981	127.91840	16						
a292	407.5431	112.68776	16						
a302	413.5856	116.73423	16						
a312	402.7525	120.44085	16						
a322	404.2869	122.04782	16						
a332	402.0575	129.08078	16						
a342	392.3481	108.11726	16						
a352	404.9956	107.87578	16						
a362	394.1650	110.23375	16						
a372	399.8113	121.50961	16						
a382	388.3106	108.45178	16						

Experiment 2: Table of means

Descriptive Statistics							
	Mean	Std. Deviation	N				
a300	368.1867	91.65247	15				
a310	361.8233	95.30115	15				
a320	363.5940	78.19555	15				
a330	357.4060	93.04741	15				
a340	367.8947	89.32106	15				
a350	351.6913	89.94932	15				
a360	357.6080	89.22158	15				
a370	352.0693	89.35618	15				
a380	354.2133	84.40780	15				
a390	345.1700	77.16640	15				
a400	353.3513	85.07892	15				
a410	362.4187	89.97247	15				
a420	362.1707	92.69227	15				
a430	347.5227	88.13039	15				
a440	350.1100	87.14400	15				
a450	350.1313	78.59239	15				
a301	373.8320	97.10772	15				
a311	367.6467	85.54879	15				
a321	363.8020	94.80708	15				
a331	365.9947	91.59360	15				
a341	356.7327	88.99075	15				
a351	354.8073	92.90408	15				
a361	348.4180	82.93322	15				
a371	348.8200	75.99935	15				
a381	347.8293	84.54553	15				
a391	350.1467	78.09518	15				
a401	354.2627	91.44475	15				
a411	346.9807	86.73900	15				
a421	354.1573	97.11604	15				
a431	358.6560	92.45569	15				
a441	343.0227	90.33416	15				
a451	351.3013	79.07760	15				

Descriptive Statistics								
	Mean	Std. Deviation	N					
a302	376.6213	80.81718	15					
a312	387.2753	102.16962	15					
a322	368.0460	83.12628	15					
a332	389.1033	110.24115	15					
a342	365.1707	95.03266	15					
a352	378.8580	96.10187	15					
a362	371.6747	93.58002	15					
a372	366.8007	93.43201	15					
a382	365.0047	97.80256	15					
a392	370.6580	101.50256	15					
a402	366.3013	105.46747	15					
a412	365.7633	95.50879	15					
a422	367.5800	91.77871	15					
a432	369.6240	94.24477	15					
a442	368.0193	90.26440	15					
a452	368.0900	94.91525	15					

APPENDICES

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Chapter four: Table of means

	Descript	tive Statistics				
	1 = Musician, 2		Std.		a351	1.00
	= Non-Musician	Mean	Deviation	Ν		2.00
a310	1.00	417.8464	61.92725	11		Total
	2.00	414.0420	59.31062	10	a371	1.00
	Total	416 0348	59 19687	21		2.00
a330	1.00	409 4891	62 10517	11		Total
4000	2.00	400 2560	54 50186	10	a391	1.00
	Total	405.0024	57 33722	21		2.00
2250	1 00	403.0324	64 00472	41		Total
assu	2.00	409.3473	04.90473 60.07674	10	a312	1.00
	2.00	400.4670	50.27574	10		2.00
	Iotal	407.9852	57.01836	21		Total
a370	1.00	415.6955	65.51517	11	a332	1.00
	2.00	404.3240	58.93767	10		2.00
	Total	410.2805	61.18111	21		Total
a390	1.00	408.5673	60.83763	11	a352	1.00
	2.00	406.9390	52.65369	10		2.00
	Total	407.7919	55.66766	21		Total
a311	1.00	418.2082	74.72395	11	a372	1.00
	2.00	427.4660	75.78803	10		2.00
	Total	422.6167	73.47790	21		Total
a331	1.00	418.4673	70.57354	11	a392	1.00
	2.00	416.7920	66.79955	10		2.00
	Total	417.6695	67.07480	21		Total

1	2.00	411.7740	74.81669	10
	Total	415.4362	74.66973	21
a371	1.00	417.0355	75.53981	11
	2.00	417.0190	69.76082	10
	Total	417.0276	71.01471	21
a391	1.00	412.4682	80.67392	11
	2.00	412.4720	69.39444	10
	Total	412.4700	73.62849	21
a312	1.00	437.7373	77.30731	11
	2.00	440.2550	82.69003	10
	Total	438.9362	77.88972	21
a332	1.00	433.8691	72.12795	11
	2.00	438.0150	72.85587	10
	Total	435.8433	70.67045	21
a352	1.00	426.6782	84.09296	11
	2.00	418.8320	81.40473	10
	Total	422.9419	80.83295	21
a372	1.00	428.3464	76.38703	11
	2.00	436.8690	91.19682	10
	Total	432.4048	81.72576	21
a392	1.00	425.4836	71.86799	11
	2.00	437.6130	87.79941	10
	Total	431.2595	78.03824	21

Chapter five: Table of means

(a) Mask condition mean corrected RTs

	Descrip	otive Statistics							
	Musicians,		Std.		M_35_1	Musician	381.3919	58.77463	16
	nMusicians	Mean	Deviation	Ν		nMusician	374.7756	79.05459	16
M_31_0	Musician	377.3781	50.97561	16		Total	378.0838	68.60628	32
	nMusician	386.7938	94.38559	16	M_37_1	Musician	386.2163	55.78099	16
	Total	382.0859	74,77202	32		nMusician	370.2625	66.48315	16
M 33 0	Musician	371.6769	50.60961	16		Total	378.2394	60.90953	32
	nMusician	385.2719	107.99576	16	M_39_1	Musician	382.8400	61.79118	16
	Total	378 4744	83 24950	32		nMusician	373.8487	94.27790	16
M 25 0	Musician	275 0025	47 20417	16		Total	378.3444	78.54398	32
W_35_0	NUSICian	375.8025	47.30417	10	M_31_2	Musician	398.5150	57.93289	16
	niviusician	365.0013	90.03862	10		nMusician	387.9188	68.13085	16
	Total	380.7769	71.22992	32		Total	393.2169	62.44190	32
M_37_0	Musician	372.7100	47.61218	16	M_33_2	Musician	402.1788	60.71086	16
	nMusician	376.3388	87.62787	16		nMusician	388.3738	71.88043	16
	Total	374.5244	69.39573	32		Total	395.2763	65.82325	32
M_39_0	Musician	377.1481	53.00391	16	M 35 2	Musician	398.2850	52.37477	16
	nMusician	383.7700	92.57797	16		nMusician	376.1250	67.62583	16
	Total	380.4591	74.28199	32		Total	387.2050	60.55498	32
M_31_1	Musician	382.2800	54.44177	16	M 37 2	Musician	400.9544	64.35820	16
	nMusician	370.8006	77.21504	16		nMusician	385.6362	62.52497	16
	Total	376.5403	65.97782	32		Total	393.2953	62.89967	32
M_33_1	Musician	385.6788	50.83487	16	M_39_2	Musician	400.2738	66.34114	16
	nMusician	379.5550	74.93078	16		nMusician	380.2475	62.02613	16
	Total	382.6169	63.06220	32		Total	390.2606	63.98947	32

(b) No-Mask condition mean corrected RTs

nM_31_0	Musician	397.6031	67.24439	16					
	nMusician	382.1313	84.31705	16					
	Total	389.8672	75.43051	32					
nM_33_0	Musician	388.3325	71.92450	16	nM_37_1	Musician	381.8375	63.24047	16
	nMusician	375.4525	88.65302	16		nMusician	366.3306	89.04135	16
	Total	381.8925	79.67971	32		Total	374.0841	76.37756	32
nM_35_0	Musician	385.6875	78.80677	16	nM_39_1	Musician	374.3531	64.87416	16
	nMusician	376.1031	84.64695	16		nMusician	365.1638	89.11114	16
	Total	380.8953	80.59638	32		Total	369.7584	76.81510	32
nM_37_0	Musician	381.6613	67.04149	16	nM_31_2	Musician	421.2100	75.70981	16
	nMusician	372.6050	87.49966	16		nMusician	368.9375	64.59714	16
	Total	377.1331	76.81511	32		Total	395.0738	74.14693	32
nM_39_0	Musician	384.6900	73.18340	16	nM_33_2	Musician	407.3563	74.12058	16
	nMusician	377.3800	78.93836	16		nMusician	384.6087	66.23110	16
	Total	381.0350	74.96958	32		Total	395.9825	70.10266	32
nM_31_1	Musician	389.4687	71.54723	16	nM_35_2	Musician	406.4319	74.83194	16
	nMusician	381.6875	81.72580	16		nMusician	372.3694	75.90666	16
	Total	385.5781	75.65970	32		Total	389.4006	76.13796	32
nM_33_1	Musician	391.2450	69.45619	16	nM_37_2	Musician	404.9063	80.96527	16
	nMusician	366.1013	76.67963	16		nMusician	375.8244	70.63349	16
	Total	378.6731	73.09221	32		Total	390.3653	76.18590	32
nM_35_1	Musician	380.4081	65.68624	16	nM_39_2	Musician	405.4063	76.29764	16
	nMusician	369.8088	87.16538	16		nMusician	379.7119	87.37000	16
	Total	375.1084	76.11241	32		Total	392.5591	81.73606	32

Appendix 2: Tables of error means

Chapter one: Tables of error means

Experiment 1: Error means

Descriptive Statistics									
	Mean	Std. Deviation	Ν						
a300	.2421	.12129	14						
a310	.2207	.11750	14						
a320	.2279	.07526	14						
a330	.2021	.06841	14						
a340	.1914	.08690	14						
a350	.2007	.12338	14						
a360	.1693	.11125	14						
a370	.1621	.11943	14						
a380	.1993	.12275	14						
a390	.2079	.09585	14						
a301	.1329	.11671	14						
a311	.1307	.11906	14						
a321	.1371	.13539	14						
a331	.1800	.13307	14						
a341	.1564	.12701	14						
a351	.1429	.13035	14						
a361	.1264	.12592	14						
a371	.1593	.14035	14						
a381	.1193	.13321	14						
a391	.1414	.12309	14						
a302	.2179	.11457	14						
a312	.2164	.14259	14						
a322	.1914	.14670	14						
a332	.1979	.16619	14						
a342	.2079	.16339	14						
a352	.2386	.11628	14						
a362	.2193	.09203	14						
a372	.2021	.13902	14						
a382	.1943	.11554	14						
a392	.1964	.11379	14						

Experiment 2: Table of error means

Descriptive Statistics

	Mean	Std. Deviation	Ν
a28086	.1906	.08668	16
a280206	.1581	.08983	16
a29086	.1788	.09472	16
a290206	.1838	.06652	16
a30086	.1863	.08032	16
a300206	.1862	.10327	16
a31086	.1594	.10208	16
a310206	.1963	.11517	16
a32086	.1838	.08570	16
a320206	.1719	.09537	16
a28186	.1475	.06708	16
a281206	.1994	.15631	16
a29186	.1575	.10927	16
a291206	.1581	.14053	16
a30186	.1488	.09722	16
a301206	.1287	.12733	16
a31186	.1150	.10132	16
a311206	.1419	.12362	16
a32186	.1531	.10756	16
a321206	.1819	.13809	16
a28286	.2169	.14079	16
a282206	.2475	.14083	16
a29286	.2238	.14156	16
a292206	.2325	.14821	16
a30286	.2363	.11921	16
a302206	.2713	.19026	16
a31286	.2325	.13254	16
a312206	.2263	.17988	16
a32286	.2469	.16414	16
a322206	.2513	.12088	16

Experiment 3: Table of error means

Descriptive Statistics								
	Mean	Std. Deviation	N					
a300	.2113	.12774	16					
a310	.2337	.11337	16					
a320	.2044	.10893	16					
a330	.2119	.14209	16					
a340	.2400	.11454	16					
a350	.2075	.11115	16					
a360	.2050	.12811	16					
a370	.1931	.09329	16					
a380	.2256	.11610	16					
a390	.2019	.09975	16					
a301	.1569	.12478	16					
a311	.1744	.11736	16					
a321	.2394	.11908	16					
a331	.1506	.15507	16					
a341	.1650	.12717	16					
a351	.1869	.11672	16					
a361	.2219	.14143	16					
a371	.1244	.10776	16					
a381	.1881	.13106	16					
a391	.1388	.12093	16					
a302	.2444	.13861	16					
a312	.3125	.14704	16					
a322	.2625	.12657	16					
a332	.3087	.11366	16					
a342	.2856	.11501	16					
a352	.2781	.15501	16					
a362	.3044	.09899	16					
a372	.2694	.12907	16					
a382	.2494	.13791	16					
a392	.2438	.13426	16					

Descriptive Statistics								
	Mean	Std. Deviation	N					
a260	.2288	.08366	16					
a270	.2312	.10404	16					
a280	.1906	.10755	16					
a290	.1944	.10733	16					
a300	.2150	.11978	16					
a261	.1644	.14047	16					
a271	.1181	.12512	16					
a281	.1638	.12033	16					
a291	.1400	.10863	16					
a301	.1619	.12200	16					
a262	.2919	.18516	16					
a272	.2938	.12225	16					
a282	.2694	.15106	16					
a292	.2575	.15550	16					
a302	.2812	.14715	16					

Experiment 4: Table of error means

Experiment 5: Table of error means

	000011						
	Mean	Std. Deviation	N	a441	.1838	.12971	16
a390	.2125	.10884	16	a451	.1406	.12487	16
a400	.2156	.10360	16	a461	.1544	.10564	16
a410	.1800	.13784	16	a471	.1519	.12249	16
a420	.2106	.12391	16	a481	.1575	.14821	16
a430	.1950	.11272	16	a491	.1494	.13354	16
a440	.1744	.10595	16	a392	.2644	.15496	16
a450	.2119	.10362	16	a402	.3213	.16272	16
a460	.1863	.09653	16	a412	.2869	.11847	16
a470	.1919	.13427	16	a422	.2781	.12172	16
a480	.1825	.10523	16	a432	.2912	.13754	16
a490	.1794	.10939	16	a442	.2850	.15170	16
a391	.1613	.11960	16	a452	.2456	.13135	16
a401	.1625	.12876	16	a462	.2819	.13949	16
a411	.1250	.13382	16	a472	.2394	.12358	16
a421	.2025	.08513	16	a482	.2488	.14278	16
a431	.1369	.12126	16	a492	.2600	.14652	16

Descriptive Statistics

Chapter three: Tables of error means

Experiment 1: Table of error means

Descriptive Statistics								
	Mean	Std. Deviation	Ν					
a280	.2563	.08648	16					
a290	.2256	.11039	16					
a300	.2206	.12715	16					
a310	.1906	.11869	16					
a320	.2050	.14904	16					
a330	.1919	.11686	16					
a340	.1994	.11096	16					
a350	.2138	.11171	16					
a360	.2381	.11606	16					
a370	.2213	.11189	16					
a380	.2025	.10649	16					
a281	.1581	.11059	16					
a291	.1444	.09832	16					
a301	.1844	.14546	16					
a311	.2494	.10497	16					
a321	.2056	.13201	16					
a331	.2100	.09599	16					
a341	.1594	.13314	16					
a351	.1844	.12149	16					
a361	.2019	.14237	16					
a371	.1875	.12562	16					
a381	.1731	.12424	16					
a282	.2312	.12355	16					
a292	.2044	.15007	16					
a302	.2569	.13994	16					
a312	.2869	.13230	16					
a322	.1863	.16872	16					
a332	.2263	.11564	16					
a342	.2294	.12567	16					
a352	.2875	.14215	16					
a362	.2369	.15768	16					
a372	.2425	.15164	16					
a382	.1963	.13063	16					

Experiment 2: Table of error means

Descriptive Statistics								
	N							
a300	.2413	.09531	15					
a310	.2153	.12495	15					
a320	.2260	.12716	15					
a330	.2080	.12260	15					
a340	.2127	.12424	15					
a350	.1960	.12281	15					
a360	.2320	.12565	15					
a370	.1807	.10780	15					
a380	.1967	.13097	15					
a390	.2087	.13032	15					
a400	.1487	.11109	15					
a410	.2087	.09665	15					
a420	.1893	.11336	15					
a430	.1773	.11202	15					
a440	.1480	.09915	15					
a450	.1920	.11378	15					
a301	.1840	.14951	15					
a311	.1727	.13247	15					
a321	.1273	.14444	15					
a331	.1500	.11446	15					
a341	.0987	.13038	15					
a351	.1927	.16294	15					
a361	.1680	.15979	15					
a371	.1827	.12781	15					
a381	.2180	.14915	15					
a391	.1373	.12538	15					
a401	.1967	.13824	15					
a411	.1807	.13301	15					
a421	.1327	.10539	15					
a431	.1933	.12630	15					
a441	.2027	.13488	15					
a451	.1433	.10279	15					

Descriptive Statistics								
	Mean	Std. Deviation	N					
a302	.2547	.14004	15					
a312	.2380	.13909	15					
a322	.2380	.15713	15					
a332	.2640	.12665	15					
a342	.1860	.12460	15					
a352	.2573	.09765	15					
a362	.2487	.16031	15					
a372	.2867	.15122	15					
a382	.2307	.12848	15					
a392	.2333	.11884	15					
a402	.2560	.17574	15					
a412	.2153	.14197	15					
a422	.2187	.14918	15					
a432	.1967	.14603	15					
a442	.2260	.13953	15					
a452	.2100	.16027	15					

APPENDICES

Chapter four: Table of error means

	Descript	ve stutist	63		L				
	1 = Musician,				a351	1.00	.2791	.16404	11
	2 =		Std.			2.00	.2440	.16840	10
	Non-Musician	Mean	Deviation	Ν		Total	.2624	.16291	21
a310	1.00	.2355	.07980	11	a371	1.00	.3155	.20052	11
	2.00	.1950	.07091	10		2.00	.2310	.16901	10
	Total	.2162	.07665	21		Total	.2752	.18662	21
a330	1.00	.2336	.13930	11	a391	1.00	.3009	.17745	11
	2.00	.1920	.08094	10		2.00	.2470	.16594	10
	Total	.2138	.11448	21		Total	.2752	.16999	21
a350	1.00	.2345	.13816	11	a312	1.00	.3391	.18234	11
	2.00	.2160	.09902	10		2.00	.2690	.10775	10
	Total	.2257	.11851	21		Total	.3057	.15210	21
a370	1.00	.2173	.11199	11	a332	1.00	.3245	.16495	11
	2.00	.2070	.10350	10		2.00	.2990	.17000	10
	Total	.2124	.10545	21		Total	.3124	.16364	21
a390	1.00	.2191	.12934	11	a352	1.00	.3455	.16831	11
	2.00	.2170	.12401	10		2.00	.2780	.13879	10
	Total	.2181	.12364	21		Total	.3133	.15499	21
a311	1.00	.3227	.18298	11	a372	1.00	.3900	.17816	11
	2.00	.2570	.15847	10		2.00	.3440	.13006	10
	Total	.2914	.17080	21		Total	.3681	.15504	21
a331	1.00	.3036	.21158	11	a392	1.00	.3118	.14992	11
	2.00	.2710	.16258	10		2.00	.2960	.15472	10
	Total	.2881	.18589	21		Total	.3043	.14858	21
-									

Descriptive Statistics

Chapter five: Table of error means

(a) Mask condition: Table of error means

	Descriptive	Statistic	s						
	Musicians,		Std.		E_M_37_1	Musician	.1638	.12748	16
	nMusicians	Mean	Deviation	Ν		nMusician	.2156	.13186	16
E_M_31_0	Musician	.1456	.13441	16		Total	.1897	.13027	32
	nMusician	.2375	.10351	16	E M 39 1	Musician	.1581	.13353	16
	Total	.1916	.12690	32		nMusician	.2250	.14962	16
E_M_33_0	Musician	.1769	.12679	16		Total	1916	14357	32
	nMusician	.2188	.12795	16	E M 21 2	Musisian	2224	17017	16
	Total	.1978	.12709	32	E_M_31_2	wusician	.2231	.1/91/	10
E_M_35_0	Musician	.1662	.10398	16		nMusician	.2394	.15563	16
	nMusician	.2444	.12447	16		Total	.2313	.16529	32
	Total	.2053	.11960	32	E_M_33_2	Musician	.2581	.15281	16
E_M_37_0	Musician	.1713	.12868	16		nMusician	.2756	.13633	16
	nMusician	.2344	.13135	16		Total	.2669	.14273	32
	Total	.2028	.13187	32	E_M_35_2	Musician	.2144	.16665	16
E_M_39_0	Musician	.1669	.12867	16		nMusician	.2575	.17506	16
	nMusician	.2319	.12172	16		Total	.2359	.16955	32
	Total	.1994	.12756	32	EM 37 2	Musician	2200	13515	16
E_M_31_1	Musician	.1513	.13500	16	L_m_0/_2	-Musician	.2200	.10010	
	nMusician	.1875	.14960	16		niviusician	.2956	.18221	16
	Total	.1694	.14137	32		Total	.2578	.16242	32
E_M_33_1	Musician	.1500	.14909	16	E_M_39_2	Musician	.2481	.16501	16
	nMusician	.2244	.13847	16		nMusician	.3088	.14665	16
	Total	.1872	.14649	32		Total	.2784	.15662	32

(b) No-Mask condition: Table of error means

L									
E_nM_31_0	Musician	.1763	.07338	16	E nM 37 1	Musician	.1300	.11063	16
	nMusician	.1781	.10413	16		nMusisian	2462	42020	10
	Total	.1772	.08862	32		niviusician	.2102	.12920	10
E_nM_33_0	Musician	.1744	.10577	16		Total	.1731	.12617	32
	nMusician	.2119	.11083	16	E_nM_39_1	Musician	.1319	.11850	16
	Total	.1931	.10825	32		nMusician	.2144	.13540	16
E_nM_35_0	Musician	.1481	.09649	16		Total	.1731	.13199	32
	nMusician	.2044	.14066	16	E_nM_31_2	Musician	.2231	.07838	16
	Total	.1762	.12205	32		nMusician	.2638	.21181	16
E_nM_37_0	Musician	.1756	.09515	16		Total	.2434	.15845	32
	nMusician	.2000	.09238	16	E nM 33 2	Musician	2631	13001	16
	Total	.1878	.09307	32	L_IIIVI_33_2	Musician	.2001	.10001	10
E_nM_39_0	Musician	.1644	.08656	16		nMusician	.2525	.17887	16
	nMusician	.2212	.10223	16		Total	.2578	.15391	32
	Total	.1928	.09756	32	E_nM_35_2	Musician	.2275	.11066	16
E_nM_31_1	Musician	.1038	.10334	16		nMusician	.2700	.19044	16
	nMusician	.1687	.14868	16		Total	.2487	.15473	32
	Total	.1363	.13020	32	E_nM_37_2	Musician	.2006	.12979	16
E_nM_33_1	Musician	.1206	.12108	16		nMusician	.2731	.20049	16
	nMusician	.1444	.13196	16		Total	.2369	.17017	32
	Total	.1325	.12516	32	E nM 39 2	Musician	2269	12065	16
E_nM_35_1	Musician	.1038	.09179	16		abdusisian	2544	40444	40
	nMusician	.1656	.13923	16		niviusician	.2544	.19114	10
	Total	.1347	.12019	32		Total	.2406	.15785	32

Appendix 3: General Consent Form

Participant Identificati	on Number:		
Title of Project:			
Name of Researcher: N	aomi du Bois	Please tick box	
I confirm that I have restudy and have had the	ead the informati opportunity to a	on sheet for the above ask questions.	
I am satisfied that I un have had enough time	rmation provided and		
I understand that my p free to withdraw at any without my legal rights	articipation is vo time, without g s being affected.	luntary and that I am iving any reason, and	
I agree to take part in t			
Name of Participant	Date	Signature	
Researcher	Date	Signature	

Appendix 4: Participant Details for Experiments without a Music Group

Participant Details

Participant Identification Number:

Title of Project:

Name of Researcher: Naomi du Bois

Age: _____

Gender:	 	
Ochuci.		

Please answer 'yes' or 'no' to the questions below.

Are you right-handed?

Do you have any known hearing problems?

Do you have any musical training?

Name of Participant

Date

Signature

Appendix 5: Participant Details for Experiments with a Music Group

Participant Details

Participant Identification Number:

Title of Project:

Name of Researcher: Naomi du Bois

Age: _____

Gender: _____

Please answer the questions below.

Are you Right-Handed?

Do you have any known hearing problems?

Do you have any formal musical training?

If Yes – what grade have you achieved, and do you still play an instrument regularly?

If No – do you play an instrument, or have you played an instrument regularly in the past 10 years?

Your email address: _____

Name of Participant

Date

Signature

Appendix 6: Participant Information Sheet for Chapter Two Experiments

PARTICIPANT INFORMATION SHEET

Title of Project: Investigating the inharmonic pop-out effect in tone perception

Invitation

You are invited to take part in a research study. Before you decide, it is important that you understand why the research is being done and what it will involve. This Participant Information Sheet tells you about the purpose, risks and benefits of this research study. If you agree to take part, we will ask you to sign a Consent Form. If there is anything that you are not clear about, we will be happy to explain it to you. Please take as much time as you need to read this information. You should only consent to participate in this research study when you feel you understand what is being asked of you, and you have had enough time to think about your decision. Thank you for reading this.

Purpose of the Study

This study is concerned with the mechanisms in the brain involved in combining separate auditory information received from the environment into whole impressions. For example, when we receive auditory information we must combine the frequencies which are coming from the same source in order to understand what the sound is and where it is coming from. This also involves deciding which sounds are different from one another. Previous findings have highlighted what is termed a pop-out effect whereby sounds that are separated by semitones are detected faster than those which are harmonically related. This study aims to examine the effect of altering the previously used paradigm on the pop-out effect. The study will take ~3 months to complete. You and 16 others have been invited to participate as you meet the inclusion criteria.

Do I have to take part?

It is up to you to decide whether or not to take part. If you do decide to take part, you will be given this Information Sheet to keep and be asked to sign a Consent Form. You are free to withdraw at any time and without giving a reason. A decision to withdraw at any time, or a decision not to take part, will not affect your rights in any way.

What will happen to me if I take part?

Should you choose to participate you will be asked to provide details of your age, gender, whether you are right/left handed, whether you have any hearing problems, and whether you have had music training. Experimental sessions will take place in a sound attenuated laboratory on the second floor of Arts Millennium building extension (AMBE) at NUI Galway. All details, including the reaction time data from your sessions will be kept securely in the sound lab. You will be seated in front of a computer and you will be required to wear head phones. At the beginning of each session a cross will be presented on the computer screen for 500ms to alert you to the commencement of each trial. Trials will consist of two tones presented over the head phones one after the other. You will be asked to attend to the first tone but not to make a response, and to focus on the second tone which is the target stimulus. If the target is absent the tone will sound flat and if it is present it will sound like two alternating

tones. You must make a response by pressing one of two keys; Yes, the target is present or No, it is absent. You must make your response as accurately and rapidly as possible. Each session will begin with a 40-trial practice block.

How long will my part in the study last?

You would be required to attend two or three experimental sessions (no more than three). You will be contacted in advance to arrange a date and time for each session. Sessions will take approximately 1 hour to complete. Therefore, you can expect that this study would take about 3 hours of your time, spread out over three separate days, arranged to suit you.

What are the possible benefits in taking part?

This would be an opportunity for you to visit a sound attenuated laboratory and see first-hand how information is collected experimentally. Also, people who have participated in similar research previously, have reported that they experienced pleasant and calming sensations as they attended to the tones.

What are the possible disadvantages and risks of taking part?

There are no risks known to be involved in taking part in this research, and your participation will not put you at a disadvantage in any way.

What happens at the end of the study?

While it could be up to 2 years before final results are published, we would be pleased to include you on an address list to receive publications arising from the study. Only general findings will be reported, without reference to identifiable individual results.

What happens if I change my mind during the study?

You are entitled to change your mind about participating in this at any time without disadvantage or penalty.

Who do I contact for more information or if I have further concerns?

Please feel free to contact the researcher for further information or if you have any concerns regarding your participation which have not been addressed here.

Details are as follows; -

Student Researcher: Naomi du Bois	Phone: +353 85 7747340 Email: n.dubois1@nuigalway.ie
Supervisor: Dr Mark A. Elliott	Email: m.elliott@nuigalway.ie

If you have any concerns about this study and wish to contact someone in confidence, you may contact: The Head, School of Psychology, National University of Ireland, Galway.

Appendix 7: Participant Information Sheet for Chapter Three Experiments

PARTICIPANT INFORMATION SHEET

Title of Project: Investigating the inharmonic pop-out effect in tone perception using temporal parameters based on Time Quantum model (TQM) theory.

Invitation

You are invited to take part in a research study. Before you decide, it is important that you understand why the research is being done and what it will involve. This Participant Information Sheet tells you about the purpose, risks and benefits of this research study. If you agree to take part, we will ask you to sign a Consent Form. If there is anything that you are not clear about, we will be happy to explain it to you. Please take as much time as you need to read this information. You should only consent to participate in this research study when you feel you understand what is being asked of you, and you have had enough time to think about your decision. Thank you for reading this.

Purpose of the Study

This study is concerned with the mechanisms in the brain involved in combining separate auditory information received from the environment into whole impressions. For example, when we receive auditory information we must combine the frequencies which are coming from the same source in order to understand what the sound is and where it is coming from. This also involves deciding which sounds are different from one another. Previous findings have highlighted what is termed a pop-out effect whereby sounds that are separated by semitones are detected faster than those which are harmonically related. This study aims to examine the pop-out effect, using temporal parameters based on Time Quantum model (TQM) theory. The study will take ~3 months to complete. You and 16 others have been invited to participate as you meet the inclusion criteria.

Do I have to take part?

It is up to you to decide whether or not to take part. If you do decide to take part, you will be given this Information Sheet to keep and be asked to sign a Consent Form. You are still free to withdraw at any time and without giving a reason. A decision to withdraw at any time, or a decision not to take part, will not affect your rights in any way.

What will happen to me if I take part?

Should you choose to participate you will be asked to provide details of your age, gender, whether you are right/left handed, whether you have any hearing problems, and whether you have had music training. Experimental sessions will take place in a sound attenuated laboratory on the second floor of Arts Millennium building extension (AMBE) at NUI Galway. All details, including the reaction time data from your sessions will be kept securely in the sound lab. You will be seated in front of a computer and you will be required to wear head phones. At the beginning of each session a cross will be presented on the computer screen for 500ms to alert you to the commencement of each trial. Trials will consist of two tones presented over the head

phones one after the other. You will be asked to attend to the first tone but not to make a response, and to focus on the second tone which is the target stimulus. If the target is absent the tone will sound flat and if it is present it will sound like two alternating tones. You must make a response by pressing one of two keys; Yes, the target is present or No, it is absent. You must make your response as accurately and rapidly as possible. Each session will begin with a 20-trial practice block.

How long will my part in the study last?

You would be required to attend two or three experimental sessions (no more than three). You will be contacted in advance to arrange a date and time for each session. Sessions will take approximately 1 hour to complete. Therefore, you can expect that this study would take about 3 hours of your time, spread out over three separate days, arranged to suit you.

What are the possible benefits in taking part?

This would be an opportunity for you to visit a sound attenuated laboratory and see first-hand how information is collected experimentally. Also, people who have participated in similar research previously, have reported that they experienced pleasant and calming sensations as they attended to the tones.

What are the possible disadvantages and risks of taking part?

There are no risks known to be involved in taking part in this research, and your participation will not put you at a disadvantage in any way.

What happens at the end of the study?

While it could be up to 2 years before final results are published, we would be pleased to include you on an address list to receive publications arising from the study. Only general findings will be reported, without reference to identifiable individual results.

What happens if I change my mind during the study?

You are entitled to change your mind about participating in this at any time without disadvantage or penalty.

Who do I contact for more information or if I have further concerns?

Please feel free to contact the researcher for further information or if you have any concerns regarding your participation which have not been addressed here.

Postgraduate Researcher: Naomi du Bois Phone: 085-7747340 Email:n.dubois1@nuigalway.ie

Supervisor: Dr Mark A. Elliott Email: m.elliott@nuigalway.ie

If you have any concerns about this study and wish to contact someone in confidence, you may contact: The Head, School of Psychology, National University of Ireland, Galway.

Appendix 8: Participant Information Sheet for the MEG Experiment

PARTICIPANT INFORMATION SHEET

Title of Project: Investigating differences in the dynamic-systems structure of auditory cognition as a function of musical training.

Invitation

You are invited to take part in a research study. Before you decide, it is important that you understand why the research is being done and what it will involve. This Participant Information Sheet tells you about the purpose, risks and benefits of this research study. If you agree to take part, we will ask you to sign a Consent Form. If there is anything that you are not clear about, we will be happy to explain it to you. Please take as much time as you need to read this information. You should only consent to participate in this research study when you feel you understand what is being asked of you, and you have had enough time to think about your decision. Thank you for reading this.

Purpose of the Study

This study is concerned with the mechanisms in the brain involved in combining separate auditory information received from the environment into whole impressions – a process called auditory binding. For example, when we receive auditory information we must combine the frequencies which are coming from the same source in order to understand what the sound is and where it is coming from. This also involves deciding which sounds are different from one another. Music cognition is the area of research that examines how these brain processes relate to our perception of music. Musicians rely on these processes for melodic prediction and to synchronise with other musicians as they play. This study aims to investigate whether musical training influences auditory binding. The study will take ~3 months to complete. You and 11 others have been invited to participate as you meet the inclusion criteria.

What will happen to me if I take part?

If you do decide to take part, you will be asked to sign a Consent Form. You are still free to withdraw at any time and without giving a reason. Should you decide to withdraw this will not affect your rights in any way.

Should you choose to participate you will be asked to provide details of your age, gender, whether you are right/left handed and whether or not you have any musical training. Experimental sessions will take place at the Northern Ireland Functional Brain Mapping (NIFBM) facility, in the Intelligent Systems Research Centre, on Magee Campus of the Ulster University. All details, including the MEG data from your sessions will be kept securely at the research centre and copies will be kept on a secure server at the National University of Ireland, Galway (NUIG). You will be prepared for the MEG, which involves attaching 5 sensors at your hairline using surgical tape. Then you will be seated in the MEG chamber in front of a screen and you will be required to wear insert ear phones. At the beginning of each session you will complete a practice block during which you will receive feedback. Following this you will complete 6 blocks. At the beginning of each trial a cross will be presented on the computer screen for 500ms. Trials will consist of two tones presented via the ear

phones one after the other. You will be asked to attend to the first tone but not to make a response, and to focus on the second tone which is the target stimulus. If the target is absent the tone will sound flat and if it is present it will sound like two alternating tones. You must make a response by pressing one of two keys; the right response pad key for Yes, the target is present or the left response pad key for No, it is absent. You must make your response as accurately and rapidly as possible.

How long will my part in the study last?

You would be required to attend one experimental session. Sessions will take approximately 2 hours to complete.

What are the possible benefits in taking part?

This would be an opportunity for you to visit an MEG laboratory and see a neuroimaging procedure first-hand, and how information is collected experimentally. Also, people who have participated in similar research previously, have reported that they experienced pleasant and calming sensations as they attended to the tones.

What are the possible disadvantages and risks of taking part?

There are no risks known to be involved in taking part in this research, and your participation will not put you at a disadvantage in any way.

What happens at the end of the study?

While it could be up to 2 years before final results are published, we would be pleased to include you on an address list to receive publications arising from the study. Only general findings will be reported, without reference to identifiable individual results.

What happens if I change my mind during the study?

You are entitled to change your mind about participating in this at any time without disadvantage or penalty.

Who do I contact for more information or if I have further concerns?

Please feel free to contact the researcher for further information or if you have any concerns regarding your participation which have not been addressed here.

Student Researcher: Naomi du Bois	Phone: +353 85 7747340 Email: n.dubois1@nuigalway.ie
Supervisor: Dr Mark A. Elliott	Email: mark.elliott@nuigalway.ie

Director of the NIFBM facility: Prof. Girijesh Prasad Email: g.prasad@ulster.ac.uk

If you have any concerns about this study and wish to contact someone in confidence, you may contact: **Dr. John Bogue**, The Head, School of Psychology, National University of Ireland, Galway. **Email:** john.bogue@nuigalay.ie

Appendix 9: Participant Information Sheet for the Masking Experiment

PARTICIPANT INFORMATION SHEET

Title of Project: Investigating differences in the dynamic-systems structure of auditory cognition as a function of musical training.

Invitation

You are invited to take part in a research study. Before you decide, it is important that you understand why the research is being done and what it will involve. This Participant Information Sheet tells you about the purpose, risks and benefits of this research study. If you agree to take part, we will ask you to sign a Consent Form. If there is anything that you are not clear about, we will be happy to explain it to you. Please take as much time as you need to read this information. You should only consent to participate in this research study when you feel you understand what is being asked of you, and you have had enough time to think about your decision. Thank you for reading this.

Purpose of the Study

This study is concerned with the mechanisms in the brain involved in combining separate auditory information received from the environment into whole impressions – a process called auditory binding. For example, when we receive auditory information we must combine the frequencies which are coming from the same source in order to understand what the sound is and where it is coming from. This also involves deciding which sounds are different from one another. Music cognition is the area of research that examines how these brain processes relate to our perception of music. Musicians rely on these processes for melodic prediction and to synchronise with other musicians as they play. This study aims to investigate whether musical training influences auditory binding. The study will take ~3 months to complete. You and 31 others have been invited to participate as you meet the inclusion criteria.

Do I have to take part?

It is up to you to decide whether or not to take part. If you do decide to take part, you will be given this Information Sheet to keep and be asked to sign a Consent Form. You are still free to withdraw at any time and without giving a reason. A decision to withdraw at any time, or a decision not to take part, will not affect your rights in any way.

What will happen to me if I take part?

Should you chose to participate you will be asked to provide details of your age, gender, whether you are right/left handed, whether you have any hearing problems, and whether you have had music training. Experimental sessions will take place in a sound attenuated laboratory on the second floor of Arts Millennium building extension (AMBE) at NUI Galway. All details, including the reaction time data from your sessions will be kept securely in the sound lab. You will be seated in front of a computer and you will be required to wear head phones. At the beginning of each session a cross will be presented on the computer screen for 500ms to alert you to the commencement of each trial. Trials will consist of two tones presented over the head phones one after the other. You will be asked to attend to the first tone but not to make

a response, and to focus on the second tone which is the target stimulus. If the target is absent the tone will sound flat and if it is present it will sound like two alternating tones. You must make a response by pressing one of two keys; Yes, the target is present or No, it is absent. You must make your response as accurately and rapidly as possible. Each session will begin with a 20 trial practice block with the experimenter present to ensure that you understand the task before beginning the experiment proper.

How long will my part in the study last?

You would be required to attend two experimental sessions. You will be contacted in advance to arrange a date and time for each session. Sessions will take approximately 1 hour to complete. Therefore, you can expect that this study would take about 2 hours of your time, spread out over three separate days, arranged to suit you.

What are the possible benefits in taking part?

This would be an opportunity for you to visit a sound attenuated laboratory and see first-hand how information is collected experimentally. Also, people who have participated in similar research previously, have reported that they experienced pleasant and calming sensations as they attended to the tones.

What are the possible disadvantages and risks of taking part?

There are no risks known to be involved in taking part in this research, and your participation will not put you at a disadvantage in any way.

What happens at the end of the study?

While it could be up to 2 years before final results are published, we would be pleased to include you on an address list to receive publications arising from the study. Only general findings will be reported, without reference to identifiable individual results.

What happens if I change my mind during the study?

You are entitled to change your mind about participating in this at any time without disadvantage or penalty.

Who do I contact for more information or if I have further concerns?

Please feel free to contact the researcher for further information or if you have any concerns regarding your participation which have not been addressed here.

Details are as follows:

Student Researcher: Naomi du Bois	Phone: +353 85 7747340 Email: n.dubois1@nuigalway.ie
Supervisor: Dr Mark A. Elliott	Email: mark.elliott@nuigalway.ie

If you have any concerns about this study and wish to contact someone in confidence, you may contact: The Head, School of Psychology, National University of Ireland, Galway.
Appendix 10: Debriefing form for the Chapter Two Experiments

Debriefing Form

Thank you for your participation in the present study concerning temporal dynamics in auditory feature binding. Previous findings suggest that when we discriminate between sounds in our environment, tones that are fractionally related are easier to distinguish between than tones that are integer multiples. This has been referred to as a 'pop-out' effect. The aim of the present study was to examine whether or not a slight alteration to a previously used stimulus would eliminate or otherwise change this 'popout' effect.

Again, I thank you for taking part in this study. If you know of any friends or acquaintances that are eligible to participate in this study, I ask that you not discuss it with them until after they have had the opportunity to participate.

Prior knowledge of the study could potentially bias participant responses. I greatly appreciate your cooperation.

If you have any questions regarding this study, please feel free to ask the researcher at this time, or in case of questions you may have at a later time the researchers' details are as follows:

Naomi du Bois Mobile number: 0857747340 E-mail: <u>n.dubois1@nuigalway.ie</u>.

Senior Researcher: Dr Mark A. Elliott E-mail: <u>mark.elliott@nuigaway.ie</u>

Thanks again for your participation

Appendix 11: Debriefing form for the Chapter Three Experiments

Debriefing Form

Thank you for your participation in the present study concerning temporal dynamics in auditory feature binding. Previous findings suggest that when we discriminate between sounds in our environment, tones that are fractionally related are easier to distinguish between than tones that are integer multiples. This has been referred to as a 'pop-out' effect. The aim of the present study was to examine whether this effect would be changed, or eliminated, by timing the presentation of the target based on a model concerning the timing of perceptual brain mechanisms (the Time Quantum model (TQM)).

Again, I thank you for taking part in this study. If you know of any friends or acquaintances that are eligible to participate in this study, I ask that you not discuss it with them until after they have had the opportunity to participate.

Prior knowledge of the study could potentially bias participant responses. I greatly appreciate your cooperation.

If you have any questions regarding this study, please feel free to ask the researcher at this time, or in case of questions you may have at a later time the researchers' details are as follows:

Naomi du Bois Mobile number: 0857747340 E-mail: <u>n.dubois1@nuigalway.ie</u>.

Senior Researcher: Dr Mark A. Elliott E-mail: <u>mark.elliott@nuigaway.ie</u>

Thanks again for your participation

Appendix 12: Debriefing form for the MEG and Masking Experiments

Debriefing Form

Thank you for your participation in the present study concerning temporal dynamics in auditory feature binding. Previous findings suggest that when we discriminate between sounds in our environment, tones that dissonant (or do not sound like they are in harmony) are easier to distinguish – they stand out. The aim of this research is to see if music training influences pitch discrimination in general.

Again, I thank you for taking part in this study. If you know of any friends or acquaintances that are eligible to participate in this study, I ask that you not discuss it with them until after they have had the opportunity to participate.

Prior knowledge of the study could potentially bias participant responses. I greatly appreciate your cooperation.

If you have any questions regarding this study, please feel free to ask the researcher at this time, or in case of questions you may have at a later time the researchers' details are as follows:

Naomi du Bois Mobile number: 0857747340 E-mail: <u>n.dubois1@nuigalway.ie</u>.

Senior Researcher: Dr Mark A. Elliott E-mail: <u>mark.elliott@nuigaway.ie</u>

Thanks again for your participation

Appendix 13: General Contact Information

Who do I contact for more information or if I have further concerns?

Please feel free to contact the researcher for further information or if you have any concerns regarding your participation which have not been addressed here.

Details are as follows; -

Student Researcher: Naomi du Bois

Phone: 085-7747340

Email:

n.dubois1@nuigalway.ie

Supervisor: Dr Mark A. Elliott mark.elliott@nuigalway.ie

Email:

If you have any concerns about this study and wish to contact someone in confidence, you may contact: Dr John Bogue, The Head, School of Psychology, National University of Ireland, Galway – john.bogue@nuigalway.ie

Appendix 14: Contact Information for the MEG project

Who do I contact for more information or if I have further concerns?

Please feel free to contact the researcher for further information or if you have any concerns regarding your participation which have not been addressed here.

Details are as follows; -

Student Researcher: Naomi du Bois

Phone: 085-7747340

Email:

Email:

n.dubois1@nuigalway.ie

Supervisor: Dr Mark A. Elliott mark.elliott@nuigalway.ie

Director of the NIFBM facility: Prof. Girijesh Prasad Email:

g. prasad @ulster.ac. uk

If you have any concerns about this study and wish to contact someone in confidence, you may contact: Dr John Bogue, The Head, School of Psychology, National University of Ireland, Galway – john.bogue@nuigalway.ie



Appendix 15: Recruitment Leaflet for the MEG Project



Dear All,

My name is Naomi du Bois. I am a PhD candidate and Irish Research Council Scholar, from the School of Psychology, in NUI Galway. As part of my research I am looking for people over 18 years of age to take part in an experimental study. This study is concerned with the mechanisms in the brain involved in combining separate auditory information received from the environment into whole impressions - a process called auditory binding. For example, when we receive auditory information we must combine the frequencies which are coming from the same source in order to understand what the sound is and where it is coming from. This also involves deciding which sounds are different from one another. Music cognition is the area of research that examines how these brain processes relate to our perception of music. Musicians rely on these processes for melodic prediction and to synchronise with other musicians as they play. This study aims to investigate whether musical training influences auditory binding. To accomplish this, I must compare the performance on an auditory task, of people who play a musical instrument and people who do not. You have been invited to participate on this basis and, should you wish to take part, this would require one experimental session.

What is involved in taking part?



The procedure involves the use of magnetoencephalography (MEG).... and takes place in the MEG lab located in the Intelligent Systems Research Centre, on Magee campus. MEG is a modern non-invasive neurophysiological technique for measuring magnetic fields generated by neuronal activities inside the brain. It is a non-invasive procedure, is completely harmless and does not hurt.

A member of the research team will meet with interested people at the Intelligent Systems Centre, to show them the set-up, provide more information, and answer any questions. If participation is agreed the next step is to sign a consent form. Please note that participants can withdraw at any time prior to, or during the procedure, regardless of having signed a consent form. Participants will be prepared for the MEG, and then seated in the chamber in front of a monitor with response pads. The entire process might take up two hours of your time as it includes the preparation time, approx. 30 - 40 minutes, and completing the auditory task, 1 hour). It is a sound-based task requiring a yes/no response and is not difficult. Everyone who participates receives £10 for their time.

Ethical approval for this experiment has been obtained from the Research Ethics Committee at NUI Galway and the Ulster University. Confirmation of this can be provided at your request. If you are interested in taking part in this experiment, please send an email, as I am more than happy to discuss the research in more detail and answer any questions you may have.

APPENDICES

You can contact me by phone or email:

Naomi du Bois BA (PhD candidate, and Irish Research Council scholar) Mobile number: +353 85 7747340 Email address: <u>n.dubois1@nuigalway.ie</u>

Also, my supervisor's details are as follows:

Dr Mark Elliott – senior lecturer at NUIG Telephone number: +353 91 495345 Email address: mark.elliott@nuigalway.ie

Contact Information for the NIFBM facility, UU, Magee Campus:

Professor Girijesh Prasad – Professor of Intelligent Systems & Director of the NIFBM facility. Location: Intelligent Systems Research Centre, Magee Campus. Telephone number: +44 28 7167 5645 Email address: <u>g.prasad@ulster.ac.uk</u>

Appendix 16: Recruitment Leaflet for the Masking Project





Dear All,

My name is Naomi du Bois. I am a PhD candidate and Irish Research Council Scholar, from the School of Psychology, in NUI Galway. As part of my research I am looking for people over 18 years of age to take part in an experimental study. This study is concerned with the mechanisms in the brain involved in combining separate auditory information received from the environment into whole impressions - a process called auditory binding. For example, when we receive auditory information we must combine the frequencies which are coming from the same source in order to understand what the sound is and where it is coming from. This also involves deciding which sounds are different from one another. Music cognition is the area of research that examines how these brain processes relate to our perception of music. Musicians rely on these processes for melodic prediction and to synchronise with other musicians as they play. This study aims to examine the effects of masking sounds with noise on music cognition in musicians compared to non-musicians. To accomplish this I must compare the performance on an auditory task, of people who play a musical instrument and people who do not. Ultimately it is considered that understanding the differences in the musically trained brain compared to the musically naive brain will help to develop interventions for people with auditory processing deficits. Therefore, in the greater scheme, participation will help significantly in reaching this goal.

What is involved in taking part?



The experiment will take place in the Arts Millennium Building Extension (AMBE), second floor sound laboratory, in the Psychology department (room 2071). I am happy to provide more information and answer any questions – my contact details

are below. On an agreed day, participants will be seated in the sound room in front of a monitor with response pads – see photo above. Completing the auditory task will take approx. 40-50 minutes, and participation involves two sessions on separate days. It is a sound-based task requiring a yes/no response, and is not difficult. Participants will receive a \in 15 One4all voucher for taking part.

Ethical approval for this experiment has been obtained from the Research Ethics Committee at NUI Galway and the Ulster University. Confirmation of this can be provided at your request. If you are interested in taking part in this experiment, please send an email, as I am more than happy to discuss the research in more detail and answer any questions you may have.

You can contact me by phone or email:

Naomi du Bois BA (PhD candidate, and Irish Research Council scholar) Mobile number: +353 85 7747340 Email address: <u>n.dubois1@nuigalway.ie</u>

Also my supervisor's details are as follows: Dr Mark Elliott BA, MSc., PhD (senior lecturer at NUIG)

Telephone number: +353 91 495345

Email address: <u>mark.elliott@nuigalway.ie</u>

Appendix 17: Copyright Permission 1

Naomi du Bois PhD Candidate – Perception, Cognition and Action (PCA) Irish Research Council Scholar Arts Millennium Building Extension (AMBE) School of Psychology National University of Ireland, Galway (NUIG) Email: n.dubois1@nuigalway.ie Tel: +353 85 7747340

Dr Mark A. Elliott Email: mark.elliott@nuigalway.ie

Sept. 22nd, 2018

Dear Dr Elliott,

I am contacting you to request permission to include the following material within the electronic version of my PhD:

Figures 1 & 4: Source taken from Elliott, M. A. (2014). Atemporal equilibria: proand retroactive coding in the dynamics of cognitive microstructures. Frontiers in Psychology, 5, 990.

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Synchronization and stimulus timing: Implications for temporal models of visual information processing. In Psychophysics Beyond Sensation: Laws and Invariants of Human Cognition.

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Process timing and its relation to the coding of tonal harmony. Journal of

Experimental Psychology. Human Perception and Performance, 37(5), 1628–1642.

I would like to include the above figures.

APPENDICES

I would like to make an electronic version of my thesis available in ARAN which is the National University of Ireland, Galway's online repository http://aran.library.nuigalway.ie/. Once available in digital format, access to the thesis will be freely available via the Web. All users of the thesis will be bound by a Creative Commons Attribution Non-Commercial No Derivatives license (http://creativecommons.org/licenses/by-nc-nd/3.0/).

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(Signature)

Dr Mark A. Elliott

Date

23rd September 2018

May 14, 2018

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