

An Evolutionary Perspective on the Human Skill of Interpersonal Musical Entrainment  
by  
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**Abstract:**

This dissertation seeks to explore the evolution of human musicality by exploiting the idea that musical ability is a complex evolutionary exaptation, related to the evolution in humans of the ability to process information across different domains and modalities. As such the 'faculty of music' is seen, not as a single entity, but as a combination of different abilities (themselves possibly composed of sets of further subskills and thus integrated into a highly complex multi-level system) which may have evolved for reasons outside of musical ability and thus may be present in other species. This paper offers a first step towards a broad evolutionary definition of the faculty of music by concentrating upon the skill of interpersonal entrainment to music. Interpersonal Musical Entrainment (IME) is viewed as a conglomeration of sub-skills including fundamental temporal processing, periodical production, perceiving synchronisation, error correction, attending to pulse and bodily movement. The dissertation investigates how these abilities manifest themselves in a variety of human behaviours and attempts to show that individual sub-skills are shared with other animals with differences of quality and behavioural manifestation rather than kind, and as such may have developed for, arguably, more directly survival oriented, skills. Hence the seemingly species-specific ability of interpersonal musical entrainment may be attributed to increased cognitive flexibility in humans as well as to the subsequent ability to abstract intrinsic abilities from one behavioural context and re-deploy these within another.

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## 1. Introduction

*'Musicality, as the activity of a unitary "self" or "individuality" expressing motives to move, is organised in one connected time frame. It cannot be synthesised or accreted in the mind from separately anarchic processes, but must have one coherent and orderly rhythmic foundation. It expresses an integral stream of events in the whole brain, which conduct separate body parts to targets in a real or imagined space-time of experience, synchronising moves so the effects of separate actions can balance one another and form anticipated sequences and coincidences in space and time, as nearly faultlessly as possible. The gracefulness of all we do depends on it.'* (Trevarthen 1999/2000, p.160).

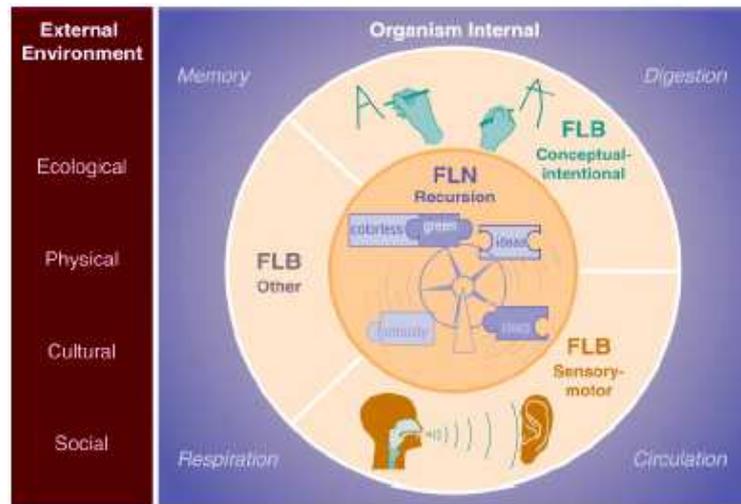
An evolutionary perspective on music and musical ability is motivated by the need to find a framework for integrating and reconciling two seemingly opposed approaches in current musical scholarship – scientific and cultural - with each other, and with recent approaches to the study of the human mind and behaviour. Recent publications (e.g. Peretz, & Zatorre, 2003; Desain & Honing, 2000; Sloboda & Juslin, 2001) and the proliferation of music and science journals (e.g. Music Perception; Psychology of Music; Musicae Scientiae; Journal of New Music Research) are testimony to the fact that music and musical ability are increasing foci of cognitive and neuroscientific exploration. Central to any scientific study of music and musical ability is the notion that music, as an universal human behaviour, has a knowable relationship to human biology and mind. The view in current musicological and ethnomusicological scholarship, on the other hand, is that music is a cultural construct detachable from biological determinants (e.g. Bohlman, 1999). Music is seen to exist only within culturally determined contexts. As such, music is thought to be cross-culturally heterogeneous to such an extent that the notion of universality in music is untenable. Additionally, research into the human mind and human behaviours is increasingly signifying the biological and behavioural continuity between humans and other animals (Brooks, 1999). An evolutionary perspective on music, by focusing upon phylogenetic progression and attributes that allow a gene, a behaviour, an organism *or* an interpersonal/group dynamic to be functional (Cross, 2003), uniquely offers an integrated framework for comprehending music, both biologically and culturally, within the general framework of human behaviour.

Interpersonal entrainment within musical contexts would seem to be particularly well suited to an evolutionary perspective as it is an universal human behaviour (Clayton, 2003) and can be interpreted both as a biological phenomenon, in that it is governed by underlying biological processes, and as a cultural phenomenon in terms of its evolutionary functionalities.

Existing evolutionary perspectives on the skill of entrainment within music have attempted to account for the adaptive strength of this ability with reference to mother-infant interaction (Dissanayake, 2000), coalition signalling (Merker, 1999/2000, 2000, 2002; Hagen & Bryant, 2003) and muscular bonding (McNeill, 1995). Furthermore, the principal proponents of these theories have tried to rationalise an increased evolutionary drive towards the skill of entrainment in humans by, respectively, linking their hypothesis to increased human infant altriciality, female exogamy and increased sociality. While these approaches all have putative value in explaining reasons for improvements to the ability to entrain one's movements to music they do little explain how this skill emerged. Part of the problem is that they view the skill of entrainment to music as a single phenomenon. Viewing bodily entrainment to music, instead, as a conglomeration of subskills allows a clearer distinction from entrainment in other contexts and suggests the possibility that bodily entrainment to music emerged as an exaptive consequence of

the human move towards increased cognitive flexibility. Additionally, breaking down the skill of interpersonal entrainment into subcomponents offers the potential for cross-species comparative data in what would seem to be an uniquely human skill, practised in a uniquely human behavioural context.

This dissertation takes its theoretical cue from recent suggestions made by Hauser, Chomsky and Fitch (2002) for an evolutionary perspective on the faculty of language. Hauser, Chomsky and Fitch suggest a distinction between what they term a faculty of language in the broad sense (FLB) and a faculty of language in the narrow sense (FLN). FLB includes an internal computational system (FLN, see below) combined with at least two other organism-internal systems; 'sensory-motor and conceptual intentional. Accepting that opinion is divided on the precise nature of these systems, and whether they are substantially shared with other vertebrates or uniquely adapted to the exigencies of language, the authors take as uncontroversial 'the existence of some biological capacity of humans that allows us (and not, for example, chimpanzees) to readily master any human language without explicit instruction'. FLB includes this capacity but excludes organism-internal systems that are necessary but not sufficient for language such as memory, respiration, digestion, and circulation. Leaving the door open to more inclusive definitions<sup>1</sup> the authors hypothesise that FLN includes a computational system (narrow syntax) that generates internal representations and maps them into the sensory-motor interface by means of the phonological system and into the conceptual-intentional interface by means of the (formal) semantic system. They suggest that the key component of FLN is recursion, which they identify as a computational system operating primarily over the syntactical domain. FLN thus takes a finite set of elements and yields a potentially infinite array of discrete expressions<sup>2</sup> (see figure 1).



**Figure 1:** A schematic representation of organism-external and -internal factors related to the faculty of language. FLB includes sensory-motor, conceptual-intentional, and other possible systems; FLN includes the core grammatical computations that Chomsky, Hauser and Fitch suggest are limited to recursion. (diagram taken from Chomsky, Hauser & Fitch, 2002, p. 1570).

<sup>1</sup>Lieberman (1996), for example, has argued that the sensory-motor systems were specifically adapted for language and thus should be a part of FLN.  
<sup>2</sup>Recursion is probably not the best term to use as it implies infinity. However, we (as the authors recognise) are restricted by other organism internal factors such as lung capacity, working memory, concept formation and motor output speed and hence exhibit a limited capacity for recursion.

Hauser, Chomsky and Fitch strongly favour a comparative approach to studying the evolution of the faculty of language. They propose, on the basis of a wide range of data (see Appendix 1) that only FLN is uniquely human and hypothesise that most, if not all, peripheral components of FLB are based upon mechanisms shared with other animals, with differences of quantity or quality rather than kind. On the other hand, FLN - the computational mechanism for recursion - is viewed as being recently evolved and unique to humans. The authors explain that 'according to this hypothesis much of the complexity manifested in language derives from the complexity in the peripheral components of FLB, especially those underlying the sensory-motor and conceptual intentional interfaces, combined with sociocultural and communicative contingencies. FLB as a whole has an ancient evolutionary, long predating the emergence of language, and a comparative analysis is necessary to understand this complex system.' By contrast, FLN as a uniquely human capacity must have evolved in the last 6 million years since our divergence from the last common relative of chimpanzees and humans.

Importantly, the authors recognise that both FLB and FLN may have evolved for reasons outside of linguistic/communicative ability such as numbers, navigation and social relations. Furthermore they view shared mechanisms across different cognitive domains (in particular music) as a valuable source of information about the structure of the faculty of language.

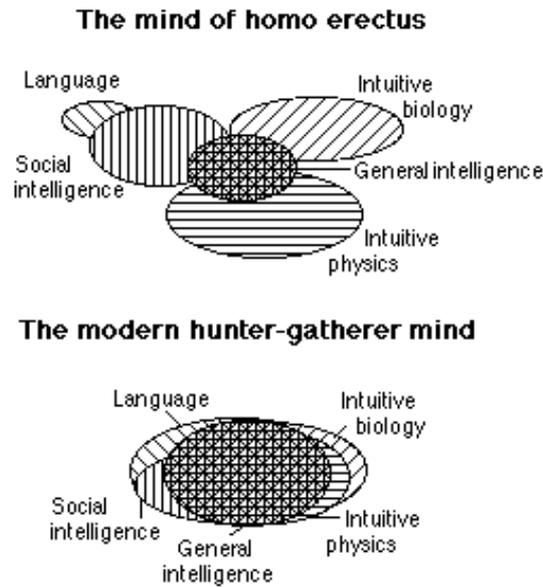
Implicit, although not explicitly mentioned, in this approach is the notion that linguistic ability requires processing information across different cognitive domains as well as across modalities. In other words for a faculty of language to operate it requires not only the individual components but also some form of integration/fluidity. Mithen (1996) has suggested, following Fodor's distinction between innate, specialised cognitive competencies and a general, central, intelligence, that the course of human cognitive evolution is *uniquely* characterised by an increase in the capacity to integrate information across domains and to transfer information or skills between domains. Mithen, with the support of the archaeological record, describes three evolutionary phases:

**Phase 1:** Minds dominated by a domain of general intelligence - a suite of general-purpose learning and decision-making rules.

**Phase 2:** Minds in which general intelligence has been supplemented by multiple specialized intelligences, each devoted to a specific domain or behaviour, and each working in isolation from the others.

**Phase 3:** Minds in which the multiple specialized intelligences appear to be working together, with a flow of knowledge and ideas between behavioural domains (p.64) (see figure 2).

The flexibility of phase 3, which according to Mithen characterises the modern mind, is seen to have emerged only within the last 100,000 years and becomes most evident in the archaeological record with the "cultural explosion" that occurred some 30,000 to 60,000 years ago. Although music is not explicitly mentioned by the author, it has particular relevance to music as musical ability requires processing information across domains and modalities (see Cross, 1999)



**Figure 2:** diagrammatic representation of the theoretically identified cognitive ‘separated’ structures of early hominids (here *Homo erectus*) compared to the ‘integrated’ cognitive structures of modern humans. (after Figures 16 and 17 of Mithen (1996)) (taken from Cross, 1999).

The only problem with the model suggested by Chomsky, Hauser and Fitch is that they do not take enough account of this species-specific cognitive fluidity and thus their approach relies too exclusively upon comparative data based upon individual components of the faculty of language. We can learn a great deal, also, by looking at other human skills which may have become adapted through increased cross-domain integration and by exploring not only unique components within the faculty of language but also upon unique combinations of integrated components.

This dissertation offers the first step towards an adapted version of the Chomsky, Hauser and Fitch model with regard to the faculty for music by concentrating upon the skill of bodily entrainment in music

## 2. Human Interpersonal Musical Entrainment

One of the most prevalent features of music, outside of the socially constructed constraints of western art music, is interpersonal bodily entrainment to the ‘pulse’ (a regular succession of events through time) or ‘beat’ (a perceptual conglomeration of usually regular multiples of pulse) of the music. Although very few examples may seem to contradict the existence of pulse being a universal feature of music, we can safely assume that pulse is a, if not *the*, salient feature of music worldwide. Arom’s study of African music, together with his knowledge of western popular and classical traditions led him to the following definition of music: “*music is a succession of sounds capable of giving rise to a segmentation of time during which it flows in isochronous units... there can only be music inasmuch as it is measured and ‘danceable’*”. The correlation between dance and music is so strong that many African cultures do not lexically distinguish between the two (Arom, 1991). Furthermore, bodily movements underlie the production of the acoustical properties of music and, as such, any form of ensemble playing is reliant upon interpersonal bodily entrainment. In production, as in reaction, African cultures lean

more heavily towards bodily involvement than does contemporary musical practice in the west. The ethnomusicologist John Blacking has noted in his studies of traditional Venda music (Blacking 1973) that Venda adults, when instructing children, concentrate largely on how one should move when producing music rather than how it should sound. Additionally, certain musical cultures do not separate between musical performance and dance in that choreography is an intricate part of the production of sound (e.g. Japanese Taiko drumming). That we as a species have not only the ability but also the motivation to entrain our movements to music is beyond doubt. One need only observe people's reaction to music in the disco, at jazz concerts or at popular music gigs for proof of this.

Interpersonal Entrainment is not a phenomenon unique to musical performance but is common to a wide range of human interactions in which a common pulse is established as a framework for interaction<sup>3</sup>. As in musical performance, deviations from expectancy are often used as a communicative, expressive device. Furthermore the precision of interpersonal entrainment achieved in musical performance and other forms of interaction can be seen to partially reflect the quality and/or efficacy of the event. However, interpersonal entrainment in music is differentiated from other forms of pulse-based interpersonal entrainment in that it involves the *synchronous* production of acoustic output and subsequently relies, arguably, upon a stricter adherence to pulse as well as a greater conscious awareness thereof. Bodily entrainment in musical context is also differentiated from other forms of entrainment that operate at time scales of little relevance to music, such as environmental entrainment in the form of circadian rhythms or the matching of brain wave frequencies, and from self-entrainment in which two or more of a single body's oscillatory systems become synchronised<sup>4</sup>. For the purposes of this paper the term Interpersonal Musical Entrainment (IME) is used and is defined as '*interpersonal behavioural synchrony based upon the perception of pulse in acoustic signals created by human movement*'. IME is not a single entity but is putatively reliant upon the concurrent operation of six sub-skills:

- **A fundamental ability to perceive and produce synchronised and temporally separated events**
- **The ability to produce a reasonably steady periodic pulse**
- **The ability to perceive synchronised events across modalities**
- **The ability to rapidly adjust to small perturbations in pulse as well as changes in tempo – phase and period correction**
- **The ability to perceive and internalise a pulse in complex auditory phenomena**
- **The ability to co-ordinate bodily movements with simple and complex phenomena**

These sub-skills should be viewed as operating at different hierarchical levels with fundamental temporal ability being an essential component of all other sub-skills and with the simpler skills of periodical production, the perception of synchronicity and error correction mechanisms inherent, at least intrinsically, in the more complex skills of dynamic attending and motor activity. In effect we have is a highly complex multi-level system requiring considerable cognitive

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<sup>3</sup> Mother-Infant interactions have been shown to adhere to a relatively strict interactive pulse (Malloch, 1999/2000) Furthermore, researchers have identified periodicities in communicative rhythms on a number of different levels, from the alternation of speech and silence in conversation down to the alternation between consonants and vowels in each phrase (see Jaffe & Anderson, 1997) and periodic rhythms of speech can continue across turn boundaries with a speaker conforming precisely to the speech rhythms of the preceding speaker (e.g. Couper-Kuhlen, 1993; Auer, Couper-Kuhlen et al. 1999; Webb, 1972).

<sup>4</sup> The notion that self-entrainment is a crucial factor in both smooth interlimb coordination and timing and as such linked to interpersonal entrainment will be discussed later. It is worth noting that self-entrainment also occurs at an external level as, for example, in gestured speech (Knapp & Hall, 1997; Mayberry et al., 1998).

flexibility. In support of the evolutionary rationales that will be put forward in the latter part of this dissertation, the following review of psychological studies of individual sub-skills will attempt to establish that the hypothesised sub-skills themselves require considerable cognitive cross-domain processing, show considerable stability across modalities, are ubiquitous (at least intrinsically) within a wide range of human behavioural contexts and that many of the sub-skills are subserved by common internal mechanisms.

## 2.1 Fundamental Temporal Mechanisms

Scientific study of periodical perception and production and sensorimotor synchronisation have largely concentrated upon an experimental paradigm in which participants are required to entrain simple movements, such as finger tapping, with predictable, isochronous auditory stimulus. Experimental paradigms of this nature have been explored since 1886 (Stevens 1886) who used this setup to explore the ability of participants to continue tapping a steady beat (200ms - 2000ms) which was set with the help of a metronome. Experimental paradigms have largely concentrated on intertap intervals of 30ms to 2000ms. This range, largely chosen instinctively at first, is not only the temporal range of intervals with seemingly the most relevance/prevalence in music but also possibly to other communicative acts with roots in fundamentals of information processing. Pöppel (1999, 1999/2000) describes three basic temporal experiences; simultaneity, non-simultaneity and temporal order, and has suggested that temporal processing of sequential information can be classified into four categories:

- **0-2ms:** Within this temporal interval range simultaneous and non-simultaneous events are perceived to be simultaneous (Hosokawa et al., 1981; Moore, 1993).
- **2/3ms-20/40ms:** Events separated by this temporal range create the impression of non-simultaneity but the temporal order of events - which of two events came first - cannot be confidently or unerringly distinguished (Hirsh, 1959; Lotze et al., 1999; Mills & Rollman, 1980; Steinbüchel et al., 1996; Pastore & Farrington, 1996)<sup>5</sup>.
- **30ms-3sec:** Events separated temporally within this range are viewed to be processed within what Fraisse (1984) has termed the 'psychological present'. Temporally separated sequences can be perceived as such and can be produced with relative ease. Intervals within this range are believed to be processed within an 'actual present' as a whole (Fraisse, 1984, & Wittmann 1999). 3secs is thought to be a time constant in perceptual tasks represents a central neural mechanism that functions to integrate successive into a "gestalt" in order to create a "subjective present" (Pöppel, 1973, 1978). Furthermore repetitive isochronous events within this temporal range, have been shown to build perceptual expectancies towards future events (Jones, 1989; Large & Jones, 1999)

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<sup>5</sup>Pöppel (1978, 1997) has theoretically identified the perception of temporal order as a 'basic mechanism in the hierarchy of elementary temporal experiences'. According to his theoretical approach 'functional system states with a duration of ca. 30ms are implemented by neuronal oscillations that define the temporal order of events. After the transduction of a first stimulus, a relaxation oscillation is triggered with a period of 30ms that is phase-locked to the stimulus. If the second stimulus is processed within this first period, temporal order of the two events cannot be indicated. Only when the second stimulus is processed in a following period -because the inter-stimulus interval is longer than 30ms - can the temporal order of the two events be established.' (Wittmann & Pöppel, 1999/2000). This view is, however, opposed by an alternative model of perceptual and dynamic representation in the brain which postulates an interval-based representation (e.g. Ivry, 1996). Aspects of this debate are discussed at a later stage.

- **3sec +:** Although the question of whether the processing of larger timing intervals is operated by similar or overlapping mechanisms is open (Gibbon, Malapani, Dale. & Gallistel, 1997), it is widely accepted that durations exceeding 3 seconds involve an additional memory process that link moments that passed with the present (Fraisse, 1984, Pöppel 1999). This further timing mechanism is thought to bind successive events in perceptual units of 2 to 3 seconds (Block, 1990; Fraisse, 1984; Pöppel, 1978; 1997). Pöppel terms this process the formation of perceptual Gestalts.

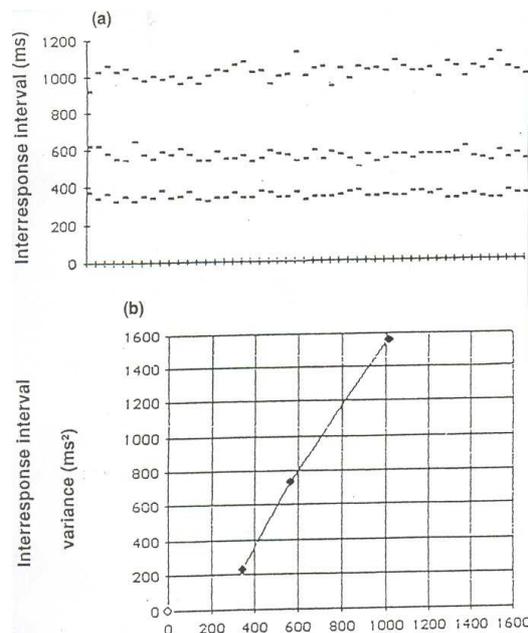
Important for the further course of argumentation in this paper is evidence suggesting that the threshold between events whose temporal order are not distinguishable and those which are is consistent for acoustic, visual and tactile stimuli (Hirsh & Sherrick, 1961). Furthermore, timing processes inherent in kinesthetic abilities is constant across a range of effectors (Franz E. A., Zelaznik, H. N. & Smith, A, 1992). Much empirical evidence has, also, been collected to support the theoretical framework of the 'psychological present' in perception across modalities and in motor behaviour (Wittmann & Pöppel, 1999/2000). Evidence cited by Wittmann & Pöppel, (1999/2000) includes the following:

- During the perception of ambiguous figures like the Rubin vase automatic shifts between the two perspectives occur at fairly regular intervals of 3 seconds (Steinbüchel et al., 1999)
- Although when listening to a dynamically unchanging metronome pulse we perceive units of integrated beats by subjectively accentuating every  $x^{\text{th}}$  beat, perceived integration units, even at lower frequencies, never exceed 3 seconds (Szelag et al., 1996; Fraisse, 1978).
- A frequency histogram of everyday repetitive movements in humans of five different cultures filmed in natural surroundings indicated that movements mostly lay in the time range of 2-3 seconds (Schleidt et al., 1987)
- Perceptual 'chunking' in linguistic and musical processing (Wingfield & Nolan, 1980; Pöppel 1985, 1989; Szelag et al., 1996) (discussed below).
- Synchronisation in finger-tapping experiments cannot be maintained when inter-event intervals exceed 2 seconds. Mates et al. (1994) have shown that in periods longer than 2 seconds the ability to anticipate when the next signal will occur will break down.

It is important for the course of taken argumentation followed in this paper to note that temporal mechanisms of perception and integration are consistent across modalities and varying skills and hence likely to be controlled by a flexible and widely connected central mechanism.

## **2.2 Periodical Production**

Stevens' pioneering study (1886) into isochronous serial interval production (ISIP), in which participants were instructed to continue a metronomically established pulse (360ms-1500ms), established some important facts. Subjects were able to adjust to the response rate according to the metronome beat provided and maintain it over extended periods. However this study showed considerable variability in performance and an increased variability with increases in temporal interval (see figure 3).



**Figure 3:** Interresponse interval data from Stevens (1886). (a) Data from three trials for a professional musician producing interresponse intervals at three different target intervals 400, 600, and 1000ms. (b) Variance computed from the data above as a function of the mean interval. (taken from Vorberg & Wing 1996 p. 184)

Stevens observed from a visual inspection of the data that variability between the target interval and the mean of the intervals produced by the subjects remained within about 5% of the standard deviation and that variability was evident on two distinct levels:

- Short-term fluctuations characterised by a zig-zag shape such that ‘two sequent variations in the same direction were rare.
- Larger, more primary, waves extending over the sequence (since termed ‘drift’).

### 2.2.1 Inter-Onset-Interval Variability

Although experimental paradigms affect the levels of dispersion later studies have confirmed a typical standard deviation of ISIP series of between 3-6 percent of the inter-onset-interval (IOI) (e.g. Keele, Pokorny, Corcos & Ivry, 1985; Madison, 1998; Michon, 1967; Wing & Kristofferson, 1973b). Furthermore, the ‘zig-zag shape’ – whereby an interval longer than the mean is frequently followed by an interval shorter than the mean – and the increased interval to interval deviations with increases in IOI observed by Stevens have been since validated (Vorberg & Hambuch, 1984; Vorberg & Wing, 1996; Wing & Kristofferson, 1973a; Wing & Kristofferson, 1973b). The former observation has been taken to imply a negative first-order correlation whereas the latter has been described as an accelerating function of the IOI (Fraisse, 1984) with breaks in the function around 250ms (Wing & Kristofferson, 1973b) and 1 sec (Madison, 1998). Madison (2000) hypothesises that ‘the latter break is probably related to qualitative changes in performance found for other temporal tasks (Madison, 1998; Szlag, 1997). These may in turn be related to a retention or integration limit around one second, which is found both for the auditory (Crowder, 1993; Kubovy & Howard, 1976; Mates, Radil, Müller & Pöppel, 1994; Pöppel, 1996; Pöppel, 1997; Warren, 1993) and visual modality (Freyd & Johnson, 1987).’

It is interesting to note that training with feedback designed to reduce deviation has shown to reduce dispersion by thirty percent (Nagasaki, 1990). However, dispersion remains reasonably substantial even in the case of extensive rhythmic training (Madison, 1992). The evidence of whether musicians produce less dispersion is as yet contradictory with some studies supporting improved periodicity (Fran ek, Mates, Radil, Beck & P oppel, 1991; Keele et al., 1985) and others showing no difference (Madison, 1999; Yamada & Tsumura, 1998).

Wing and Kristofferson (1973b) proposed a theoretical model to account for negative first order correlation in self-paced tapping for which they assumed that a succession of timed pulses are generated by an internal timekeeper ©. In this model each internally generated interval (C<sub>j</sub>) is subject to a delay in motor implementation (M<sub>j</sub>) before the occurrence of an observable response I<sub>j</sub>, I<sub>j+1</sub>. Internally generated intervals and motor implementation delay are seen to be independent and subject to random variability such that over successive responses I<sub>j</sub> have variance:

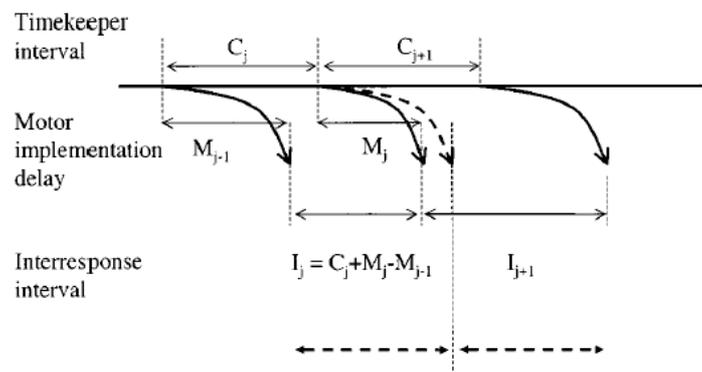
Eq. 1) 
$$\text{Var}(I) = \text{var } \textcircled{C} + 2\text{var}(M)$$

The model predicts dependence between adjacent I<sub>j</sub>I<sub>j+1</sub> with lag-on autocovariance:

Eq. 2) 
$$\text{Acov}(I(1)) = -\text{var}(M)$$

This led the authors to the following prediction for the autocorrelation at lag k:

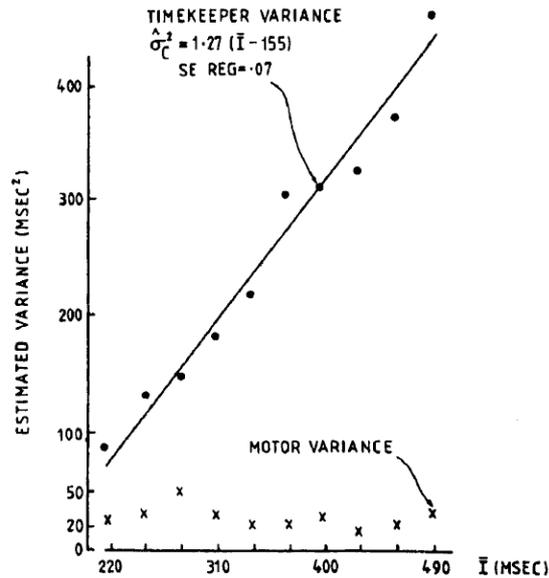
Eq. 3) 
$$\begin{aligned} \text{Acorr}(I(k)) &= \text{acov}(I(k))/\text{var}(I) \\ &= -1/\{2 + \{\text{var}\textcircled{C}/\text{var}(M)\}\} & k = 0 \\ &= 0 & k > 0 \end{aligned}$$



**Figure 4:** Diagrammatic representation of the Wing-Kristofferson two-level timing model. Timekeeper intervals © are subject to motor implementation delays (M) in defining interresponse intervals (I). Average I is equal to the average C. However, variation in I reflects both C and M. In particular, variation in M results in negatively correlated I (tendency for short and long intervals to alternate), as suggested by the dashed lines

It should be noted that the WK model predicts that the lag-one autocorrelation (the correlation between adjacent pairs of intervals taken through the sequence of intervals) occurs as a result of the two-level architecture and not from some feedback mechanism, and should, in accordance with equation three, remain within the limits of zero and minus one-half of the previous interval. Support for the model has been given by a variety of different studies each emphasising different variables such as age of the participants, levels of ‘clumsiness’, time perception as well as using a variety of effectors (see appendices 2 and 3). In each case equation 1 and 2 have been solved to

yield estimations for var. © and var. (M) with fluctuations supporting the case for timekeeper and motor implementation processes being distinct and behaviourally dissociable. Of particular note is Wing's unsurprising finding (1980) that var. © is entirely responsible for increased variance with increases in inter-tap-intervals (Stevens 1886) (see figure 5).

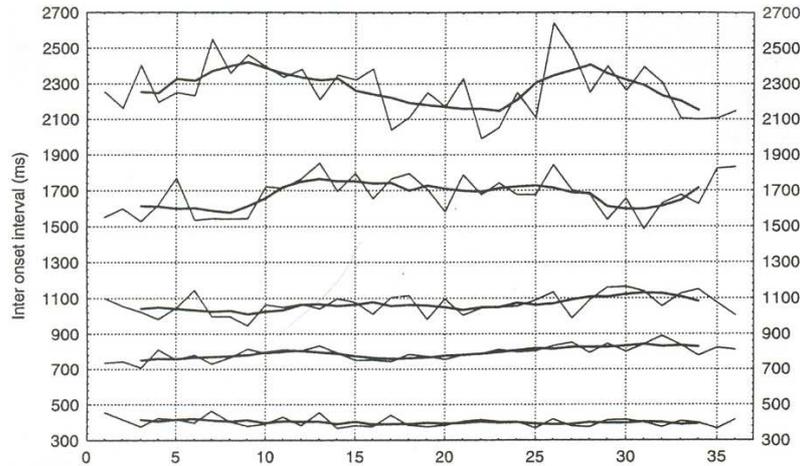


**figure 5:** Variability of timing. At longer intervals, timekeeper variance (var©) increases but motor implementation variance (Var(M)) is relatively constant. (diagram taken from Wing, 1980).

Proponents of the model accept that some studies of repetitive tapping have produced results outside the scope of the model. However, these have been attributed to bias in autocorrelation estimators in the relatively short sequences which have to be used in support of the model in order to avoid the factor of 'drift' (producing positive higher-order correlations, see below). Attempts have been made to adapt the model to make explicit allowance for estimator bias (e.g. Vorberg & Wing, 1996).

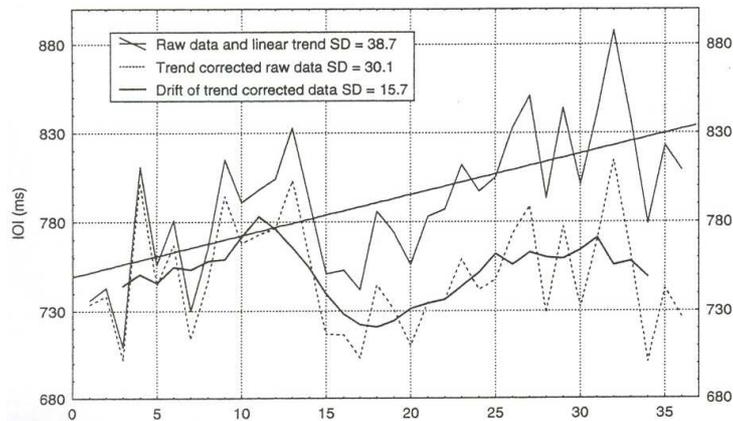
### 2.2.2 Drift as Factor of Variability

As mentioned previously the other factor contributing to variability in isochronous tapping tasks is drift. Due to the influence of the Wing-Kristofferson model 'drift' has not been given as much study as it merits. However, recent models (Madison, 1998; Madison, 2001) have attempted to incorporate drift as a key factor in tapping variability. Drift refers to involuntary substantial fluctuations in the mean over time – musically speaking subconscious accelerando and ritardando – and constitutes a positive higher-order dependency as several intervals in succession become increasingly shortened or lengthened. Figure 6 - a typical set of data from the continuation phase of an isochronous tapping task (Madison, 2000) - clearly shows substantial fluctuation in the means. The smoothed plots – 5 point moving average – emphasise this point. Furthermore, fluctuations in the mean seem to be proportional to the IOI and have no specific period (i.e. are random).



**Figure 6:** Raw data from one participant in the continuation (production) phase. The thicker lines are five point moving averages.

Madison (1998, 2001) has attempted to create a model of variability that accounts for and distinguishes between negative first-order correlation and drift by subtracting a linear marked trend in a sequence from total dispersion and hence calculating the percentage of mean dispersion caused by drift. Madison considers that drift can operate at multiple levels. Without going into the complex mathematics of the model the diagram below shows the idea behind the approach very clearly (see figure 7). In the example – an enlarged diagram of the 700ms series given above - trend (overall change in IOI over the production interval) alone yields a standard deviation (SD) which is 40 percent of the total SD for the data. What is particularly noticeable, however, is that even after subtraction of the trend the remaining variability retains positive higher-order dependence as shown by the 5 point moving average of the trend corrected data.



**Figure 7:** Raw data from one participant in the continuation (production) phase after synchronising to 700ms IOIs. The straight line shows the linear trends, and the dotted line is the residuals when the trend is subtracted. The thicker line is a five point moving average of the trend corrected data.

It is clear from studies of variability in isochronous tapping studies that, although we possess an impressive ability to produce periodical events, we do not have an absolute ability in this area<sup>6</sup>. This suggests that we have evolved a system that is *sufficient* for building expectancy, and

<sup>6</sup> Although reproduction of exact tempos is much enhanced in musical production where people will often reproduce the tempo used on, for example, a favourite recording (Levitin, 1996)

coordinating internal and external events, but without need for absolute precision. Furthermore, it is worth noting that periodic behaviour (albeit not necessarily production) is not restricted to musical activity and is ubiquitous to tapping to simple acoustic patterns (Essens & Povel, 1985; Helmuth & Ivry, 1996; Ivry & Hazeltine, 1995; Jones & Pfoordresher, 1997; Mates, Radil, & Pöppel, 1992; Parncutt, 1994; Povel, 1981, 1984, 1985; Povel & Collard, 1982; Povel & Essens, 1985; Robertson et al., 1999; Vos Mates & van Kruysbergen, 1995), tapping to music (Drake, Penel & Bigand, 2000; Schreier, 1998; van Noorden & Moelants, 1999; Vos, van Dijk, & Schomaker, 1994) tapping to polyrhythms (Deutsch, 1983; Klapp et al., Peper, Beek, & van Wieringen, 1995), speech rhythms (Cummins & Port, 1998), limb coordination (Diedrich & Warren, 1995; Schmidt, Beek, Treffner, & Turvey, 1991; Schmidt, Bienvenu, Fitzpatrick, & Amazeen, 1998), time perception (Large & Jones, 1999; McAuley, 1995; McAuley & Kidd, 1998), and infants' postural adjustments (Berenthal, Rose & Bai, 1997).

## 2A An Exploration of the 'Timing Mechanism'

### 2A.1 The Nature of the Timing Mechanism

The production and perception of temporal intervals and periodical behaviour suggests the existence of some kind of internal timing mechanism. There is considerable disagreement in the psychological literature as to how timing is achieved (see Brain and Cognition Vol. 48 for a comprehensive overview). In this field of enquiry timing has largely been explored with regard to temporal duration processing and in relation to timings inherent in the external and inter-limb co-ordination of movements. Two theories dominate the literature the first of which – Kelso's **dynamic model** of movement co-ordination (Kelso 1981; 1984) - is concerned, largely with the study of timing inherent in rhythmic and non-rhythmic human movements. As such it is less relevant at this stage in the argument and will be discussed at a later stage.

The other prevalent notion in the study of timing in kinesthetic tasks *and* temporal processing is the existence of a mechanism somewhat analogous to a clock mechanism. Models of this nature seem more relevant to kinesthetically simple periodical behaviour as they incorporate the abilities to perform stationary temporal perception tasks whereas dynamic models are largely concerned with the achieving of fluent coordinated movement. Evidence in support of an internal clock, without necessarily discounting the role of dynamic inter-limb interaction in kinesthetic co-ordination, comes from a variety of sources (see Ivry, 1997) including significant correlations between measures of temporal variability in motor tasks across different effectors (Keele, Pokorny, Corcos, & Ivry, 1985; Franz, Zelaznik, & Smith, 1992) as well as correlations between motor and perceptual tasks (Keele et al., 1985; Ivry & Hazeltine, 1995). The idea of an internal clock seems to accord more strongly with the wide array of procedural and perceptual methodologies inherent in musical behaviour ranging from complete embodiment of the pulse in dance musics to the passive aesthetic appreciation of classical music concert-goers. Proponents of the internal clock have accepted that results from studies of bilateral and bimanual tapping necessitate the extension of the analogies to incorporate at least two clocks. Recent researchers Ivry & Richardson (2001) even suggest that each effector is associated with a unique set of timing elements whose harmonious interactions lead to decreased variability (the variability has been attributed to decreased var. (C) in Wing-Kristofferson

models). Furthermore, evidence of decreased variability in bilateral and bimanual tapping<sup>7</sup> suggests inter-clock flexibility or a multiple effector advantage (Ivry & Richardson, 2001)

### 2A.2 The Workings of the Internal Clock

Attempts to characterise the internal processes of the **internal clock** have generally defined two different theoretical possibilities which can be described metaphorically as oscillatory pacemakers and an hourglass mechanism respectively (Ivry, 1996; Schöner, 2001). The **pacemaker** approach is based on the assumption that representation of events is based on a reproducible oscillatory period combined with some type of counting device. The oscillatory pacemaker is thought to operate at a fixed speed which could either be adjusted based on task demands or there could exist a bank of such oscillations, with different intervals resulting from their interactions (Church & Broadbent, 1991; Miall, 1996).

The fundamental difference of the **hourglass** model is that the pacemaker mechanism, when activated, is always preset to represent a specific interval. The timing of a movement is thus thought to be dependent upon a prediction of the final destination and the timing thereof. As such, the representation of different intervals is seen to require sets of timers each tuned to different durations. Another important difference from the pacemaker model is that, if required to represent the same interval repeatedly, the timekeeper must be retriggered each time by a form of reset process.

Largely due to the ubiquity of oscillatory processes in the nervous system researchers have, by and large, viewed the pacemaker model as being the more likely of the two hypotheses. Furthermore, if we assume that processes underlying temporal processes and rhythmic movement are the same as those involved in musical production and perception, the internal continuation of an established pulse during musical involvement (Cooper & Meyer, 1960) is suggestive of an open-loop (i.e. oscillatory) system. The build-up of expectancy (Jones, 1989) in perception of partly periodic phenomena such as music seems to further support the case for an oscillatory pacemaker system. For these reasons I will be concentrating on the pacemaker hypothesis in the further course of argumentation. It is, however, probably worth noting the possibility that, as is often the case with seemingly irreconcilable dichotomies, aspects of both approaches are correct. It is undeniable that we have an ability to program movements (one need just think of a gymnast preparing a routine or a musical virtuoso preparing a concert performance for confirmation of this). However, we also need to make very quick adjustments to movements depending upon random circumstances. It is, for example, possible that the hourglass approach is an

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<sup>7</sup> Synchronous bimanual tapping leads to reduced within-hand variability for both hands in untrained participant and professional percussionists (Helmuth & Ivry, 1996; Richardson & Ivry, unpublished taken from Ivry & Richardson, 2001)

Tapping bilaterally with different effectors has also shown to produce reduced within effector variability for both effectors (Helmuth & Ivry, 1996; Turvey et al., 1986). Estimates with the WK model show improvements to be a manifestation of improvements of central variability (Turvey et al., 1986)

Patients demonstrating greater timing variability on one side compared to the other due to unilateral cerebellar lesions unfailingly showed significantly decreased variability for the impaired hand in bimanual tapping (Franz, Ivry & Helmuth, 1996) (The unimpaired hand showed stable variability in unilateral and bimanual tapping)

extension to the pacemaker model in which sequences of multiple oscillations are pre-programmable.

### **2A.3 Evidence for a Common Mechanism**

It is, of paramount importance for the course of argumentation taken in this paper to explore whether or not the mechanism involved in timing tasks are 'flexible' and, as such, stand up to Mithen's view of the integrative modern human mind. In other words is it constant across perception, production and differing modalities? Is it able to interact with other cognitive functionalities to achieve complex conglomerative functionalities? Or is the perceptual and procedural skill of temporal differentiation in itself a combination of cognitive capacities?

As previously discussed evidence for similar perceptual thresholds suggests interactive flexibility across differing modalities. The evidence provided below suggests that this flexibility extends to perception and production both of which seem to be subserved by the same mechanism. Furthermore it seems likely that the mechanism underlying the perception and production of shorter temporal intervals is congenital to processing temporal duration beyond the psychological present. Larger intervals can be seen to be processed by a memory-based counting mechanism analogous to an orchestral percussion player silently counting out the bars prior to his entry. Finally, there is evidence showing a positive correlation between periodical ability and acuity in temporal discrimination:

#### Perception and Production

- The human ability to entrain movements to an external stimulus such as music.
- Similarities between the individual performance in tasks of time perception and time production (Ivry & Hazeltine, 1995)

#### Shorter and Larger Intervals

- Significant correlation between individual performance across a wide range of temporal intervals in periodical and stochastic temporal discrimination tasks (Stevens, 1888; Michon, 1967)

#### Periodical Ability and Temporal Discrimination

- Significant correlations between performance in repetitive tapping tasks and duration discrimination tasks such as those found by Keele et al (1985). Importantly, acuity on the perception tasks was found to have no correlation to non-temporal motor tasks supporting the notion of an overlap in the neural systems subserving these tasks.
- Frequency of inter-interval isochronous clicks has been shown to be a factor in time perception and production; particular frequencies of inter-interval clicks systematically increase or decrease perceived or produced intervals (Treisman et al, 1990; Treisman et al, 1992). A significant negative correlation has been observed in that frequencies that shorten estimates of perceived time, most likely by slowing down the internal 'clock', tend to lengthen movement times.

### 2.A.3 Neural integration in temporal and periodical tasks

Neurological studies offer an invaluable insight into the nature of the timing mechanism. Various areas of the brain have been shown to play a part in various timing tasks suggesting that timing is reliant upon interaction between different cortical areas. Jeuptner et al (1995) demonstrated increases in regional cerebral blood flow (rCBF) with positron emission tomography (PET) in the cerebellum, basal ganglia as well as cerebellar temporal, prefrontal and cingulate cortex when subjects judged the duration of tone intervals.

The **cerebellum**, traditionally labelled as a motor structure, has been most widely associated with timing functions and shown to be an essential component for a wide variety of them. Patients with cerebellar lesions show marked increases in variability in repetitive tapping tasks as well as impaired performance on temporal discrimination tasks<sup>8</sup> (Ivry & Keele, 1989). Interestingly, analysis using the Wing-Kristofferson model has shown the nature of the variability to be dependent upon the locus of the pathology suggesting multiple functions. Ivry, Keele & Diener (1988) through application of the Wing-Kristofferson model, identified elevated var. (I) with increased var. (C) in patients who had lesions of the dentate nucleus (the output of the lateral cerebellum). By contrast, patients with medial cerebellar lesions demonstrated raised var. (I) as a result of increased var. (M). Furthermore some of the primary symptoms of cerebellar dysfunction – dysmetria and unintentional tremor – have been attributed to a loss in coordination of the temporal pattern between antagonist muscles (Hallett, Shahani & Young, 1975; Hore, Wild & Diener, 1991). Cerebellar dysarthria is most evident on sounds that require precise timing between sets of articulators (Ivry & Gopal, 1992).

The **basal ganglia** has also been shown to be involved in timing functions. Patients with Huntington's and Parkinson's disease (both diseases, which affect the basal ganglia) have shown impaired response timing, duration discrimination and increased IOI variability in repetitive tasks (Freeman et al: O'Boyle, Freeman & Cody (1996). Studies attempting to partition the disorder into var. (C) and var. (M) in Parkinson patients have brought conflicting evidence. Some studies (Pastor, Jahanshahi, Artieda & Obeso, 1992; O'Boyle, Freeman & Cody, 1996) have shown no differential effects of the disorder on var. (C) and var. (M), whilst others (Harrington & Haaland, 1998; Harrington, Haaland & Hermanowicz, 1998) reported a selective increase in var (C).

**Cortical structures** are also involved in timing tasks and 'seem to contribute different, perhaps more integrative computations in timing tasks than those attributed to the cerebellum or the basal ganglia' (Hazeltine & Ivry, 1997, p. 165). For example, premotor and or supplementary motor cortical lesions have been associated with deficits in rhythm production (Halsband et al, 1993). Furthermore, laterality effects have been reported on tests of temporal perception: for intervals ranging from 1 to 5 s, patients with precentral left hemisphere lesions tend to produce shorter time intervals than control subjects, whereas patients with precentral right hemisphere lesions tend to produce longer time intervals (Von Steinbüchel, Witmann & Pöppel, 1996).

An intuitive interpretation of the information provided suggests that different cortical areas contribute different aspects to timing tasks or that different mechanisms operate at

<sup>8</sup> Other factors, such as loudness discrimination ability, were shown not to be a factor of the impaired performance.

different temporal intervals. It is interesting to note that research examining the role of the basal ganglia has concentrated on intervals of 3 s and more and has viewed drift as the primary factor in increased variability due basal ganglia dysfunctions (Meck, 1996; Pastor et al, 1992; Maricq & Church, 1983). Research examining the role of the cerebellum, on the other hand, has used intervals of less than 1 s and have shown increased timing variability due to cerebellar lesions to be less effected by drift (Hore, Wild & Diener, 1991; Ivry & Keele, 1989).

Although this may seem at first sight to support the idea that different mechanisms operate at different temporal intervals, it is more likely to support the notion that as target intervals lengthen, additional processes, such as attentional and memory functions, become involved (see above for temporal processing thresholds). Ivry & Mangles (1997) found that cerebellar patients perform poorly at temporal discrimination tasks centred at 400ms and 4 s, whereas frontal patients were impaired only when stimuli were separated by 4 sec. This suggests that frontal contribution may not be specific to timing but instead involves itself in timing tasks when working memory or attentional requirements are increased. Theories that suggest two differentiated timing processes, one for non-conscious (i.e. operating below temporal thresholds) timed motor behaviours in the basal ganglia and one for consciously timed motor behaviours in the cerebellum have received recent support from a study (Stephan et al., 2002) that identified additional dorsolateral prefrontal cortex involvement.

The differences viewed between the type of increased variability produced by cerebellar and basal ganglia patients have been interpreted as noisy timing systems and changes in clock speed respectively. An interesting hypothesis is that the basal ganglia patients produce increases in drift because the basal ganglia is critical for shifting cognitive sets (Brown & Marsden, 1988; Downes et al, 1993; Hayes et al, 1997). Patients with Parkinson's disease take longer to switch from one task to another, particularly when both tasks use the same stimuli. Hazeltine et al (1997, p.166) hypothesise that 'if timing long durations, in the absence of external cues, requires the accumulation of short intervals and the updating of internal states, then dopamine<sup>9</sup> depletion may slow this process, leading to timing problems in parkinsonian patients.'

It is fair to say that, although neuropsychological data do not, yet, unequivocally distinguish between basal ganglia, cerebellar and other cortical contributions, humans demonstrate considerable cortical flexibility in the performance and perception of a wide variety of periodical and temporal tasks.

### **2.3 The Perception of Sensorimotor Synchronisation – Evidence from Asynchronies**

Isochronous tapping with a metronome is characterised, unsurprisingly, by considerably less variability than tapping without a metronome (Dunlap, 1910) and must therefore be dependent upon on an additional error correction mechanism based on the desire for perceived synchronisation (Mates, 1994; Schulze & Vorberg, 2001; Semjen, Vorberg & Schulze, 1998). The nature of the correction mechanisms will be discussed below but first of all it is necessary to consider how sensorimotor synchronisation is perceived. The most observed phenomenon in experiments requiring the production of simple synchronous movements with a metronomic beat

<sup>9</sup> Meck (1995) proposes that a dopamine-dependant, basal ganglia system forms the pacemaker-accumulator mechanism.

is negative synchronisation error (NSE) – people tend to tap before the click (Dunlap, 1910; Fraisse, Oléron & Paillard, 1958; Fraisse, 1966; Franěk, Radil, Indra, and Lánsky, 1987; Mates, Radil & Pöppel, 1992; Aschersleben & Prinz, 1995). The absolute value of the negative synchronisation, however, varies with the alterations in the experimental method. Changes to NSE with changes in experimental paradigm have provided the impetus for a number of diverse theories regarding how the perception and production of sensorimotor synchronisation is achieved.

### 2.3.1 The Evidence

A variety of factors have been shown to influence the value of the negative synchronisation. Experiments into the various influences are summarised in the table below in which variable factors have been classified into nine categories: Effector organ; modality of the pacing signal; external sensory feedback; internal sensory feedback; training; tempo; duration of the pacing signal; kinaesthetic nature of the tap; and nature of the intertap interval.

<b>Variable Factor</b>	<b>Effects on the negative synchronisation error (NSE)</b>
<u>The effector organ</u>	<ol style="list-style-type: none"> <li>1. Anticipatory error is substantially more pronounced (45ms) with foot than hand tapping under controlled feedback situations independent of the body side involved and of whether one or two simultaneous effectors - two hands, two feet or one foot and one hand - are employed (Aschersleben &amp; Prinz, 1995; Billon, Bard Blouin &amp; Teasdale, 1996).</li> <li>2. Wohlschläger &amp; Koch (2000) ordered four effectors - finger, toe, elbow and knee – according to the negative asynchrony (NA) produced starting with the least error as follows: 1. Finger (61ms NA); 2. Elbow (72ms NA); 3. Knee (86ms NA); 4. Toe (105ms NA).</li> </ol>
<u>Modality of the pacing signal</u>	<ol style="list-style-type: none"> <li>3. Negative synchronisation is most pronounced with <b>auditory</b> pacing signals such as clicks (Kolers &amp; Brewster, 1985)</li> <li>4. <b>Visual</b> pacing signals result in a reduction in asynchronies and even positive asynchronies under conditions with very short intertap intervals (Dunlap, 1910; Kolers &amp; Brewster, 1985)</li> <li>5. In studies employing <b>tactile</b> pacing signals intermediate size asynchronies between those for visual and auditory have been reported (Kolers &amp; Brewster, 1985). However, Müller et al (2001) observed no asynchrony under conditions applying visual pacing signals.</li> </ol>
<u>External sensory feedback</u>	<ol style="list-style-type: none"> <li>6. Adding auditory feedback to the tap leads to reduced NSE. (Ascherleben, 1995, 1997; Mates &amp; Aschersleben, 2000; O’Boyle &amp; Clarke, 1996; Mates, Radil &amp; Pöppel, 1992)</li> <li>7. Subliminal delays (less than 100ms) in auditory feedback proportionally increase NSE. (Aschersleben &amp; Prinz, 1997; Mates &amp; Aschersleben, 2000)</li> </ol>
<u>Internal sensory feedback</u>	<ol style="list-style-type: none"> <li>8. Participants injected with local anesthesia to the right index finger showed marked increases in NSE both in air-taps and contact taps (Aschersleben, Gehrke &amp; Prinz, 2001)</li> <li>9. An almost completely deafferented patient (see Cooke, Brown, Forget &amp; Lamarre, 1985 for a description) did not show a differentiated NSE between finger and foot tapping. (Bard et al., 1992)</li> <li>10. A deafferented patient (see Cole &amp; Sedgwick, 1992 for a description), suffering from a purely sensory neuropathy leading to a total loss of kinesthetic and tactile sensitivity for the whole body below the neck whilst leaving the motor system intact, showed marked performative improvements with increases of extrinsic sensory feedback. (Aschersleben, Stenneken, Cole &amp; Prinz, 2003b)</li> </ol>
<u>Training</u>	<ol style="list-style-type: none"> <li>11. Musically untrained persons exhibit an asynchrony that is, on average, 10ms larger than that produced by amateur instrumental musicians (Aschersleben, 1994). The mean synchronisation error is further decreased in highly trained musicians (Ludwig, 1992)</li> </ol>

	<p>and some professional pianists are able to tap in exact synchrony. (Repp, 1999).</p> <p>12. Training with informatory feedback leads to participants being able to tap in exact synchrony after 10 sessions (about 10'000 taps) although participants report that they have to delay their tap subjectively and that perceptual synchrony is not achieved (Aschersleben 2000a). Training without feedback mechanisms does not change the mean asynchrony. (Aschersleben, 2000b)</p>
<u>tempo</u>	<p>13. Several studies have identified increases in negative asynchronies with increasing interval durations (Woodrow, 1932; Kolers &amp; Brewster, 1985; Mates et al., 1994; Miedreich, 2000; Pressing, 1998). However, Gehrke (1996) demonstrated that faster tapping rates were collated to more powerful taps which in turn affects the synchronisation error. Participants trained to filter out variability caused by variations in the power of the tap showed no variation in synchronisation errors across different interval durations (Gehrke, 1996 – Experiment 3)</p>
<u>Duration of the pacing signal</u>	<p>14. Modifications to the duration (1 - 300ms) of the pacing signal have been shown to affect negative asynchrony with increases in duration leading to decreases in synchronisation error (Vos, Mates &amp; Kruysbergen, 1995). A stimulus duration of 300ms can even lead to the disappearance of negative asynchrony if combined with a tempo of 120bpm.</p>
<u>Kineasthetics nature of the tap</u>	<p>15. When participants produce large amplitudes (7cm), (and subsequently greater force and velocity) the corresponding asynchrony (25ms NSE) is substantially less than when participants are instructed to produce small amplitudes (1cm amplitude; 60ms NSE). (Aschersleben et al., 2003a; Gehrke, 1996)</p> <p>16. Wohlschläger &amp; Koch (2000) observed that the motion of finger tapping tends naturally to incorporate a secondary intermediate tap into thin air. By instructing participants to incorporate this and even tertiary 'air-taps' they achieved a mean decrease in negative asynchrony across a range of different effectors.</p>
<u>Intertap interval</u>	<p>17. By comparing performance in which intervals between successive stimuli is empty and tapping to a piece of music Thaut et al (1997), observed a decrease in asynchrony in the latter.</p> <p>18. The introduction of randomly distributed (not rhythmically) tones in between clicks also decreased negative asynchrony (Wohlschläger &amp; Koch, 2000)</p>

### 2.3.2 Theoretical Perspectives

Variability in the quantity of NSE with changes to experimental conditions has led to widespread theories regarding the perception of synchronisation, as well as other factors, which can be seen to cause/affect NSE in experimental conditions. Each of the approaches is supported by a subset of the data presented above. However none singularly manage to explain all the data nor do any of the posited theories avoid contradicting evidence if viewed autonomously. Four theories have been put forward;

According to the **Nerve-Conduction (Paillard-Fraille) Hypothesis**, NSE is seen to have its origins in peripheral processes. The idea is that because it takes more time for the sensory information from the tip of the finger (resulting from the tactile and kinesthetic feedback from the tap) to travel to the brain than that from the ear (from the auditory pacing signal), the tap has to precede the click to establish synchrony at the level of central representation. (Aschersleben & Prinz, 1995, 1997; Fraisse, 1980; Paillard, 1949) see figure 8.

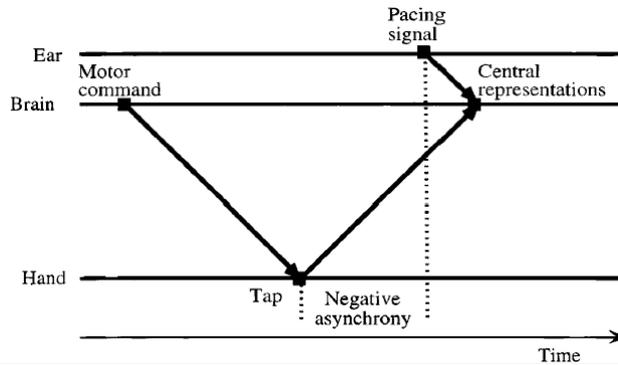


Figure 8: The nerve-conduction hypotheses (taken from Aschersleben, 2002 p.69)

The nerve-conduction hypothesis is supported by increased NSE in foot-tapping versus finger-tapping<sup>1</sup>, (from the table of evidence above) as well as studies employing additional and delayed auditory feedback<sup>6,7</sup>. The model can also account for the effect of the pacing signal's sensory modality on the magnitude of NSE<sup>3,4,5</sup> if the number of synaptic transmissions are taken into account. However the hypothesis fails to account for the differences in NSE produced by finger, toe, elbow and knee<sup>2</sup> and does not explain the effects on NSE of practice<sup>11,12</sup>, expertise<sup>11</sup>, changes in the duration of the tap<sup>14</sup>, the nature of the inter-interval space<sup>15-18</sup>, and changes in the force of the tap<sup>15</sup>.

The **Sensory Accumulator Model** also takes the view that synchrony is established at the level of central representation. The model assumes that for an external event to be experienced and timed, its central representation has to be experienced as one neural entity. The processing times necessary for the creation of the neural state is dependent upon a threshold which is determined by the density of afferent neural signals generated by the physical events. The model, thus, assumes that the steepness of an accumulation function determines the time elapsed between an external event and its central representation. The primary factor of the steepness of the accumulation function is the density of afferent signals arriving at a central level; the more afferent signals per unit of time the earlier the threshold should be reached. In simple metronomic tapping tasks NSE is believed to be a result of the tap having a less steep accumulation function because auditory information is accumulated faster than tactile/kinesthetic information. (Aschersleben et al., 2003a; Gehrke, 1995, 1996) (see figure 9).

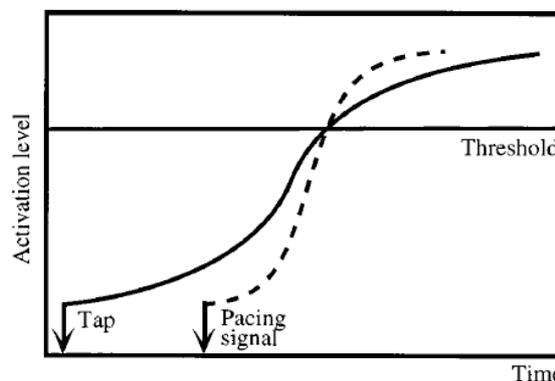


Figure 9: The sensory accumulator model (taken form Aschersleben, 2002)

The sensory accumulator model also takes support from increased NSE in foot-tapping<sup>1</sup> as it views the receptor density and the representational area in the brain as being smaller for the foot than the hand. As such its accumulation function is hypothetically less steep. The model also receives backing from modifications to the amplitude and force of the tapping motion<sup>15</sup> as well as from studies altering the nature of the internal sensory feedback<sup>8,9,10</sup>. Furthermore, it can theoretically account for the effects of training and expertise<sup>11,12</sup> by assuming a dependence of the speed of accumulation on these factors. Evidence that contradicts the autonomy of this approach includes the NSE magnitude of the four effectors finger, elbow, knee and toe<sup>2</sup> and changes to NSE as a result of changes to the inter-tap interval<sup>17,18</sup>.

The **Perceptual (P)-centre hypothesis** of synchronisation suggests that it is not the onsets of tap and click that are synchronised, but instead their P-centres. The temporal position of the p-centre of an auditory stimulus depends on the duration of the stimulus: the longer the duration of the stimulus, the more the p-centre is shifted away from the stimulus onset. Thus, NSE in finger tapping experiments is seen to result from finger taps having a delayed p-centre when compared to the very crisp clicks often used. (Vos, Mates & van Kruysbergen, 1995). The p-centre hypothesis is only really useful in explaining the effect on NSE of changes in the duration of the pacing signal<sup>14</sup> with other data being out of theoretical grasp.

Although not a factor in the perception of synchrony **errors in time perception** have also been viewed as a factor in the production of NSE. Wohlschläger & Koch (2000) hypothesise that we structure time with the aid of auditory signals and bodily movements. As such the simplicity of movement employed in experimental circumstance as well as the bareness of the inter-tap-interval are seen as factors in the production of NSE. This is the only theory that is able to account for the NSE magnitude of the four different effectors<sup>2</sup>, as the level of NSE has been matched to the simplicity of the movement. It also gains support from alterations to the kinesthetic nature of the tap<sup>15,16</sup> and from decreases in NSE with tone and musical additions<sup>17,18</sup> to the intertap interval. Errors in time perception cannot, however, account for results obtained from changes to internal and external sensory feedback<sup>6-10</sup> nor from changes to the duration of the pacing signal<sup>14</sup>.

Considering the multifarious nature of the evidence, and the partial validity and contradiction inherent in all of the theoretical perspectives upon the production of NSE if viewed autonomously, the most likely verity is an integration of the theories, or aspects thereof, discussed above (Aschersleben, 2002). Once again for the line of argumentation taken in this paper it is worth pointing out that the perception of synchronisation is based upon the almost instantaneous integration of information across a wide range of modalities and, as such, is reliant upon considerable cognitive flexibility.

#### **2.4 Error Correction in Isochronous and Perturbed Synchronisation**

As mentioned in the previous section, sensorimotor regular periodic synchronisation with isochronous events requires some form of corrective mechanism without which timing errors due to internal timekeeper variance (Wing & Kristofferson, 1973) would simply accumulate and lead to a loss of synchrony (Hary & Moore; Vorberg & Wing, 1996). Furthermore, pulse in music is subject to involuntary fluctuations (not just in the form of ‘mistakes’ but also as a feature of individual style (Collier & Collier, 1996; 2002)) as well as deliberate expressive and structurally motivated modulations of tempo and microtimings (Schaffer, 1981, 1982; Gabrielsson, 1986; Palmer, 1989; Repp, 1992; Iyer, 2002). As such, bodily entrainment to music requires constant

error correction to compensate for internal and external asynchronies. Two theoretical internal error correction processes have been theoretically and mathematically explicated: phase correction and period correction (Mates, 1994a, b; Repp, 2000, 2001; Semjen, Vorberg & Schulze, 1998; Vorberg & Wing, 1996).

#### 2.4.1 Phase Correction and Period Correction

**Phase correction** describes a correction procedure which creates an adjustment to the interval generated by an internal timekeeper and leaves the period of the timekeeper unaffected. This mechanism is thought to adjust for phase errors between stimulus and response events taking the perceived (conscious or unconscious) phase error (e.g. asynchrony) between the last response and stimulus events as input and correcting the next internal timekeeper interval by increasing or decreasing it by some fraction of that error (for a discussion of the nature of the mechanism see Schulze & Vorberg, 2001). A phase correction mechanism is generally believed to be sufficient for maintaining synchronisation with a metronomic pulse (Pressing, 1998; Semjen et al, 1998, Semjen, Schulze & Vorberg, 2000; Vorberg & Wing, 1996). In isochronous synchronisation tapping tasks phase errors are due to random variability in the timekeeper mechanism. However, experiments in which deliberately introduced fluctuations around a constant mean period have also been accounted for through phase correction models (see Repp, 2001).

Another correction model – **period correction** - assumes a correction mechanism to modify the next target interval on the basis of discrepancies between the timekeeper interval and the last inter-stimulus interval. As such, this mechanism alters the period of the timekeeper that paces the period. In contrast to phase correction, period correction only seems to play a part in synchronisation tasks if the external stimulus sequence is altered in some way (i.e. non-isochronous) (Repp, 2001). The clearest example of period correction is to be found in tempo changes to the pacing signal. Michon's influential experiments concentrated on the mechanism of period correction by introducing sudden tempo changes (of 8% or more) to isochronous sequences (Michon, 1967). Michon found that participants were generally able to synchronise (to within pre-alteration variability levels) after 4 to 5 taps. Further Michon showed by plotting inter-tap-intervals (ITIs) that an initial overshoot was followed by an individually varying gradual approximation. Although Michon's hypothesis that period correction is *solely* responsible for tracking pulse changes has subsequently been renounced, his statistical findings have since been corroborated and accounted for by conglomerate models of error correction incorporating both phase and period corrections (see below)

An important question in error correction has been whether or not they operate below thresholds of temporal perception. There is, as Repp (2001a) points out, 'mounting evidence that sensory information can guide action without (or before) being consciously perceived'. Neumann (1990), for example, argues against the widespread tendency to assume that conscious perception mediates between sensory input and actions. Neumann terms the phenomenon of sub-perceptual guidance direct parameter specification and draws in his argument on a wide range of evidence from research undertaken in the field of vision<sup>10</sup>. The phenomenon has also been termed perception-action coupling (Kelso & Kay, 1987), and entrainment (Large & Jones, 1999)

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<sup>10</sup> 'Masked visual stimuli that are not consciously perceived can nevertheless cue manual responses (Fehrer & Raab, 1962; Klotz & Neumann, 1999; Klotz & Wolff, 1995; Neumann & Klotz, 1994; Taylor & McCloskey, 1990) and activate corresponding motor areas in the brain (Eimer & Schlaghecken, 1998; Leuthold & Kopp, 1998). Manual actions such as pointing, grasping, and gesturing seem to be controlled directly by visual information and thus immune to illusions that distort conscious perception (Adam et al., 1996; Agliotti, DeSouza & Goodale, 1995; Bridgeman, Kirsh & Sperling, 1981; Creem & Proffitt, 1998; gentilucci, Chieffi, Daprati, Saetti & Toni, 1996; Haffenden &

#### 2.4.2 Supraliminal vs. Subliminal Error Correction

It is widely accepted that phase correction can occur below perceptual threshold levels (Repp, 1999, 2000). However, although adjustments to subliminal pulse changes occur, it is less clear whether period correction occurs below perceptual thresholds. Psychophysical data suggest a detection threshold of about 2% for step changes relative to a baseline IOI (Michon, 1967; Drake & Botte, 1993; Friberg & Sundberg, 1995; McAuley & Kidd, 1998). The first study to employ subliminal (-1.3% (10ms)) of the baseline IOI (700ms) was undertaken by Hary & Moore (1985, 1987a). On the basis of computer modelling of the auto and cross-correlations of the IOIs and it is, Hary & Moore proposed a mixed phase resetting model in which period correction occurs slowly in combination with 'mixed resetting'. In this model the interval preceding the next tap (the internal delay) is sometimes measured from the previous tap (no phase correction) and sometimes from the previous tone (phase correction). This has subsequently been shown to be the formal equivalent to a phase correction model in which the current timekeeper interval is constantly adjusted by a proportion of the most recent asynchrony (Schulze, 1992). This model has become widely known and employed as the **linear phase correction model** (Mates, 1994; Vorberg & Wing, 1996; Pressing, 1998; Semjen et al., 1998, 2000; Repp, 2000, 2001) (see Schulze & Vorberg, 2001 for an overview). Mates (1994) has argued against the linear phase correction largely because it fails to account for the initial ITI overshoot in response to large step change (Michon, 1967). Mates argues in favour of a model incorporating both linear phase corrections and period correction processes (Mates, 1994). In this model, phase correction is a proportion  $\alpha$  of the most recent internally perceived asynchrony and period correction is a proportion  $\beta$  of the internally perceived difference between the most recent IOI and the timekeeper period. The model can, theoretically, account for the initial ITI overshoot in response to a large step change by assuming a simultaneous imperfect phase correction ( $\alpha < 1$ ) and perfect period correction ( $\beta = 1$ ). However, the same result can be achieved by interchanging the values (Repp, 2001) and as such the model does little to explore which of the two mechanisms is the more efficient. A key problem with the model is that Mates does not distinguish between the supraliminal and subliminal. There is a growing amount of evidence suggesting that different correction strategies are used in the two cases.

Thaut, Tian & Azimi-Sadjadi (1998) used cosine-wave modulated metronome sequences employing both subliminal and supraliminal step changes. Their results supported the earlier studies by Michon (1967) and Hary & Moore (1985) in that the results for supraliminal (50ms) step changes showed a fairly rapid adaptation following an initial overshoot whereas results for subliminal (10/20ms) step changes showed a rapid adaptation without an initial overshoot. Thaut et al. (1998) also found that asynchronies returned rapidly to the pre-step change level with supraliminal step changes, however, only very slowly after subliminal step changes. This shows that internal period correction increases with step change magnitude and suggests that this is a direct result of supraliminality. These results have been corroborated by Repp<sup>11</sup> (2001b) who

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Goodale, 1998; Rumiati & Humphreys, 1998; but see Franz, Gegenfurtner, Bühlhoff & Fahle, 2000, for a recent critique). Following the seminal work of Ungerleider and Mishkin (1982), Goodale and coworkers have accumulated evidence for anatomically and functionally separate visual pathways subserving object perception and the control of action (see, e.g., Goodale & Humphrey, 1998; Goodale & Milner, 1992). Striking cases of functional dissociation of these pathways have been observed in neurological patients in the form of blindsight and visual form agnosia on one hand, and optic ataxia on the other (Goodale & Humphrey, 1998; Köhler & Moscovitch, 1997).’ (Summary taken from Repp, 2001 p. 600)

<sup>11</sup> Although adjustments were made as Repp’s participants were more practiced and as such were believed to have shown lower perceptual thresholds.

concludes that 'period correction is affected by awareness of temporal change whereas phase correction seems to be insensitive to such awareness'. Repp further hypothesises that this is due to 'period correction requiring memory for at least one preceding event and as such greater computational complexity calling for greater neural resources, thus making the process more extensive in brain space and in time, and hence more accessible to higher-level cognitive processes'. (Repp, 2001b, p.310-311). The hypothesis has received support from a recent study (Stephan et al., 2002), which shows that while ventral prefrontal cortical areas are engaged in subconsciousness motor adaptations to auditory stimulus, conscious motor adaptations includes *additional* dorsolateral prefrontal cortex involvement.

The fact that adaptations occur below perceptual temporal thresholds shows that internal processes that control the timing of synchronised action are directly coupled to the sensory information without any mediation by awareness or perceptual judgement (Repp, 2001). Perception or awareness is not a pre-requisite of synchronised behaviour, but instead is an additional less precise mechanism which is preceded by a highly accurate level of temporal perception subserving motor control. (Thaut et al., 1998a, 1998b). Importantly, this implies that entrainment is not a centralised process that relies on concurrent abstraction of periodicities from multiple inputs, but an obligatory coupling of internal processes of perception and action.

## **2.5 The Induction of Pulse**

### 2.5.1 The Perception of Pulse

Entrainment to music requires not only the ability to entrain movements to a isochronous train of events, but also the ability to perceive a constantly modified pulse in what is, more often than not, a continuous and rhythmically constructed auditory phenomenon. Pulse denotes any periodicity inherent or perceived in any actual, discerned or inferred temporal organisation of events (i.e. rhythm) and connotes a real, or at least perceived, isochrony of external events based upon perceived underlying periodical divisions of time. An external event in musical terms can refer to a variety of temporally distinguished perceptual phenomena including signal/tone onset, dynamic accentuation, as well as changes in pitch, dynamic level, timbre and harmony. Significantly, people exhibit preferences for temporal structures that embody simple time ratios (e.g. 2:1, 3:1, 3:2) (see Drake & Bertrand, 2000) and inferences of temporal organisation generally lead to the perception of proximate simple time ratios even if the auditory signal is more complex (Jones & Yee, 1997). It is also worth noting that, although a perception of pulse generally arises in response to an actual periodicity present in the musical signal, it is 'stable' in that once established it may continue even if auditory periodicity is disrupted in some way (Cooper & Meyer, 1960). The perception of pulse is restricted to temporal ranges within the perceptual present (Pöppel, 1999) and creates expectations about likely timing of future events ('future-oriented attending') (Jones, 1989).

Pulse is traditionally seen to exist at various hierarchical bi- or tri-nominally constructed levels (Lerdahl & Jackendoff, 1983). Perceived beats are seen to occur at different metrical levels (see figure 10) with two metrical levels - tactus and metre - generally being viewed as particularly significant:

**Figure 10:** opening section from 2-part invention in D-minor by J.S. Bach with three depicted metrical levels.

Tactus is a moderate-tempo pulse present in most rhythmic music. It is the metrical level at which listeners are inclined to choose to tap a finger or foot. It is usually within the approximate range of 300 to 800 ms (Fraisse; 1982, Large & Jones, 1999; Synder & Krumhansl, 2000; Drake, Penel, & Bigand, 2000)). As the music gets slower a listener will tend to find faster pulses to coincide with this tapping range and vice versa. The range of 300 to 800ms is also the range for ‘instantaneous’ (i.e. not cued) tapping (Fraisse, 1982) and has been described as incorporating an internal ‘referent’ level that varies individually and across age-groups and levels of musical experience/familiarity (Large & Jones 1999; Drake, Jones, & Baruch, 1999).

Metre is a metrically organised periodic grouping of perceived pulses somewhat akin to formalised temporal gestalt formation. It is important to note that the traditional ethnocentric view of the perception of metre as an unambiguous interpretation of the properties of the audio signal based upon a hierarchy of weak and strong beats is flawed. Iyer (1998, p.3) argues, with reference to African music, that ‘metre connotes *but does not strictly imply* a hierarchy of weak and strong beats’. Furthermore, studies of rhythm perception of both test patterns and musical performances show that metre is an ambiguous, if not wholly imaginary, property of the audio signal (Parncutt, 1994). Additionally, there is evidence to suggest that the perception of metre (and tactus) in musical styles is in part socially constructed (Ladzekpo, 1995; Stobart & Cross, 2000). Metre is, in short, a cognitive/perceptual phenomenon.

### 2.5.2 Attending to Dynamic Events

Musical performance, as previously mentioned, involves considerable temporal flexibility in terms of the structural shaping of melodies and rhythms, playing ahead of the beat, tempo modulations, expressive temporal modifications as well as inadvertent periodical inaccuracies. As such music can be seen to have a lot in common with other dynamic events such as interpersonal interactions and, for example, the dribbling of a football. These events all comprise actions and movements that display distinct beginnings, recognisable rhythms, characteristic tempos and lawful endings (Berthenthal & Pinto, 1987; Boltz, 1992; Johansson, 1973; Johansson, von Hofsten & Jansson, 1980; Jones, 1990; Neisser & Becklen, 1975; Pickett, 1980; Pike 1945). As with music, temporal relationships modulate as events unfold; rates change, rhythms vary, and structures transform. In all of these events we are able to apprehend clear temporal structures despite the fact that the periodicities that compose these structures fluctuate extensively. It seems likely, therefore, that the mechanism for attending to music is the same as that which regulates attending to other forms of quasi-periodic dynamic events.

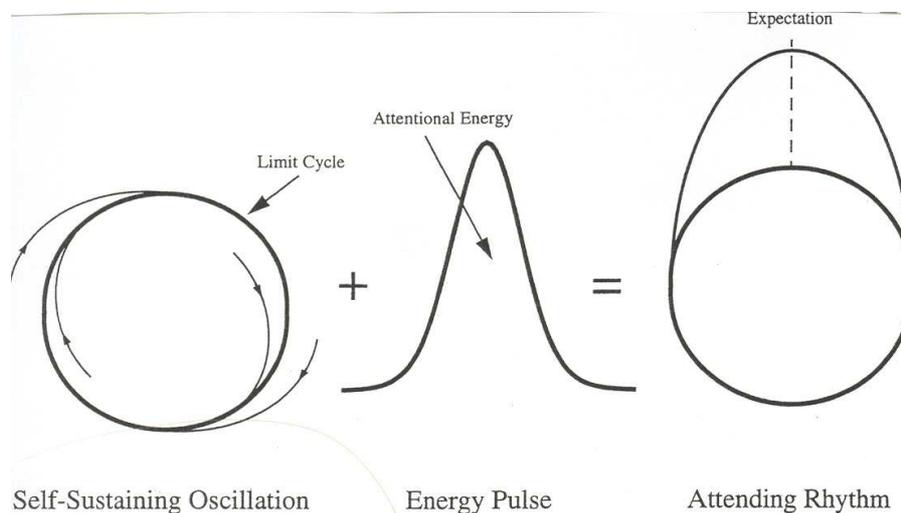
Large & Jones (Large & Jones, 1999) have developed a model of attending to music and other auditory and visual dynamic events – Dynamic Attending Theory - in which internal attending

oscillatory rhythms entrain to external events and so permit selective targeting of attention to expected points (Jones, 1976; Jones & Boltz, 1989; Large, 1994; Large & Kolen, 1995; McAuley, 1994, 1995).

Ordinate to their theory is the notion that attention is not a continuous operation but rather one in which we build expectancies and efficiently direct energy pulses toward the expected whilst reacting to the unexpected. Large and Jones take their cue from static visual attention theories in which attention is seen as involving both a long-term, goal-oriented attentional process and a transient, stimulus-driven mechanism (Egeth & Yantis, 1997). Large and Jones (1999) explain that:

The goal-oriented mechanism reflects expectancy and attentional set; it is concerned with deliberate changes in focal attending (e.g., Folk, Remington & Johnston, 1992). For instance, an individual may react faster to an object in an attended-to-location or may be successfully instructed to ignore certain objects in a forthcoming display. By contrast, the stimulus-driven mechanism reflects fast (some claim automatic) attentional shifts, usually caused by a single salient feature or an abrupt display change. For instance, the abrupt onset of a non-target object may provoke a rapid attentional shift to it and away from a target object – (i.e. attentional capture) (Jonides & Yantis, 1988; Yantis & Hillstrom, 1994). (p.123)

Dynamic attending theory shares with visual attention theories an emphasis on the immediacy of attending, the role of expectancy, and focal attending. However, the central tenet of the theory is the entrainment hypothesis in which internally generated *self-sustaining oscillations* entrain to an external event's perceived pulse by means of *additional attentional energy pulses*<sup>12</sup>. The subsequent internal *attending pulse* (see figure 11) generates expectancies that enable anticipation of future aspects of the event.



**Figure 11:** Schematic overview of a single attending pulse shown as a function of two model components: a self-sustaining oscillation and an energy pulse. Attentional targeting is suggested by mapping a given point on the limit cycle to the modal point of the energy pulse (taken from Large and Jones, 1999, p.126).

<sup>12</sup> Associations between energy and attention has a long-standing history dating back to McDougall (1911) and has been depicted in a variety of different ways (see Neumann, 1996 for a review)

Self-sustaining oscillations are viewed as involuntary and permanently operating within the temporal range of instantaneous tapping and responsible for the individually determined referent level. According to the theory, attending rhythms are subject to rapid attentional shifts akin to models of phase and period corrections thus keeping a constant entrainment to the perception of external pulse. All that remains to achieve simple bodily entrainment is to match periodic kinaesthetic actions (such as finger tapping) to the internal attending pulse (see below).

Significant for the course of argumentation taken is that by employing multiple internal oscillatory systems the mechanisms involved in dynamic attending can be seen to overlap considerably with those involved in temporal and periodic processing and production.

## 2.6 Bodily Movement

Just as the perception of pulse involves much more than simply listening out for an isochronous sequence of separated events, bodily entrainment to music generally involves more than a simple tapping action (i.e. dance but also concurrent production of 'music'). Furthermore, its nature depends, not solely on the pulse, but also upon other features of the music, individual interpretations and, more often than not, upon socially constructed routines of movement. The universality of dance as a feature of musical performance has long suggested a close relationship between music and movement (Nettl, 1984, 2000; Brown, 1991) and has resulted in many attempts to describe the connection between music and motion in an intuitive way (Truslit, 1938; Gabrielsson, 1973; Repp, 1993; Shove & Repp, 1995; Das et al., 1999). More recent scientific approaches have suggested that tempo variations in music originate from, and thus correlate to, theoretical models of motion (Todd, 1992, 1995; Feldman et al., 1992; Kronman & Sundberg, 1997). Furthermore, as compensation for the lack of real motion in theoretical modelling (Desain & Honing, 1996), direct measurements of locomotion have been used to generate music performances with considerable success. Sundberg & Friberg (1999), for example, demonstrated striking similarities between musical tempo curves and locomotional patterns and showed that aesthetically pleasing final-phrase ritardandos in western baroque music could be constructed from locomotive data taken from runners final steps. There could be a simple explanation for these observations and other theoretical correlations between music and motion. It seems likely that a subset of the mechanisms involved in musical behaviour, temporal processing and dynamic attending are involved, also, in timed, rhythmic and untimed motor behaviour. Certain overlap between mechanisms subserving the various functions is intuitively sensible. After all, human motion, temporal processing, and dynamic attending are components of musical performance, timing is inherent in a wide range of motor behaviours (see Schöner, 2002), and kinaesthetic movements have been showed to influence temporal perception (Wohlschläger & Koch, 2000). However, there is an important differentiation to be drawn between interaction between mechanisms and the sharing of a common substrate as the former allows the possibility of an entirely combinatory perspective whereas the latter implies genuine overlap. A common substrate could take the form of the multiple oscillatory systems discussed above with regard to temporal processing, periodic behaviour, and dynamic attending.

### 2.6.1 Dynamic models share Common Internal Oscillatory Mechanisms

Kugler, Kelso, & Turvey (1980) proposed an alternative, model of timing in motor behaviour to the clock mechanism discussed earlier. In this dynamic model of movement coordination,

rhythmic, non-rhythmic timed *and* non-timed<sup>13</sup> movements are understood as self-sustaining, periodically stable organisations with co-ordination resulting from complex interlimb interactions (Kugler, Kelso & Turvey, 1980; Kelso, Holt, Rubin & Kugler, 1981; Kelso, 1981; 1984;). Beek, Peper & Daffertshofer, 2002) explain that this model has famously been extended through association with observed qualitative changes described by Haken (1977) in his theory of pattern formation in open systems far away from thermal equilibrium. The resulting theoretical model for the phase transitions of interest – the Haken, Kelso and Bunz model (HKB model) -capitalises on the theory of nonlinearly coupled nonlinear oscillators. Stochastic versions of the initial deterministic model (Schöner, Haken & Kelso (1986) have provided the theoretical foundation for the study of a wide range of coordination phenomena including the coordination between nonhomologous limbs (Carson, Goodman, Kelso & Elliott, 1995; Kelso & Jeka, 1992); the coordination of rhythmic limb movements and the perceptual environment (Kelso, DelColle & Schöner, 1990; Wimmer, Beek & van Wieringen, 1992); learning (Schöner & Kelso, 1988; Zanone & Kelso, 1992); handedness (Treffner & Turvey, 1995); mirror movements (Daffertshofer, van den Berg & Beek, 1999); and pattern formation in brain and behaviour (Frank, Daffertshofer, Beek & Haken, 1999; Fuchs, Kelso & Haken, 1992; Jirsa, Friedrich, Haken, & Kelso, 1994) (see Beek, Peper & Daffertshofer, 2002 for an overview).

It is important to note that although psychologists have tended to argue for a clock mechanism or dynamic model at the expense of each other and although they concentrate upon temporal processing and dynamic co-ordination respectively, there is considerable overlap in the two models. They both can be seen to incorporate multiple internal oscillatory systems whose harmonious interaction with each other is an essential component of both models (and indeed whose opposition leads to decreased temporal processing skill and motor co-ordination). Comprehensive models reconciling dynamic models of smooth inter-limb coordination with additional clock mechanisms for timed and rhythmic/periodical action have been attempted with some success (e.g. Pressing, 1998), thus supporting the notion that motor ability and periodical and perceptual timing skills share common oscillatory mechanisms with each other, and, by association, with musical production and dynamic attending.

### 2.6.2 Neuropsychological Evidence for Shared Mechanisms

Neuropsychological studies support the existence of a common mechanism through shared brain structures across temporal processing and motor output (Keele et al., 1985; Treisman et al., 1992), as well as across time perception and motor timing (see Schobotz, 2000). Further studies have identified the cognitive role of body motion in music perception and production (Peretz, 1993; Carroll-Phelan & Hampson, 1996). From a meta-analysis of studies of brain-damaged patients with lesions localized in various regions of the brain, it has been suggested that ‘the rhythmic component... of an auditory image cannot be activated without recruiting neural systems known to be involved in the planning of motor sequences (Carroll-Phelan & Hampson, 1996). With support from the neuropsychological data, Todd (Todd, 1999; also Todd, Lee & O’Boyle, 1999) has proposed that listening to music (although not explicitly mentioned this can be taken to extend to rhythmically organised sound) involves the same mental processes that generate bodily movement. According to his hypothesis, the induction of a sense of beat or pulse (e.g. dynamic attending) occurs in the form of a ‘*sensorimotor loop*’, which includes the

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<sup>13</sup> a timed action has been defined for experimental purposes been as “a motor act, whose temporal form is reproducible and stable in the face of varying environmental conditions or perturbations and which is compensatorily altered to account for perturbations that either hold up or accelerate the movement thus restoring as much as possible the movement time” (adapted from Schöner, 2002).

posterior parietal lobe, premotor cortex, cerebrobellum and basal ganglia. As such, it is held to overlap considerably with the mental structures serving timed motor action, in which cortical structures involved in motor timing functions, such as the scaling of amplitude and velocity of movement are organised in a combined open and closed loop with subcortical structures - the 'motor circuit'<sup>14</sup> (Alexander et al., 1986, 1990; Picard & Strick, 1996; Joel & Weiner, 1997; Kischka et al., 1997; Kitano et al., 1998; Strick et al., 1998). Motor timing, in accordance with Todd's proposed sensorimotor loop, has been attributed to several structures of the motor circuit including the cerebellum, (Buonomano & Mauk, 1994; Ivry, 1996, 1997; Raymond et al., 1996; Penhune et al., 1998; Casini & Ivry, 1999) the basal ganglia, (Jüptner et al., 1995; Hinton et al., 1996; Harrington & Haaland, 1998; Harrington et al., 1998; Turner et al., 1998) and the premotor cortex (Kubota & Hamada, 1978; Weinrich et al., 1984; Halsband et al., 1993; Rao et al., 1997; Rubia et al., 1998)<sup>15</sup>. In the sensorimotor perspective a perceived rhythm is, thus, literally an imagined movement: 'If the spatiotemporal form of certain sensory stimuli are matched to the dynamics of the motor system, then they may evoke a motion of an internal representation, or motor image, of the corresponding synergetic elements of the musculoskeletal system, even if the musculoskeletal system itself does not move' (Todd, 1999 p.119 [emphasis in original]). This may be worded too strongly as it seems to imply a precise correlation between auditory input and the motor image for which there is little evidence. Although we are able, within limits, to match dynamic visual events such as gait styles and dancing with correspondingly converted sound envelopes of tones (Friberg et al., 2000), bodily entrainment to a given stimulus varies considerably, and would seem to be dependent upon mood, social constructs and a degree of randomness. The supporting notion that musical perception is, first and foremost, audible human motion (Shove & Repp, 1995) is appealing. However, one needs to consider that the auditory stimulus is not always deductible from a performer's motion and often relies heavily upon understanding the mechanisms of the musical instrument employed. Nevertheless, the central concept remains that the act of listening to rhythmic music involves the same mental processes that generate bodily movement and that as such one motivates and partially induces the other.

### 2.6.3. Periodical Rhythmic Facilitation in Neurological Disorders

Further evidence of strong links between motor and periodic and rhythmic auditory phenomenon comes from the field of music therapy in which auditory rhythmic cuing has been shown to affect kinaematic improvements in a wide range of motor tasks. Kinaematic parameters of gait and arm movements (Prassas et al., 1997; Thaut et al., 1996; Thaut et al., 1997; Safranek et al., 1982), kinaematic limb instability (Thaut et al., 2002), and speech motor control (Thaut et al., 2001) have shown immediate and long-term (McIntosh et al., 1998) improvements as a result of rhythmic auditory stimulation treatment in patients with a wide range of motor dysfunctions including stroke, traumatic brain injury, cerebral palsy, Huntington's disease, and Parkinson's disease (Adler & Ahlskog, 2000; Hummelsheim, 1999; Morris, 2000; Thaut et al., 1999). Prassas et al., for example, studied the effect of auditory rhythmic cuing on gait kinematic parameters of stroke patients and summarised their results in the following table (see figure 12).

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<sup>14</sup> The motor circuit comprises the premotor cortex, primary motor cortex, primary motor cortex, primary somatosensory cortex and medial wall motor areas in the cingulate cortex as well as parts of the basal ganglia and the thalamus.

<sup>15</sup> It is worth noting the considerable overlap to timing abilities. Indeed as some form of output is required to test timing abilities motor timing and general timing abilities are experimentally almost impossible to differentiate.

Means and *F*-scores for rhythm and no-rhythm conditions

	No-rhythm	Rhythm	<i>F</i> (df = 1, 19)
Stride length (paretic side) (% of height)	44.2	41.9	1.78
Stride length (non-paretic side) (% of height)	41.0	42.0	< 1
Hip joint range of motion (paretic) (°)	29.0	30.0	1.92
Hip joint range of motion (non-paretic) (°)	36.0	33.0	2.02
Knee joint range of motion (paretic) (°)	47.0	47.0	0.03
Knee joint range of motion (non-paretic) (°)	56.0	55.0	< 1
Trunk angle (°)	96.0	96.0	< 1
Center of mass horizontal velocity (m/s)	0.6	0.6	< 1
Center of mass vertical displacement (cm)	3.3	2.8	5.32*
Center of mass lateral displacement (cm)	11.0	10.1	< 1
Pelvic tilt (°)	181.0	180.0	< 1

Linear measurements are rounded to first decimal and angular measurements are rounded to the nearest degree.  
\* *P* = 0.032

**Figure 12:** Mean and *F*-scores for rhythm and no-rhythm conditions (taken from Prassas et al., 1997 p.220).

The authors conclude that the analysis of the parameters studied showed the following positive modifications in gait patterns of stroke patients due to musical-rhythmic cues:

- the stride lengths of the affected/non-affected sides became more symmetrical.
- hip joint range of motion of the affected/non-affected sides became more symmetrical.
- Centre of mass vertical displacement decreased, indicating improvement in mechanical efficiency.

The neuroanatomical and neurophysiological basis for the improved kinematic parameters are not yet fully understood. Thaut et al. (1999) has suggested a model of rhythmic auditory-motor entrainment in which the enhanced time information in the temporal structure of rhythm serves as an optimisation function for motor planning, programming, and execution. It is interesting to note that, although rhythmic auditory stimulation has, also, been shown to positively affect gait parameters in normal subjects (possibly reflecting imperfections in our ability to produce periodic output) (Thaut et al., 1993), the benefit level seems to increase with the severity of motor dysfunction, thus suggesting some kind of compensatory operation. It is possible that motor dysfunctions partially reflect an impaired ability to produce voluntary internal periodic oscillations and that entrainment to rhythmic stimulus provides access to periodic oscillations which are crucial to motor control. This, once more, suggests that, at least, a subset of the mechanisms involved in dynamic attending (beat induction) are involved, also, in motor behaviour.

### **3. Interpersonal Musical Entrainment: An Uniquely Human Skill?**

Of overarching concern to the study of music evolution is whether individual components are unique to humans and, thus, can be viewed to have evolved specifically for musical activity or other uniquely human skills. As previously noted, rationales for the evolution of interpersonal entrainment include coalition signalling, interpersonal interaction and muscular bonding. However, these rationales are, in effect, offering theoretical accounts for evolutionary improvements to an already existing ability and so do little to explain the emergence of the skill nor do they satisfactorily account for the species-specificity of musical interpersonal entrainment. Comparisons with other species should enable us to establish more clearly *how* the skill of interpersonal entrainment evolved, and offer clues as to its emergence and continued development. Unfortunately, cross-species comparative data on inter-individual entrainment and its hypothesised sub-skills is, as yet, rather thin on the ground. However, existing evidence together with some intuitive suppositions would seem to suggest that interpersonal entrainment is

a recent adaptation (i.e. since the divergence from our last shared relative with the chimpanzee – six million years ago) in humans, whilst the hypothesised sub-skills are shared with other animals with differences of quality and behavioural manifestation rather than of kind. When assessing the hypothesised sub-skills it is important to recognise that we should not expect to find them in a ‘musical’ context, but instead may need to explore the possibility that behavioural skills in other (non-musical) contexts are subserved by similar mechanisms.

### **3.1 Interpersonal Pulse-based Synchronous Behaviour**

Behavioural synchrony involving many individuals is not wholly absent from species other than humans (although none display the same level of flexibility as humans in that entrainment occurs within a very narrow range of tempos). Merker (2000) notes that some species of fireflies synchronise their bioluminescent flashing in the tropical night (Buck, 1988). A number of other insects synchronise their chirps in multi-male chorusing (Otte, 1977; Greenfield & Shaw, 1983), synchronous chorusing is found among chorusing frogs (Wells, 1977; Klump & Gerhardt, 1992) and clusters of male fiddler crabs wave their claws in synchrony to attract females for mating (Backwell, Jennions, and Passmore, 1998). Synchronous behaviour of this sort generally occurs in the context of multi-male displays of sexual advertisement and have been variously interpreted as the epiphenomenal outcome of timing strategies in male competition to signal first (Greenfield & Roizen, 1993; Backwell, Jennions, and Passmore, 1998); as an anti-predator strategy to dilute predator attention to a signalling male (Walker, 1969; Otte, 1977; Tuttle & Ryan, 1982) and as a means of increasing peak signal output from a group of males competing with other groups of males to attract mobile females (Wells, 1977; Buck & Buck, 1978; Morris, Kerr, & Fullard, 1978). However, these examples are, perhaps, of little direct relevance to similar displays in our species due to the extreme phylogenetic distance between humans and the species mentioned. Furthermore, similar human displays generally occur in a social context, in which synchrony, rather than occurring as a result of competitive signalling, requires a motivational mechanism for mutual entrainment. The rather limited evidence gathered so far suggests that our closest relative, the chimpanzee, is unable to keep time with and entrain to a repetitive beat, even with training (Williams, 1967). It has been suggested, however, that synchronous chorusing does exist in selected primate species. De Waal (1988: 202-203) describes the pant-hooting of captive bonobos in the following way: ‘During choruses, staccato hooting of different individuals is almost perfectly synchronised so that one individual acts as the ‘echo’ of another, or emits calls at the same moments as another. The calls are given in a steady rhythm of about two per second’. De Waal’s statement must, however, be treated with caution as it is based entirely upon subjective observation and may thus reflect a human propensity to ‘seek out’ pulse. Furthermore, a later study on bonobo distance calls reports only alternate and not simultaneous calling (Hohmann & Fruth, 1994). As of now there is no direct evidence of higher animals, other than humans, exhibiting pulse-based behavioural synchrony. This is, however, an area which requires much more study before any definite conclusions can be made.

### **3.2 Hypothesised Subskills of Interpersonal Entrainment**

Fundamental temporal processing must be seen to exist in a wide range of animals. Indeed it could be argued that, as any form of movement or perception is a movement or perception *in time*, temporal processing at a perceptual and sensorimotor level is common to all animals with sensorimotor capacities (Piaget, 1966, Richelle, 1968). As Skinner (1938) notes: ‘the problem is how time as a dimension of nature enters into discriminative behaviour’. Although, experimental cross-species comparative data on discriminative temporal perception is somewhat limited (see below), circumstantial evidence would seem to suggest that other animals share precise temporal

representation. Gibbon & Church (1990), for example, argue that efficient foraging in avian species, particularly when feeding their young, requires precise temporal representation of travel and waiting periods. Experimental studies of single-interval timing tasks have shown that rats and pigeons can be conditioned to respond at a range of temporal intervals (Catania, 1970; Church, Meck & Gibbon, 1994; Gibbon & Church, 1990; Meck & Church, 1984; Roberts, 1981) and, in accordance with human temporal processing, have shown that variability increases with increases in temporal distance (Gibbon, 1991). These experiments have, however, concentrated on intervals of 20 sec and above. To the author's knowledge experiments exploring smaller temporal ranges within single-interval timing paradigms have not been undertaken. However, it has been established that healthy rats can discriminate between intervals centered at 500 msec (Clarke et al., 1996); that rats and pigeons can be trained to respond differently to 2s and 8s stimuli (Meck & Church, 1982; Roberts & Mitchell, 1994); and that both are also able to transfer this latter discrimination across modalities (Meck & Church, 1982; Roberts, Cheng & Cohen; 1989). It is worth noting, also, that a statistical overlap between counting and temporal perception, has been identified (Meck & Church, 1983; Roberts, W. A., 1995, 1998), suggesting that, as with humans, other animals process larger temporal intervals by cognitively adding successive smaller, and therefore more easily processable, temporal intervals. Further suggestion for cross-species similarities in temporal processing is to found in neuropsychological studies which report similar cortical areas and chemical releases being involved in timing tasks in rats and humans (Meck, 1996). In rats, as in humans, it has been suggested that different cortical areas perform different functions in timing tasks and so are involved to differing degrees depending upon the interval range concerned. For example, cerebellar lesions in rats lead to a selective deficit on duration discrimination task when the stimulus range is centered at 500 msec but does not affect performance when the range is centered at 30 sec (Clarke et al., 1996). Comparative studies of discriminatory temporal perception in our primate relatives are, to date, unfortunately, lacking.

Brown, Merker and Wallin (2000 p.12) state that 'most animals (including humans) have the ability to move in a metric, alternating fashion'. It is unfortunate that they were seemingly unable to find any scientific backing for this statement. Nevertheless, it is probably safe to assume that various forms of animal and human locomotion require some form of intrinsic periodical ability. Broadbent (1994) has argued that periodic behaviour is evident in the guarding of territory and foraging of animals that partake in these activities. According to her approach, periodic behaviour in these contexts represents the statistically most productive method of proceeding. She supports her view with experiments in which rats were presented with random-interval 60 sec and 120 sec schedules and in which power spectra revealed a periodicity of responding of 20-50 sec for all animals regardless of condition. A second periodicity of 5-10 sec was evident in 60 sec random-interval schedules. It remains to be seen, however, whether this form of animal periodic behaviour pervades through to smaller time scales which must be viewed to be more relevant to human musical behaviour. Statistical analyses of periodicities in animal vocal output have, to the author's knowledge, not been undertaken. However, a visual inspection of sonograms of chimpanzee pant-hooting (Goodall, 1986), kloss gibbons (Tenaza, 1976;), winter wrens (Kroodsma, 1980), whale 'songs' (Payne, 2000) and gibbon pairs (Geissmann, 1993; 2000) would seem to suggest some periodic vocal output in a range of animals (see appendices 3-8).

The question of whether other animals share a perceptual concept of synchronised events is, most likely, out of the reach of experimental exploration. However, from a philosophical perspective, one can argue that others animals must possess, at least intrinsically, the ability to perceive synchronised events (and very closely separated events) as happening at the same time. Any

animal with perceptual ability perceives events through time and as such must perceive separate events as being temporally differentiated. Beyond certain, most likely species-specific, limits, animals will be unable to temporally differentiate between two or more events and will therefore view them as being synchronised. One possible way into this could be looking at one of the key features of the perception of synchronisation in human musical performance – intermodal processing. Stein & Meredith (1990) observed that they know of no organism with a nervous system in which the sensory modalities maintain absolute exclusivity from one another. In other words, ‘intersensory interaction is a basic neural design feature that is found at most phyletic levels’ (Lewkowicz, 2000 p.281). The adaptive strength and prevalence of intermodal processing has been demonstrated with reference to the male gypsy moth, who constantly integrates information about his position in space vis-a-vis the olfactory gradient created by the female, the wind speed gathered by his tactile and proprioceptive senses and his position in space determined from visual cues (Stein & Meredith, 1993). However, the evolution of multimodal processing is complex and cannot be viewed as a gradually increased ability to integrate across different sensory receptors. Grossenbacher (1996 p.120) notes that whereas ‘rat brains contain a relatively undifferentiated cortex with incomplete segregation of sense modalities..., the primate cortex boasts fully independent primary receiving areas which do not interconnect’. Any argumentation describing increased human ability to process across modalities should therefore restrict itself to comparative data from other primates. It remains possible that perception across modalities was primarily a unitary processing mechanism which evolved towards multiple specific segregated receiving areas in primates, which, in turn, are more competently integrated in our species.

Considering that other animals appear not to entrain their movements to external stimuli, error correction mechanisms operating in contexts analogous to human musical activity must also be a uniquely human trait. However, if we accept that mechanisms involved in periodical perception and production overlap considerably with those involved in rhythmic and coordinated motor skill, then it is reasonable to expect that the same error correction mechanisms subservise both periodical behaviour and internal periodicities (most likely in the form of a multiple internal periodic oscillatory mechanism) intrinsic to timing, timed motor action, and smooth inter-limb coordination in humans and that consequently this capacity may be operational for other animals which have these abilities.

That we share with at least a subset of other species the ability to perceive and internalise pulse in auditory phenomena is evident from observations of pulse-based interactions in various avian and primate species. Some birds feature rhythmic repetition of signals in conformity with a regular beat or pulse (Greenfield, 1994) and non-human primate species – bonobos (see above) and gibbons - have been observed to participate in pulse-based interaction. Geissmann (2000, p. 103) writes of gibbon vocal ‘duetting’ that: ‘Typically, mates combine their partly sex-specific repertoire in relatively rigid, precisely timed, and complex vocal interactions to produce well-patterned duets.’ In these duets males ‘produce one or several distinct types of short phrases that often become gradually more complex as the song bout proceeds. At more or less regular intervals, females insert long female-specific phrases that are commonly referred to as great calls. In most species, great calls consist of a particularly rhythmic series of long notes uttered with increasing tempo and/or peak frequencies’ (Geissmann, 2000, p. 107). A visual inspection of duetting sonograms clearly demonstrates these interactions to be based upon substantially periodic behaviour (see appendix 8). Whether or not the perception of pulse and subsequent generation of expectancy in human attending to dynamic events can be seen to be shared with other species is unknown. The efficiency of the dynamic attending model would, however, seem

to suggest considerable adaptive strength, and hence it is reasonable to speculate that it could pervade a wide range of perceptual capacities in numerous species.

Obviously, bodily movement is not a uniquely human skill. Furthermore, it is highly unlikely that the mechanisms that subserve bodily movement in humans is fundamentally different from that subserving kinaesthetic movement in other animals and must certainly be similar across primate species. Arguments for comparative qualitative differences in human kinaesthetic ability to other specifically primate species have been constructed with reference to the human evolutionary drive towards bipedalism. Human bipedalism has a long evolutionary history, and has, amongst many other things, considerably affected the anatomy of the vocal tract, paving the way for a respiratory and vocal system with the potential for considerable variability in acoustic production, as well as freeing the hands for object manipulation and gestural expression (Klein, 1999; Lewin, 1999). Subsequent improvements to fine vocal and manual control in humans have been comparatively recognised and can easily be accounted for by dint of evolutionary drives towards increased communicative and technical ability (Lieberman & Crelin, 1972; Lieberman, 1984; Fitch 2000; Wilson, 1998). Trevarthen (1999) has argued that ‘while walking, we freely turn and twist, glance with eyes jumping to left and right, extend waving limbs, make intricate gestures of the hands, talk, all in coordinated phrases of flowing rhythm’ and that ‘this moving has a multiplicity of semi-independent impulses, a potentiality for multi-rhythmic coordination that is surely richer than any other species possesses’ (p. 171). This latter line of argumentation must, as yet, be treated with caution as it relies solely on the author’s supposition.

### 3.3 Why is Interpersonal Musical Entrainment unique to Humans?

Evidence seems to suggest that interpersonal musical entrainment (IME) is an innate, and consequently universal, human ability<sup>16</sup> (although partially socially conditioned in the context of musical production and subject to developmental improvement). This, together with the notion that IME is unique to humans amongst primates, strongly suggests that the development of this skill *or* the acquisition of abilities requisite for the procurement of this ability was a defining event in the divergence from our last shared relative with the chimpanzee. If the supposition is correct that IME is unique to our species, despite a cross-species sharing of the its sub-skills, then the human skill of IME must be viewed as a unique combination of integrated skills within a given behavioural context. The most obvious and simple supposition is that we uniquely possess the ability to integrate all of the sub-skills into a conglomerative function. However, one must consider that, IME constitutes not only a conglomeration of sub-skills, but also a conglomeration of sub-skills *within a uniquely human behavioural context*. Many of the hypothesised simpler sub-skills such as temporal processing and periodical production can be interpreted as existing intrinsically in more complex abilities common to a range of species (e.g. kinaesthetic abilities but also more general social interaction). For example, temporal processing, error correction mechanisms, and periodical behaviour are all intrinsic to controlled bodily movement, both internally, in the form of periodic oscillatory mechanisms, and externally (e.g. periodicities evident in locomotion)<sup>17</sup>. I hypothesise that humans have uniquely evolved, in addition to the conglomeration of sub-skills, the abstraction of sub-skills from intrinsic abilities in more directly survival-oriented, (and putatively effector and modality specific/biased), behaviours into the behavioural context of musical performance and interaction. I believe the most likely sources of

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<sup>16</sup> On top of being able to participate in pulse-born alternating interactions with their mothers (Malloch, 1999/2000), newborns have been reported to entrain arm movements to the syllabic rhythms of adult speech in any language (Condon & Sander, 1974).

<sup>17</sup> Trevarthen (1999/2000) makes a similar argument in the context of what he terms the Intrinsic Musical Pulse.

such a process of abstraction of the simpler sub-skills of IME to be dynamic attending and motor ability due to the theoretical possibility that all of the other sub-skills are intrinsically constitutive of these abilities and because they can be viewed as crucial to existence across a huge phyletic distance. As such the suggestion is that IME be viewed as a highly complex evolutionary exaptation emerging as a consequence of the human move towards increased cognitive flexibility and a consequent ability to abstract skills from one context to another<sup>18</sup>. The notion that all sub-skills of IME, except for the perception of synchronicity, share common internal periodical oscillatory mechanisms as well as evidence showing that individual sub-skills are constant across modalities, require, even individually, considerable cross-domain processing and are ubiquitous to a range of human behaviours support the hypothesis. Constancy across modalities and behaviour and shared internal mechanisms are exactly what one should expect from evolutionary exaptations. Another important feature of this hypothesis is that improvements to any of the hypothesised sub-skills can theoretically account for improvement to the ability of IME even if they do not occur directly for reasons related to IME.

This approach has the capacity to provide a theoretical foundation for a more unificatory study of IMP (and potentially other complex human skills). It opens up the possibility of cross-species comparisons of human musical abilities (possibly in unique human behavioural contexts) to intrinsic abilities in other animals. Very little such comparative data has been collected. However, a couple of studies (and interpretations thereof) may demonstrate possible directions for future study:

- Evidence has been collated showing that the time constant of 3 sec associated with “gestalt formation” in humans (Pöppel, 1973, 1978) is consistent with chimpanzees’ movement patterns (Pöppel, 1988; Schleidt, 1988; Schleidt et al. 1987; Kien et al. 1991) as well as movements studied in a wide range of other mammalian species (Gerstner & Goldberg, 1994) This indicates that a similar mechanism subserves both human perceptual and mammalian motor skills, which, in turn, can be interpreted to suggest that intrinsic timing abilities in mammalian motor skill is consistent with human temporal perception and that the latter can be viewed as a partial exaptation of the former.
- Studies of learning ability in mice have shown that they are no less distracted by periodic noise than by random acoustic interjections (Prior, 2002). An interpretation of this evidence could be that mice are unable to build expectancies based upon pulse and are thus equally distracted by periodic acoustic signals. If we accept that intrinsic periodical ability is involved in motor skill and therefore common to mice, then this evidence would seem to suggest the possibility that what mice lack is the ability to abstract intrinsic periodical ability to perceptual behaviours.

Of course, these studies were not undertaken within the framework suggested here and constitute only peripheral evidence in support of the argument made here. They should be viewed primarily as demonstrations of the kind of future studies required to explore the validity of the evolutionary rationales put forward in this dissertation. Much more scientific and statistical data on externally observable and intrinsic musical abilities in a wide range of species and behavioural contexts is required before any definite conclusions can be made.

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<sup>18</sup> Abstraction as a result of increased cognitive flexibility can also be seen to operate at a more conscious quasi-symbolic level (see Mithen, 1996). A relevant example of this could be the human ability to ‘abstract’ expressive communicative intent from deliberate deviations from pulse in musical performance.

## Summary and Conclusion

The skill of interpersonal musical entrainment (IME) operates within the wider frame of the 'Faculty for Music' - a conglomeration of skills, which individually may have evolved for reasons other than musical activity and may or may not be shared with other animals. IME, itself, is dependent upon concurrent operation of a number of subskills: fundamental temporal processing abilities; precise but not absolute periodical production; the perception of synchronicity; error correction; pulse perception; and dynamic attending. These sub-skills, in turn, are constructed at different hierarchical levels with fundamentally temporal ability being an essential component of all other sub-skills and with the simpler skills of periodical production, the perception of synchronicity and error correction mechanisms inherent, at least intrinsically, in the more complex skills of dynamic attending and motor activity. In effect, we have a highly complex multi-level system requiring considerable cognitive flexibility. Furthermore, the hypothesised sub-skills themselves require considerable cognitive cross-domain processing, show considerable stability across modalities and are ubiquitous (at least intrinsically) to a wide range of human behavioural contexts. Furthermore, temporal processing, periodical behaviour, error correction mechanisms, dynamic attending and motor skill/coordination are all subserved by a common internal periodic oscillatory system and IME can operate at temporal levels below perceptual thresholds suggesting that the internal processes which control the timing of synchronised action are directly coupled to the sensory information without any mediation by awareness or perceptual judgement.

The notion has been put forward that IME is a uniquely human skill despite all sub-skills thereof being shared, at least intrinsically, with other animals. It was subsequently hypothesised that humans have uniquely evolved, in addition to the conglomeration of sub-skills, the ability to abstract sub-skills from more primary intrinsic, and possibly effector or modality specific, functions into the behavioural context of musical performance and interaction. IME is thus viewed as a highly complex evolutionary exaptation emerging as a consequence of the human move towards increased cognitive flexibility. The psychology of IME in humans as described in this paper supports this view, as does existing (albeit slight) cross-species comparative evidence. I conclude that this is a highly plausible rationale having the advantage over previous approaches in providing a constructive theoretical foundation for future, more experimentally determinant, study into interpersonal musical entrainment, within a general framework of human behaviour.

**Appendices****Appendix 1)**

<b>Empirical problem</b>	<b>Examples</b>
	<b><u>FLB - sensory motor system</u></b>
Vocal imitation and invention	Tutoring studies of songbirds, analyses of vocal dialects in whales, spontaneous imitation of artificially created sounds in dolphins (Doupe & Kuhl, 1999; Marler, 1970; Nottebohm, 1999; Janik & Slater, 2000)
Neurophysiology of action-perception systems	Studies assessing whether mirror neurons, which provide a core substrate for the action-perception system, may subserve gestural and (possibly) vocal imitation (Rizzolatti & Arbib, 1998; Rizzolatti et al., 1999; Lacaboni et al., 1999)
Discriminating the sound patterns of language	Operant Conditioning studies of the prototype magnet effect in macques and starlings (Kluender et al., 1998; Kuhl, 1991)
Constraints imposed by the vocal tract anatomy	Studies of vocal tract length and formant dispersion in birds and primates (Fitch, 1997, 2000; Hauser, Evans & Marler, 1993, Owren & Bernacki, 1988; Owren, 1990; Rendall, Owren & Rodman, 1998; Negus, 1949; Fitch & Reby, 2001)
Biomechanics of sound production	Studies of primate vocal production, including the role of mandibular oscillations (MacNeilage, 1998; Studdert-Kennedy, 1998)
Modalities of language production and perception	Cross-modal perception and sign language in humans versus unimodal communication in animals (Hauser, 1996; Petitto & Marentette, 1991; McGurk & MacDonald, 1976)
	<b><u>FLB - conceptual-intentional system</u></b>
Theory of mind, attribution of mental states	Studies of the seeing/knowing distinction in chimpanzees (Premack & Premack, 2002; Hare et al., 2000; Hare, Call & Tomasello, 2001; Heyes, 1998; Povinelli & Eddi, 1996)
Capacity to acquire nonlinguistic conceptual representations	Studies of rhesus monkeys and the object/kind concept (Cheney & Seyfarth, 1990; Meyes & Huber, 2000; Shettleworth, 1998; Santos, Sulkowski & Spaepen, 2002)
Referential vocal signals	Studies of primate vocalisations used to designate predators, food, and social relationships (Hauser, 1996; Cheney & Seyfarth, 1998; Seyfarth, Cheney & Marler, 1980; Dittus, 1984; Fischer, 1998; Gouzoules & Gouzoules, 1984; Zuberbuhler, Cheney & Seyfarth, 1999)
Imitation as a rational, intentional system	Comparative studies of chimpanzees and human infants suggesting that only the latter read intentionality into action, and thus extract unobserved rational intent (gergerly, Bekkering & Kiraly, 2002; Melzoff & Moore, 1994; Whiten, Custance, 1996)
Voluntary control over signal production as evidence of intentional communication <sup>36</sup>	Comparative studies that explore the relationship between signal production and the composition of a social audience <sup>36</sup> (Hauser, 1996; Cheney & Seyfarth, 1990; Evans & Marler, 1995; Mahler, Karakashian & Gyger, 1991)
	<b><u>FLN - Recursion</u></b>
Spontaneous and training methods designed to uncover constraints on rule learning	Studies of serial order learning and finite-state grammars in tamarins and macaques (Hauser, Newport & Aslin, 1999; Hauser, Weiss & Marcus, 2002; Fitch & Hauser, 2003; Terrace, Son & Brannon, 2003)
Sign or artificial language in trained apes and dolphins	Studies exploring symbol sequencing and open-ended combinatorial manipulation (Hermann, Richards & Wolz, 1984; Savage-Rumbaugh, 1993)
Models of the faculty of language that attempt to uncover the necessary and sufficient mechanisms	Game theory models of language acquisition, reference, and universal grammar (Nowak, Komarova & Niyogi, 2001; Nowak & Komarova, 2001; Nowak & Plotkin, 2000)
Experiments with animals that explore the nature and content of number representation	Operant conditioning studies to determine whether nonhuman primates can represent number, including properties such as ordinality and cardinality, using such representations in conjunction with mathematical operands (e.g., add, divide) (Gallistel & Gelman, 2000; Carey, 2001; Boysen & Bernston, 1989; Kawai & Matsuzawa, 2000; Matsuzawa, 1985; Brannon & Terrace, 1998)
Shared mechanisms across different cognitive domains	Evolution of musical processing and structure, including analyses of brain function and comparative studies of music perception (Lerdahl & Jackendoff, 1983; Wallin, Merker & Brown, 2000; Zatorre & Peretz, 2000)

**Table 1:** A sampler of empirical approaches to understanding the evolution of the faculty of language, including both broad (FLB) and narrow (FLN) components (adapted from Hauser, Chomsky & Fitch, 2002; see original article for references).

Appendix 2)

**Wing-Kristofferson model in Normal Studies of Repetitive Timing**

Ref.	Movement manipulandum	T (ms)	Acorr(I(1))	Var © (ms <sup>2</sup> )	Var (M) (ms <sup>2</sup> )	Comment
1	Wrist; Morse key	180 - 400	-0.43 to -0.10	90	40	Linear functions for increase in var © with T had negative intercepts
2	Finger; touch key press (P) and release @ times	400	X	X	P: 120 R: 150	Key release intervals more variable than press intervals; but release not hierachically triggered by key press
3	Finger; touch key	220 - 490	X	280	25	Functions showing linear increase in var © with T had negative intercepts
4	Finger; computer keyboard	550	<0 on 78% trials	(SD) 10 years: 28 7 years: 41	(SD) 15 16	Reliable decrease in var © in 10-year-olds; var © (but not var (M)) greater in clumsy children.
5	Finger; computer keyboard	550	<0 on 98% trials	(SD) 6 years: 42 9 years: 29 21 years: 15 43 years: 18 67 years: 23	(SD) 9 12 8 10 10	Children and older adults reliably greater var ©; males reliably lower var © than females (no interaction with age); no differences in var (M)
6	Finger; microswitch	400	X	350	100	Simultaneous solving of anagrams increased var © but not var (M)
7	Finger; lever on microswitch	325 - 550	X	250	50	Included demonstration of parallel increase in variability of time perception and var ©
8	Finger; touch key	200 - 640	-0.30 to -0.02	(SD) 11	(SD) 5	Included analysis of synchronisation phase
<p><i>Note:</i> (1) Wing &amp; Kristofferson (1973b); (2) Wing (1980a); (3) Wing (1980b); (4) Williams, Woollacott, &amp; Ivry, 1992; (5) Greene &amp; Williams (1993); (6) Sergent et al. (1993); (7) Ivry &amp; Hazeltine (1995); (8) Semjen et al. (2000)</p> <p>➤ Where a range of intervals was tested the single values indicate means observed in the middle of the target interval range. X signifies no estimate reported.</p>						

*(taken from Wing 2002 p.10)*

**Appendix 3)**

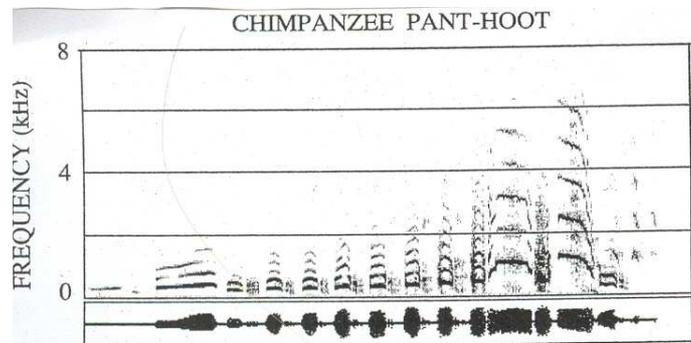
**Effect of using different effectors on Wing-Kristofferson model of Repetitive Timing**

Ref.	Movement manipulandum	T (ms)	Acorr(I(1))	Var © (ms <sup>2</sup> )	Var (M) (ms <sup>2</sup> )	Comment
1	Finger (F); wrist (W); arm pronation (AP); arm elevation (AE); touch key	400	X	F: 300 W: 220 AP: 150 AE: 150	140 80 80 60	For model with correlated (+0.4) response delays, revised estimates were var © 80-90 ms <sup>2</sup> , var (M) 140-340 ms <sup>2</sup>
2	Speech (Sp); finger (F); voice key; microswitch	400	-1/2 < Acorr(I(1)) < 0 on 80% trials	(SD) Sp: 10 F: 11	(SD) 10 9	Included bimanual (var©) < unimanual) and bimodal (var (M) > unimodal) conditions
3	Speech (Sp); jaw (J); wrist (W); forearm (F); strain gauge to lip, microswitch	400	X	J: 8685 Sp: 7840 W: 717 F: 540	(-1369) (-703) 145 134	Individual differences: Var © positively correlated across tasks (except nonsig. between W, F)
4	Horizontal saccadic eye movement; intervals between medial-lateral direction reversals	500, 700, 1000	-1/2 < Acorr(I(1)) < 0 on 84% trials	(SD) 40 to 75	(SD) 30 to 60	Var © and var (M) both increase with interval

*Note:* (1) Wing (1977); (2) Hulstijn et al. (1992); Franz, Zelaznik, & Smith (1992); Collins, Jahanshahi, & Barnes (1998) X indicates no values reported

*(taken from Wing 2002 p. 11)*

**Appendix 4)**



**Figure I:** A sound spectrogram of a single pant-hooting sequence of an adult male chimpanzee recorded at the Gombe National Park, Tanzania. Sound is produced on inhalation and exhalation. The bottom trace shows the amplitude envelope (Goodale, 1980).

Appendix 5)

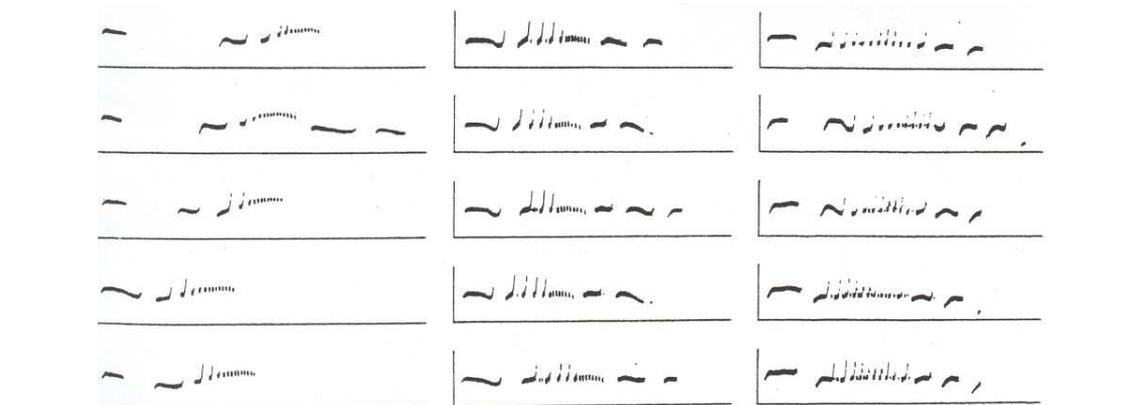


Figure II: Sample of songs of three female Kloss gibbons (Tenaza, 1976).

Appendix 6)

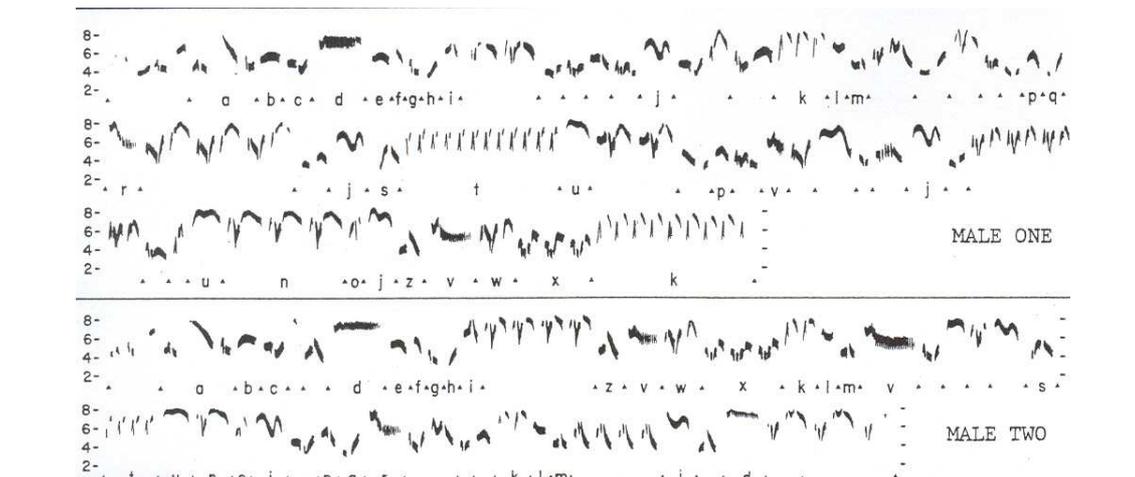


Figure III: Songs of two neighbouring winter wrens, marked with an alphabetical code to illustrate sharing of sound components between individuals. The song of male one is about seven seconds in duration (Kroodsma, 1980).

Appendix 7)

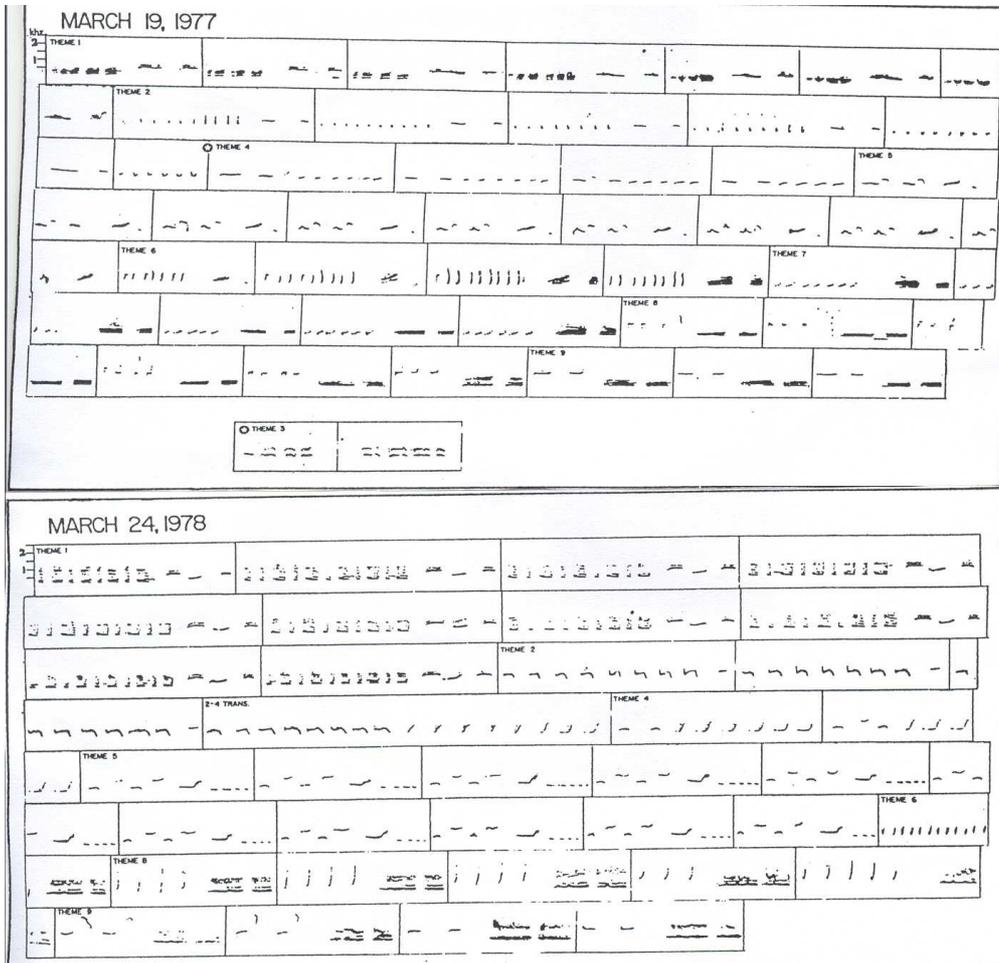
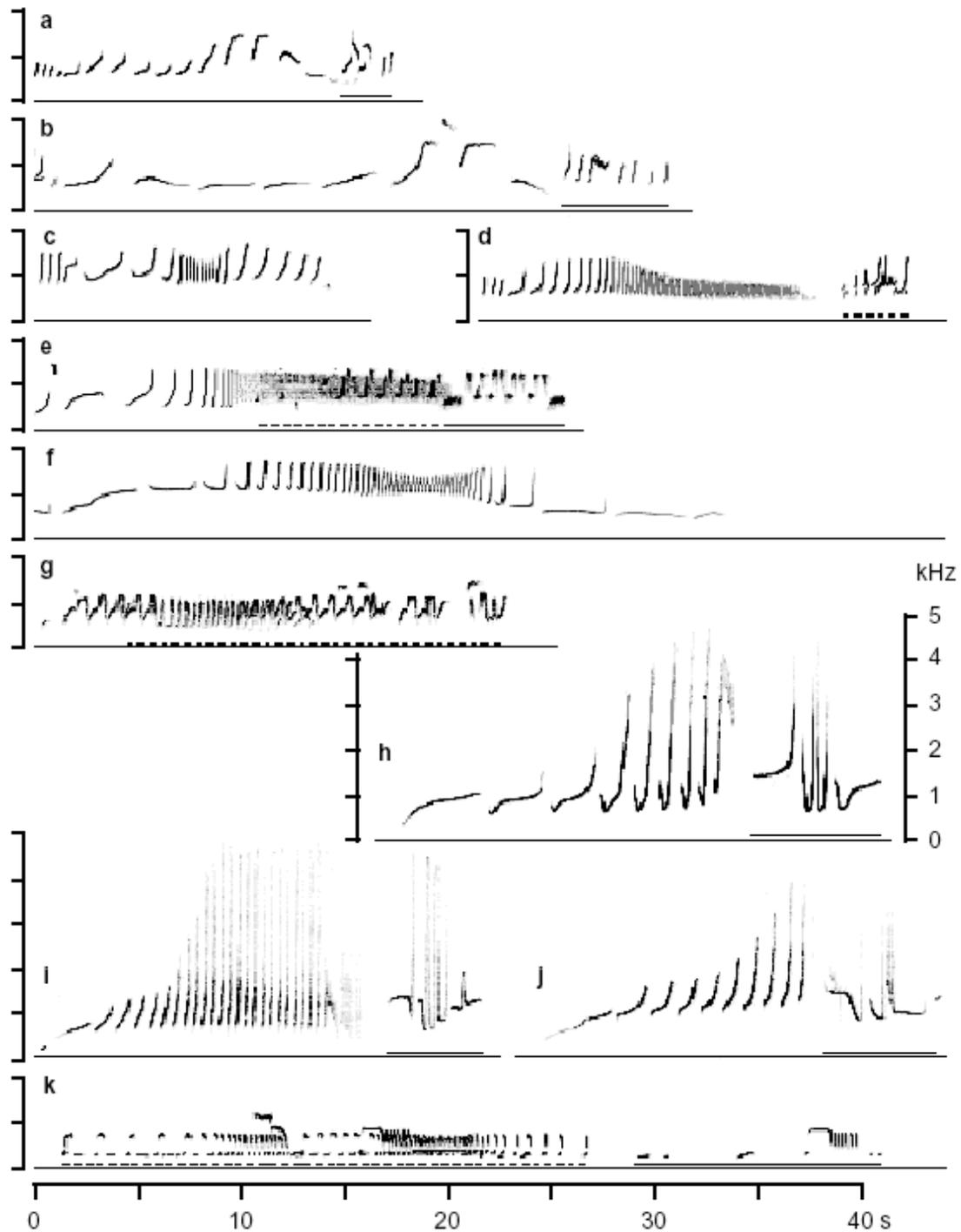


Figure IV: Tracings of spectrograms of representative songs of whales from March 1977 and 1978 (from Payne, Tyack, and Payne, 1983).

**Appendix 8)**



**Figure V:** Sonogram of gibbon great call sequences. Sonograms c and d are excerpts from female solo song bouts; all others show duets. Male solo contributions to duets are underlined with a solid line, synchronous male and female contributions are underlined with a dashed line. **a.** *Hylobates agilis*; **b.** *H. lar*; **c.** *H. moloch*; **d.** *H. muelleri*; **e.** *H. pileatus*; **f.** *H. klossii*; **g.** *H. hoolock*; **h.** *H. concolor*; **i.** *H. leucogenys*; **j.** *H. l. gabriellae*; **k.** *H. syndactylus*. (Geissmann, 1993; 2000)

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