Do we dance because we walk? The impact of regular vestibular experience on the early development of beat production and perception

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Originality Statement

I hereby declare that this submission is my own work and to the best of my knowledge it contains no materials previously published or written by another person, or substantial proportions of material which have been accepted for the award of any other degree or diploma at the University of London or any other educational institution, except where due acknowledgment is made in the thesis. Any contribution made to the research by others, with whom I have worked at University of London or elsewhere, is explicitly acknowledged in the thesis. I also declare that the intellectual content of this thesis is the product of my own work, except to the extent that assistance from others in the project's design and conception, or in style, presentation and linguistic expression is acknowledged.

This thesis includes work that appears in the following article:

- Rocha, S. & Mareschal, D. (2017). Getting into the Groove: The development of tempo-flexibility between 10 and 18 months of age. *Infancy, 22*(4), 540-551.

Pilot data for the study reported in Chapter 2 appeared in the following thesis, submitted to Birkbeck, University of London in September 2014, as a partial requirement for the award of MSc Developmental Science:

- Rocha, S. (2014). Born to Dance? An EMG investigation of movement to music in infancy.

Signed:________________________________

Abstract

Movement to music is a universal human behaviour (Savage, Brown, Sakai & Currie, 2015). Whilst the strong link between music and movement is clearly bidirectional, the origins are not clear. Studying the emergence of rhythmic skills through infancy provides a window into the perceptual and physical attributes, experience, and contexts necessary, to attain the basics of human musicality. This thesis asks whether the human experience of bipedal locomotion, as a primary source of regular vestibular information, is crucial for sensorimotor synchronisation (SMS), spontaneous motor tempo (SMT), and impacts rhythm perception. The first experiment evidences the emergence of tempo-flexibility when moving to music between 10- and 18-months-of-age. The following study is the first to show that experience of locomotion, including from infant carrying, predicts the temporal matching of infant movement to music. Curious if carrying practices influence the very rhythms that we naturally produce, a large-scale correlational study finds infant SMT is predicted by parent height, but not infant's own body size, such that infants with taller caregivers show a slower SMT than those with shorter caregivers. We contend that this reflects infant experience of being carried by their caregiver. The fourth experiment confirms that experience of being carried at a novel tempo can alter the rhythms infant spontaneously produce. Finally, we asked how information from being carried during locomotion might be changing rhythm perception; specifically, if infants show greater activation of their sensorimotor system when hearing rhythms that match the tempo at which they were carried. Combined, these studies present a highly original piece of research into the ways in which early experiences of locomotion may impact fundamental musical skill.

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Mum, I dedicate this thesis to you. Nye and Gwen, always know that you can be
anything you want to be, because our Mum has made it so.

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Introduction

'The music is not in the notes, but in the silence between.'

- Wolfgang Amadeus Mozart

We are highly rhythmic animals, with rich beat perception and synchronisation capabilities that set us apart from other species (Iversen, 2016). All known human societies produce some kind of music, and a propensity for a regular, isochronous, beat has been shown as a remarkable universal in music produced across disparate cultures (Savage, Brown, Sakai, & Currie, 2015). Rhythm is an important and growing subject of scientific study, with evidence that fundamental beat processing and production skills are crucial for human interaction, benefitting social outcomes (e.g. Demos, Caffin, Begosh, Daniels & Marsh, 2009; Hove & Risen, 2009; Valdesolo, Ouyang & DeSteno, 2010), language and educational outcomes (e.g. Goswami et al., 2002; Tierney & Kraus, 2013; Leong & Goswami, 2014), and even the ability to safely navigate the world without falling (e.g. Grahn & Brett, 2009; Nombela, Hughes, Owen & Grahn, 2013).

One of the most intriguing aspects of music is that it makes us want to move (Janata, Tomic & Haberman, 2012). The bidirectional relationship between auditory rhythms and movement has been well documented (Phillips-Silver & Trainor, 2005; 2008; Trainor, Gao, Lei, Lehtovaara, & Harris, 2009). It is not clear why such a relationship exists. Why do we synchronise movement to an auditory beat, but not a visual one (Repp & Penel, 2004)? Why do we only really move rhythmically at certain rates (Repp, 2003), and when we do, why do we move certain parts of our bodies in certain ways (Toiviainen, Luck & Thompson, 2010; Burger, Thompson, Luck, Saarikallio & Toiviainen, 2014)? How is our brain geared towards rhythmic movement to music, and how do auditory and motor areas of processing interact (Grahn & Brett, 2007; Stupacher, Hove, Novembre, Schutz-Bosbach & Keller, 2013)?

Timing is at the heart of these questions. Rhythm is a sequence of short repeated intervals, with regularities that allow us to build expectancies as to when the next beat will arrive (Jones, 1976). The underlying pulse, or tactus, is the simplest form of rhythm. In adult humans, it is this beat that we tap along to when listening to our favourite song, defining the tempi of our movement. Whilst most animals move rhythmically, it is the ability to move with an external timekeeper (Wallin, Merker & Brown, 2000), or an internal, volitionally controlled attentional pulse (Drake & Bertrand, 2001), which is special to human beat production (Bispham, 2006). These abilities are perhaps as special to humans as is language (Merker, Madison & Exkerdal, 2009). The core skills, of *sensorimotor synchronisation* (SMS), the ability to move in time with an external auditory stimulus, and *spontaneous motor tempo* (SMT), the ability to produce a consistent beat at one's natural pace, will be examined in this thesis. Also at the heart of the above questions, is the human. It is the complexity and specificity of our rhythmic skill that makes it so intriguing. Dancing is effortful, and does not seem to have any obvious survival value (Trainor, 2007), so why is it so pervasive? The ontogeny of our rhythmic behaviours has been the focus of much recent research, and can provide vital clues to the evolution of musical skill (Ravignani, Honing & Kotz, 2017).

The current thesis holds a central hypothesis that the sensorimotor nature of our musicality may be a product of our bipedal locomotion, and the multimodal, but primarily vestibular, experience that this provides. Whilst many theories of human musicality emphasise links with language or social bonding (Huron, 2001; Brown, 2003; Patel, 2006; Cross, 2009; Merker, 2009), the vestibular hypothesis put forward in this thesis builds on research showing that vestibular stimulation disambiguates auditory rhythms (Phillips-Silver & Trainor, 2005; 2008; Trainor, Gao, Lei, Lehtovaara, & Harris, 2009); the idea that the upright body structure in bipedal locomotion, with a multiplicity of degrees of freedom, gives us rich rhythmic capacities (Trevarthen, 2000); the possibility of transfer between the rhythm of walking and the rhythm of music making, which are predominantly at the same tempi (Fraisse, 1984); evidence that body size, as a proxy for walking cadence, predicts preferred tempo to move at and listen to (Mishima, 1965; Todd, Cousins & Lee, 2007; Dahl, Huron, Brod & Altenmüller, 2014); and that early infant carrying practices predict rhythmic preferences within cultures (Ayres, 1973).

In order to test this vestibular hypothesis, the current thesis takes a *developmental approach*. One way to understand SMS and SMT is to start at the beginning, and tease apart how motor and cognitive skills, and experiences, impact upon and are impacted by, developing humans' rhythmic capacities. The utility of studying infant rhythm has been recognised for many years, with many studies illuminating infants' sophisticated perceptual skills from early in development. For example, infants are able to detect violation of rhythms from birth (Winkler et al., 2009), and by seven-months-of-age process complicated variations in rhythmic structure (Trehub & Thorpe, 1989). Movement to an ambiguous beat biases the perception of a rhythm from seven-months-of-age

(Phillips-Silver & Trainor, 2005).

However, though infants spend up to 40% of their time performing rhythmic movements (Thelen, 1979; 1981), less attention has been given to the study of infant rhythm production. With some notable exceptions (see review by Provasi, Anderson & Barbu-Roth, 2014), studies of production tend to start from the pre-school years. This may be partially due to the difficulties in measuring production skills in infants who cannot easily be task directed, and infants' lack of fine motor skills to engage in traditional rhythm tasks, such as tapping. More recently, increased attention on early development and technological advances have led to studies that have used motion-capture to accurately measure spontaneous gross motor movements to music in infants (Zentner & Eerola, 2009; Fuji et al., 2014; Ilari, 2015), providing detailed observations of infant rhythm production. In order to understand an organism, we need to observe it, and only by doing so can we specify clearly what is to be explained (Tinbergen, 1963).

Though the core of the current thesis is thus the further documentation of infant rhythmic behavior, the overarching aim of this body of infant work is to contribute knowledge to our understanding of human musicality. Our objectives are discussed in more detail below.

Research aims

The broad aim of this thesis is to illuminate the role of locomotion on human musicality, through the investigation of how infants' beat production and perception is impacted by the experience of locomotion; both self-propelled, when crawling, cruising, and walking themselves, and other-propelled, when carried by the caregiver.

The first study documents infant SMS behaviour at ten and eighteen months of age. Motivated by research showing the impact of auditory tempi (e.g. Provasi & Bobin-Begue, 2003) and a social partner (Kirschner & Tomasello, 2009) on the accuracy of young children's movement to music, this study asks if there is developmental change in the tempo-matching and quantity of SMS across these parameters over the first two years of life. Inspired by the developmental change from 10 to 18 months evidenced in the first study, the next study asks if SMS improvement is indeed due to the impact of locomotion, as is hypothesised in Chapter 1. The highly novel evidence for carrying impacting SMS seen in the second study inspired a focus for the rest of the thesis on how experience of caregiver locomotion may impact infants' most basic rhythmic abilities, and so measured the impact of caregiver walking cadence on infant SMT. First, via a large-scale correlational study asking if infant rhythm is related to their own or their parent's body size, to disentangle the impact of biomechanics (own body size) from rate of predominate locomotive experience (using parent body size as a proxy for parent cadence). Second, by experimentally manipulating the walking cadence that infants were exposed to, in order to confirm that walking cadence impacts SMT. Finally, we asked if a behavioural change in SMS following carried walking experience is underpinned by neural changes, in sensorimotor alpha oscillatory activity. The following section gives a breakdown of each chapter.

Thesis Overview

As outlined above, the aim of this thesis is to further our understanding of the development of both SMS and SMT, with a particular focus on the role of locomotive experience.

Chapter 1 provides an overview of why the vestibular information that we receive from upright, bipedal, locomotion may be critical for human beat perception and production abilities, laying out a vestibular hypothesis for human musicality.

Chapter 2 presents an EMG study testing the early SMS abilities of 10- and 18-month-olds during a bell ringing to music task. The impact of the tempi of music played to infants, and the impact of the presence or absence of a social partner, is investigated.

Chapter 3 asks if the developmental change in early SMS skill observed in Chapter 1 is related to experience of locomotion, using the same SMS task to test infants before and after locomotive treadmill training. Caregivers were also asked if their infants were able to crawl or cruise, and whether they regularly carry their infant in a sling, to explore if long term first or third party locomotive experience (of being carried by the caregiver), predict infant tempo-matching.

Chapter 4 charts the development of infants' natural tempo of rhythm production. SMT is measured in a large-scale behavioural study of infants from four to 33 months of age using a free drumming task. Through use of anthropometric measurements of parents as a proxy for walking tempo, the study further explores if experience of being carried by the caregiver may set the tempo of infants' spontaneous drumming.

Chapter 5 explores if the correlational evidence found in Chapter 4 is indeed a product of walking experience, reporting an experiment on the impact of novel carrying experience on infant SMT measured through the same free drumming task as in Chapter 4.

Chapter 6 presents the final study, which tests the idea that carrying may enhance an infant's motor programme for events with that timing, such that they show greater activation of the motor system, as indexed through measurement of sensorimotor alpha suppression using EEG, when hearing sounds that correspond to the rate at which they were carried. Infants were walked at a novel tempo and then played auditory rhythms that matched or did not match the rate of walking they experienced, with the hypothesis that if infants are making use of the information they received when carried, they should show more sensorimotor alpha suppression during the auditory presentation of the congruent tempo.

Chapter 7 discusses the contribution of the presented studies to our understanding of the relationship between music and movement through development. It is argued that experience of being carried, and self-produced locomotion, is a possible key contributor to human musicality. The limitations of the current studies are discussed, and novel interdisciplinary ways to further test these ideas, from both proximate and evolutionary standpoints, are suggested.

Précis

To anticipate, in Chapter 2 we show that older infants show better SMS, providing the first evidence of the development of tempo-flexibility between 10- and 18-months-of-age. In Chapter 3, we show that infants with more locomotive experience, both self-propelled and from being carried, are better at matching rate of movement to rate of music. In Chapter 4 we evidence that older infants have a faster and less variable SMT, and that infants with taller caregivers display a slower SMT, which we attribute to experiencing slower gait when carried by the caregiver. In Chapter 5, we confirm that giving novel carrying experience impacts upon the rhythms that infants spontaneously produce, such that being carried at a slower pace engenders slower SMT and vice versa. Each experimental chapter begins with a self-contained review of the pertinent literature. First, in the following chapter (Chapter 1), we put forth the vestibular hypothesis that motivated the work herein, such that our empirical findings can be viewed in the larger framework from which they were inspired.

Chapter 1

A vestibular hypothesis of human musicality

1.1 Human Musicality

Music is an art form. In order to clarify how we can ask and answer scientific questions about our proclivity and aptitude for song and dance, Honing (e.g. Honing, ten Cate, Peretz & Trehub, 2015) dissociates 'music' from 'musicality'. According to Honing, music can be defined as the social and cultural construct that overarches musicality; musicality is therein a set of natural, spontaneously developing cognitive and biological traits that contribute to music. What exactly constitutes these traits is a contemporary research issue, in a field that is still evolving: In order to study musicality, one has to identify and examine the basic underlying mechanisms, their functions, and critically, their development (Honing et al., 2015). Whilst the end behaviours and cognitive processes might be highly complex, breaking them down into smaller components can help us unlock the 'recipe' of musicality. Rhythm, and specifically the perception and production of the beat, pulse, or tactus of music, is a core ingredient.

The current thesis examines the ontogeny of early rhythmic behaviour to answer questions on the origins of human musicality. In this chapter we put forth a vestibular hypothesis for the link between music and movement. First, we briefly summarise the prevailing schools of thought on human musicality. Second, we detail the current hypothesis, expanding on existing vestibular hypotheses to argue that the complex human movement and music relationship is at least in part the product of our vestibular system, *specialised to deal with the* *complexities of bipedal locomotion*, and give particular consideration to i) the effect of vestibular stimulation on rhythm perception, ii) the unique human upright body structure, iii) parallels between musical tempi and the tempi of locomotion, and iv) the impact of infant carrying practices on rhythm production. Finally, we summarise the research questions tested empirically within the thesis.

1.2 Theories of Human Musicality

For centuries, academics studying aspects of music have considered its evolutionary basis. Darwin himself speculated that music and dance might have contributed to sexual success, as an attractive mating display (Darwin, 1872). However, it has been argued that most acts of sexual selection exhibit high sexual dimorphism (i.e. males *or* females possess the trait), and so this is an unlikely explanation for human musicality (Huron, 2001).

The many similarities between music and language, and the more obvious survival benefits of language, have led to suggestions that language is the adaptation, and music a pleasant but not useful result, a form of 'auditory cheesecake' (Pinker, 1997). The distinctions between language and music, including the predominance of the isochronous beat in music that does not exist in language, speaks against this idea; we appear to have specific rhythmic skills that are not a direct by-product of language (Patel, 2006). Alternatively, the 'grooming and gossip' hypothesis (Dunbar, 1996), suggests language may be a means of maintaining group cohesion when group size gets too large for grooming to be a predominant affiliative activity. Music, which can be louder, more synchronous, and more emotive than language, may have improved the success of collective actions, aiding the survival of the group (Huron, 2001). Huron (2001) argues that music aids social bonding, by raising arousal and synchronising the moods of individuals, with the singing of 'Happy Birthday' and of common football chants prime examples of what the original function of music may have been. The idea of music as a 'social glue' has been popular (Brown, 2003; Cross, 2009; Merker et al., 2009). Merker advances that synchronous movement to isochronous beats may be advantageous in aligning group behaviours that are not only social but also have defensive functions, allowing for coalition signaling, or moving as one to appear larger (Merker, 2000). Larsson (2014) suggests that detecting a rhythm and moving to it reduces noise when groups are walking together, reducing the masking of critical sounds in the environment, such as of prey or stalkers.

Whilst the above theorise on human rhythmic skill from an evolutionary standpoint (i.e. what was the benefit for survival and reproductive success?), understanding the phylogenetic history of how we came to have such skills, where other species do not, is a separate question. This is especially critical for the understanding of beat perception and production, which unlike other elements of musicality such as pitch, timbre and meaning, is not as obviously also apparent in language.

A prevailing current theory is the *Action Simulation for Auditory Prediction* (ASAP) hypothesis (Patel & Iversen, 2014). The ASAP hypothesis postulates that beat perception is the product of closely integrated auditory and motor processing, such that we use our temporally precise motor cortex to generate predictions of auditory stimuli that lie within the same range of timings as our periodic actions. Motor planning areas of the brain that monitor and predict actions such as stepping or reaching, with durations in the order of hundreds of milliseconds, are utilised for discrete auditory events such as the beat in music. Accordingly, actions are simulated, but importantly, need not involve motor imagery, or use of the same effectors as would produce a correspondingly timed action, rather working at an abstract level. This idea is in line with the proposal by Schubotz (2007), that the motor system predicts events by exploiting an audiomotor or visuomotor representation. Such simulations can account for the predictive nature of movement to the beat, and the complexity of human actions can account for our superior rhythmic skill, and coordination over multiple timescales (and effectors) compared to other species. At a neural level Patel proposes that the auditory system provides timing information on the audio signal to the motor system, impacting the timing of motor planning signals, and this information is sent back to the auditory system to predict when the next beat occurs. ASAP thus stresses a specific bidirectional, rather than more general synchronous or contingent interaction, between the auditory and motor systems. Patel aligns the ASAP hypothesis with the vocal learning hypothesis (Patel, 2006), suggesting that the bidirectional auditory-motor connections just described may result from the specialised link between auditory and vocal control centers necessary for complex vocal communication, such as human speech. The human brain is accordingly specialised for audiomotor links as it must learn to produce sounds that match a desired heard model (Patel, 2006).

The vocal learning hypothesis primarily suggests that only species with the ability to acquire new, complex, patterns of sound throughout life, will show human-like beat perception and production skill, and receives support from the first experimental comparative work to show human-like SMS in a cockatoo named Snowball (Patel, Iversen, Bregman & Schulz, 2009), and observations of SMS in other variations of parrots (Schachner, Brady, Pepperberg & Hauser, 2009). However, since these pioneering studies, there is also evidence of entrainment to a beat in a sea lion (Cook, Rouse, Wilson & Reichmuth, 2013), an ape (Hattori, Tomonaga & Mastuzawa, 2013), and bonobos (Large & Gray, 2015). These last three species are not known vocal learners, and although there is argument that the sea lion, as a relative of vocal learning seals and walruses, may have abilities not yet measured (for argument for this interpretation see Patel, 2014, and against, Wilson & Cook, 2016), the primate evidence more positively speaks against the vocal learning hypothesis.

Patel concedes there are other shared traits with such species, including imitation of movement and living in complex social groups, such that vocal learning may not be the only necessary foundation for SMS (Patel, et al., 2009). However, others have argued that what is special about vocal learners may not be the vocal learning per se, but rather the development of complex fine motor control, honed motor programs and use of real-time feedback for error correction that vocal learning entails (Schachner, 2012). If true, animals with other diverse but equally fine-tuned relevant behaviours, such as well-trained dressage horses, may also show SMS (Schachner, 2012). Critically, if this is the case, rhythmic skill may still be exaptive, but the trait that beat perception and production is a by-product of may be entirely different in composition. Moreover, what we see in other species, especially those phylogenetically far from ours, are likely analogous, rather than homologous traits, and convergence on rhythmic abilities may be linked to different specialisations across species (cf. Fitch, 2015). Further, a topic largely ignored in comparative work is the impact of learning and experience. Evidence of a trait in human infancy is often taken to suggest 'innateness' (e.g. Phillips-Silver & Trainor, 2005; Winkler, Haden, Ladinig, Sziller & Honing, 2009), despite the fact that the fetus is known to learn in the womb, and the young infant learns rapidly. Within the rhythm literature, evidence across species rarely considers the potential role of experience that animal has, both in relation to its conspecifics and with humans, when describing similarities or differences (Wilson & Cook, 2016). Subjects are discussed as if they are created at the moment of testing: Would a songbird or an ape, raised as human young, show the more human-like SMS skill? Ignoring the wealth of experience of animals beyond the directly measured trait is a disservice to the process of development.

The hypothesis presented herein fully appreciates the ASAP hypothesis, and does not attempt to refute or negate the vocal learning hypothesis, but rather argues that vocal learning may not be the only specialisation that is critical to the complexity of human SMS and beat perception skill, a view magnified by the primate findings discussed above. In the constraint of only considering the vocal apparatus and speech, much of the complexity of human movement and gross motor control is left out in the cold. The hypothesis we will put forth situates itself within the realm of literature that argues for specialised mechanisms for beat perception and production, such as Patel's, and against the idea of sexual selection through mating displays and 'auditory cheesecake' described by Darwin and Pinker, respectively. Linguistic or social glue theories of musicality may well be a process by which human musicality has propagated to take such a ubiquitous hold over our species. The consideration of these aspects is not highlighted in this thesis only because it is already under deep consideration by the field, with a current zeitgeist that we believe is weakened by the lack of emphasis on a critical element of musicality: the importance of vestibular information, and the rhythmic skill and information we gain from bipedal locomotion. The question motivating the thesis is not asking 'what is ***the*** trait that allows complex human beat perception and production?', but rather 'are we missing out a critical element from our discussion?'. In the following section I elaborate why consideration of the whole body, and the uniqueness of our locomotion, may be crucial to a full understanding of human rhythm.

1.3 The Vestibular Hypothesis

In the study of rhythmic movement to a rhythmic auditory stimulus, the workings of the ear make a logical starting point for trying to understand how we integrate movement and music. When we hear music, we often spontaneously move, and as adults, move in time with the stimulus: This is unique to the auditory domain –

we do not feel compelled to synchronise with a beat presented visually (Repp & Penel, 2004; Patel, Iversen, Chen & Repp, 2005). The hair cells of the cochlea sense the vibrations of sound waves. The neighbouring vestibular system, concerned with movement, shares many pathways with the auditory system, and in the following sections we consider how the two might work together to form our overall perception of the beat.

1.3.1 The vestibular system

The vestibular system has been termed our ‘sixth sense’, and monitors our position in space, providing us with the knowledge of movement and balance requisite for normal functioning. Housed in the inner ear, the system is evolutionarily ancient, and comprises of two components, semicircular canals, that sense rotational movements of the head, and otolith organs, that sense linear accelerations. The vestibular system is thus constantly active, as even in the absence of movement, the otolith organs are monitoring the pull of gravity on the body (Angelaki & Cullen, 2008).

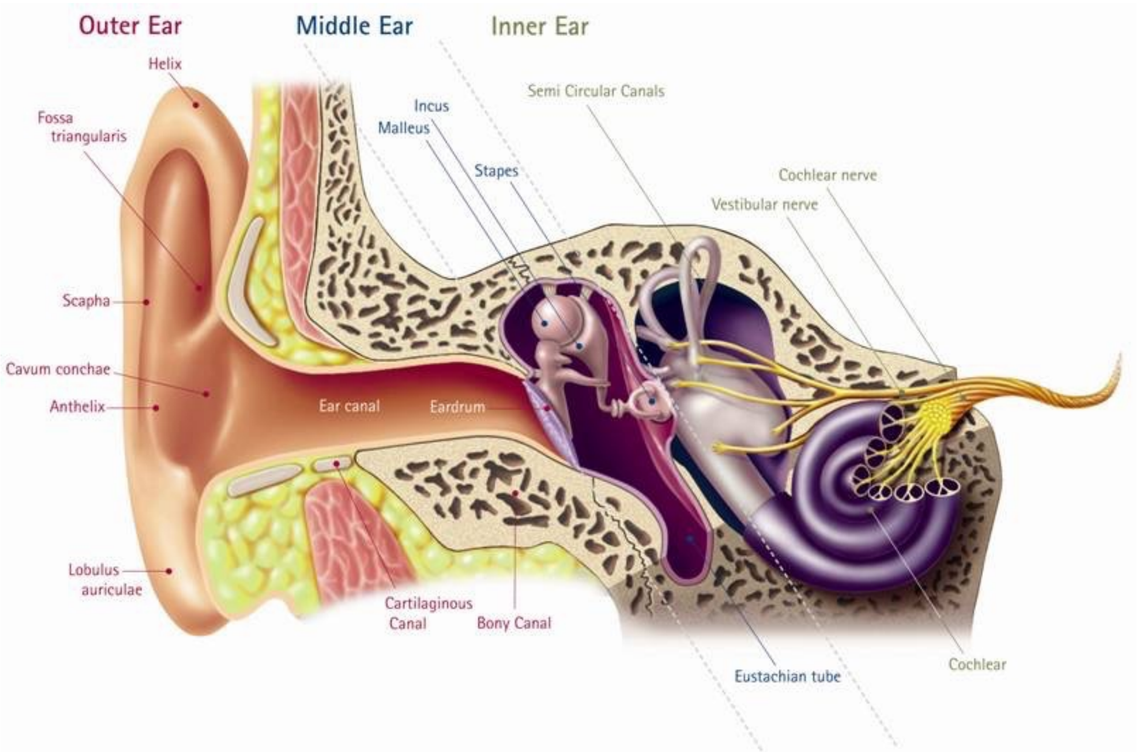

Figure 1.1 Pictorial representation of the ear. The vestibular system is housed in the inner ear, above the cochlea. (Retrieved from http://aakaarcdc.in, 11th December 2017).

This sense is unique in that the vestibular system does not provide conscious signals; we do not perceive input in the same way as we perceive a taste or smell. Signals do not project directly onto unique vestibular pathways, but rather are projected across the brain, shared with the other senses, becoming truly multimodal (Ferre, Bottini, Jannetti & Haggard, 2013). Motor, visual and auditory signals are continuously integrated with vestibular signals for a wide range of purposes, from basic to complex processing.

Though the auditory organs of the ear and the vestibular system are clearly anatomically close, it does not seem possible that direct stimulation of the vestibular system by sound waves are responsible for the link between movement and music. Though it retains some acoustic sensitivity, the auditory and balance instruments are divided, and only very loud sounds (95 decibels, akin to that of a rock concert) would be strong enough to stimulate the semi-circular canals of the vestibular system directly (Todd & Cody, 2000). It is additionally worth noting that the beat of a song is not an intrinsic property of music, but rather something that we perceive (Honing, 2012). Beats can be strong and clear, or difficult to follow, and this may vary dependent on the listener (Honing, 2012). It therefore seems unlikely that there is a direct mapping of the physical sound signal onto movement, as there is no constant property of the sound to map reliably (i.e. volume or duration, though both can be used to emphasise a beat, do not have inherent properties that signal a ‘beat’ out of context; cf. Honing, 2012).

1.3.2 Vestibular information and rhythm perception

Over the past two decades, researchers have thus focused on the multimodal properties of the vestibular system, and a possible reciprocal relationship between movement and music in our perception of a rhythm. In an attempt to understand the effect of movement on beat induction, Phillips-Silver and Trainor (2005) presented infants with an ambiguous auditory rhythm that followed the pattern ‘Beat-rest-beat-beat-beat-rest’, but were disambiguated to either a duple rhythm (‘BEAT-rest-BEAT-beat-BEAT-rest’) or a triple rhythm (‘BEAT-rest-beat-BEAT-beat-rest’), by bouncing the infant on the beat indicated in capital letters.

Following this movement training, infants chose to listen longer to the rhythm that matched their bounce rate. Interestingly, when blindfolded, the result held, but when infants passively observed bouncing rather than being bounced themselves, the effect was no longer present (Phillips-Silver & Trainor, 2005), suggesting that movement is critical, but that visual input is not.

Driven by the finding of a strong connection between audition and movement in perception of the beat, possibly suggesting vestibular input, the authors were keen to pinpoint what about movement is critical. They therefore attempted to reduce the potential role of motor, proprioceptive and tactile information by adapting passive movement of the participant to either full body, head only, or leg only movements (Phillips-Silver & Trainor, 2008). The relevant body parts of adult participants were bounced on a seesaw bed, and they were then asked whether an ambiguous, duple, or triple beat rhythm, was closest to that they had experienced during the movement training. The authors reported a diminishing effect whereby full body movement elicited the strongest perception of the intended beat, followed by head-only movement, with leg-only movement not sufficient for correct identification. Though the head-only movement, which stimulates the vestibular system, did not produce as clear an input as full-body movement, the authors speculate that there may be a reduction in vestibular stimulation with a head-only action, as full body motion naturally requires more reorientation and balance, and that head-only rocking may be a more unnatural movement.

In order to provide more direct evidence for the role of the vestibular system, galvanic vestibular stimulation was used during presentation of the same rhythms to give the feeling of a sideward movement of the head on each of the accented beats (Trainor, Gao, Lei, Lehtovaara, & Harris, 2009). A control group experienced the same tempo of stimulation but to the elbows, which was experienced as a mild tingling sensation: Only galvanic vestibular stimulation was sufficient for disambiguation of the rhythm.

This body of work clearly demonstrates that stimulation of the vestibular system impacts rhythm perception. Lacking in the literature is any discussion of whether this is a product of experience. Phillips-Silver and Trainor (2005) argue that their findings with seven-month-olds show that no *special* experience is necessary for this bimodal relationship. However, the vestibular system is the first to develop in the fetus, online by 14 weeks gestation (Lecanuet and Schaal, 1996), and thus by seven months post-partum, infants have had many months of experience. Heart-rate measurements show the fetus is sensitive to maternal movements, such as walking (Cito et al., 2005), and react to vestibular stimulation as induced by rocking the mother (Lecanuet & Jacquet, 2002). The newborn is sensitive to being carried, rocked and swung (Gordon & Foss, 1966; Pederson & Ter Vrugt, 1973; Pederson, 1975; Hunziker & Barr, 1986; Elliott, Fisher & Ames, 1988; Esposito et al., 2013; Yilmaz & Arikan, 2015). A primary experience that infants will have had exposure to is of synchronised auditory and vestibular stimulation caused by mother's locomotion (Teie, 2016). This consideration will form a primary tenet of the current thesis and is expanded in section 1.3.5.

1.3.3 Human body structure

In a reply to the emphasis on the vestibular stimulation placed by Phillips-Silver and Trainor (2005), Todd and Lee (2007), though proponents of a core role of vestibular stimulation on rhythm perception, sought to highlight that the vestibular system has evolved from fish and frogs, where the otoliths are used for hearing, and that the otolith organs exist in all vertebrates. Todd and Lee (2007) therefore reject the idea that such an audiovestibular relationship is unique to humans. How then to explain the apparently unique relationship between music and movement that exists in our species? One distinction from even our closest relatives is the uniquely human trait of bipedal locomotion. According to Trevarthen's (2000) theory of musicality, the unique structure of the human body, with all limbs stacked up one on top of the other, could be the key distinction between humans and our closest relatives. Trevarthen's hypothesis states that standing upright on two legs and walking in this position provides us with a rhythm, the sound and sensation of one foot hitting the floor after the other at a regular rate. This provides an underlying beat to daily life, but we can also move our upper body and limbs in quasi-independent motions, providing the possibility of a multiplicity of rhythms all at once[1]. According to Trevarthen (2000), although many species show agile and well-coordinated movement, bipedal locomotion

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[1] An additional point to note is that the upright body structure of bipedal humans had the knock-on effect of the descent of the larynx. This increased the length of the vocal tract and allowed for much more diverse vocalisations: It has additionally been argued that this, in addition to the control and degrees of freedom discussed by Trevarthen, was the 'musical revolution' of bipedal locomotion, two million years ago (Mithin, 2009).

means that our movement capabilities are richer and freer, and this is the origin of human musicality. The idea of humans having special, richer and freer, motor capacities, is present in the physiological literature on human locomotion. Whilst other animals may primarily rely on spinal rhythm generators, Nielsen (2003) stresses that humans are not monkeys walking on two legs; the breadth of adaptation to walking bipedally is reflected in supraspinal, as opposed to spinal, control, resulting in vastly different kinematics, cortical involvement and muscular coordination. Further, in studies of natural movement to music, there is evidence that different parts of the body synchronise with different aspects of music, sometimes at once, and with the location and direction of eigenmovements somewhat specific, so that the pulse (beat level) of music tends to be represented over the body in vertical actions, especially of the torso, compared to the meter level, often embodied as mediolateral movement over the arms or body sway (Toiviainen, Luck & Thompson, 2010; Burger, Luck, Saarikallio & Toiviainen, 2014). It may be that the strong vertical action-beat relationship reflects walking behaviour.

1.3.4 Locomotion and preferred tempo

The link between locomotion and musical rhythm has been heavily investigated in clinical populations, with strong evidence that the presence of beat-based music enables better locomotion in patients with disorders such as Parkinson's Disease, who show both gait ataxia and impaired rhythm processing in perceptual tasks (e.g. Grahn & Brett, 2009), by providing an external cue to movement (for a review see Nombela, Hughes, Owen & Grahn, 2013). The beat and expression of music can also adjust the tempi of healthy walkers and runners whilst exercising (Styns, van Noorden, Moelants & Leman, 2007; Karageorghis & Priest, 2012; Leman et al., 2013). In the current thesis we argue that this relationship is bidirectional, such that locomotion can also change rhythmic tendencies. Further, we argue that the link may also be causal, such that the cadence of locomotion sets the rate at which we prefer to create and listen to music.

It has been well observed that the tempo of most music and human locomotion coincide (Mishima, 1965; Ayres, 1973; Fraisse, 1984; Styns et al., 2007; Trainor, 2007). The rate at which an individual walks is in part determined by the length of their limbs and other such anthropometric features, due to the pendulum nature of the leg swing and aerobic cost optimisation that depends on stature (e.g. Bertram, 2005). Anthropometrics correlate with Spontaneous Motor Tempo (SMT), as measured through tapping (Mishima, 1965), and naturalistic full body dancing (Dahl, Huron, Brod & Altenmüller, 2014). Critical to the argument that these relationships could be the product of locomotion is that anthropometrics are also correlated with preferred tempo in a perceptual listening task (Todd, Cousins & Lee, 2007). As there is unlikely to be a genetic mechanism that directly matches body size to auditory preferences (Trainor, 2007), locomotion is a sensible, pervasive, candidate experience for such a transfer (Todd et al., 2007, Trainor, 2007). Walking provides a strong vestibular input, and we can also hear our own steps. Vestibular deficits impede normal gait, and information from the other senses has to be well integrated with the vestibular signal in order to control posture (Ouchi et al., 1999). Taken together, this evidence highlights that if we hypothesise any advantage of sensitivity to the multimodal activity of walking, strong vestibular-auditory synchronisation skill may also be advantageous.

1.3.5 Carrying practices

The difficulty of achieving bipedal locomotion requires the caregiver to carry the infant in her arms, for the long period of development before an infant can locomote herself. Infants may not walk until the end of their first year of life (Storvold, Aarethun & Grete, 2013), but for a long period before they can move independently, and likely for a long period after they take their first steps, a pervasive and highly rhythmical experience for infants is to be carried or rocked by the caregiver. At the same time, the infant may hear the sound of the caregiver's steps. It is possible that experiencing such *third-party* locomotion through our protracted development, with the coordination of sound and balance this initiates, may explain the vestibular-beat induction relationship. It is a well-documented phenomenon that when we tap along with a song, we consistently anticipate the beat by some milliseconds (Repp, 2005). It would be insightful to know if the fetus or infant is using vestibular and auditory information as some kind of predictive mechanism in anticipation of the mothers' step.

One paper that inspired much of the work in this thesis is an anthropological report conducted by Barbara Ayres, published in 1973. Ayres hypothesises that the regular rhythmic movement experienced by an infant when the caregiver is walking, working, and rocking the infant, may be associated with the ‘rewards’ of contact, temperature control, feeding and sleeping: The reinforcement of such behaviours with such rewards leads to a sustained preference for rhythmicity in adulthood, which may then be expressed in the music that we produce. Accordingly, she predicts that societal preference for a regular rhythm should be correlated with the nature and frequency of infant carrying in that population. Ayres analysed data on carrying practices collected from 54 traditional, historically independent societies, which spanned North America, the Mediterranean, Africa, Eastern Europe/Asia and the Pacific. The societies were grouped by their prevalent carrying method, into three types: i) carried in a sling, pouch or shawl, ii) carried in arms, on hip or on shoulder, and iii) kept in cradle, cradleboard of hammock. Across the world areas examined, carrying method was fairly evenly distributed, except in North America, where all but one of the eight traditional societies analysed used a cradleboard. Samples of music (at least ten examples from each society) were collected and analysed. The music was categorised as ‘regular’, if it met criteria as a single beat rhythm (just a pulse), a simple rhythm (measures divisible by two or three, forming units of equal length, and an accented beat occurs at the beginning of each measure), or a complex meter (measures not divisible by two or three, but still of equal length, and still with accents at the beginning of each measure). Music was categorised as ‘non-regular’ if it had an irregular rhythm (measures not of equal length, accents occur at irregular intervals) or a free rhythm (also known as parlando rubato, where no recurring beat or accent is evident). The dependent variable was the percentage of music from each society that fell into the ‘regular’ category, and across all samples, the median score was 40%. Ayres found that societies where infants are carried, either in a sling or on the body without support, produce a higher percentage of music with a regular rhythm than societies that use the cradle, cradleboard or hammock.

Whilst to our knowledge the hypothesis put forward by Ayres has yet to be empirically tested, in the following sub-sections we attempt to draw upon several strands of research to formulate how carrying may be just as informative for early rhythmic skill as self-achieved locomotion. As the impact of carrying on rhythm will be the element of our hypothesis most tested through the thesis, the rest of this section explores the scientific literature on infant carrying in some detail; why carrying may be important, the changes it may make to the developing child, and how carrying may be experienced as an active movement rather than a passive one by the infant.

1.3.5.1 Humans as 'carried young'

Human infants are born incompetent creatures, who require extensive attention from the caregiver for a protracted period of development. Accordingly, in contemporary hunter-gatherer societies, infants are held or carried for most of the day (Lozoff, Brittenham & Klaus, 1978). Evidence for human infants as belonging to a mammalian category of the ‘carried young’ includes observations of newborn and infant posture, with their characteristic rounded spine and flexed leg position beneficial for being carried at the hip over standing upright, a clinging response when moved suddenly, and extensive frequent feeding and defecating that suggest near constant contact with the caregiver (for a review see Schon & Silven, 2007).

Infant carrying is an effortful task, potentially costing more energy than even breastfeeding (Wall-Scheffler, Geiger & Steudel-Numbers, 2007). The amount of time that modern Western infants are carried is likely to vary hugely depending on specific cultures and parenting style, and at six weeks of age time spent in arms and not feeding has been estimated from as low 61 minutes per day (Baildam et al., 2000) to as high as 2 hours 11 minutes per day (St. James-Roberts, Hurry, Bowyer & Barr, 1995). Whilst infants may sleep in the arms, young infants carried in a forward-facing sling are likely to be awake and looking at the environment, and are engaging in arm movements more than 17% of the time (Field, Malphurs, Carraway & Paelez-Nogueras, 1996). Walking whilst holding an infant is different from walking alone, with shorter steps observed (Wall-Shceffler et al., 2007), but is still smooth and rhythmic, and does not seem to be more cautious than walking holding any object; maximal stepping height is not different when carrying an infant as an equally heavy bag of shopping (Hodges & Lindhiem, 2006).

1.3.5.2 The impact of carrying on infant development

Historically, much of the literature on infant carrying focuses on the impact of carrying on soothing infants. A randomised control trial on the effects of supplementary carrying demonstrates that approximately two hours of extra time spent in the arms of the caregiver is related to a decrease in time crying and fussing of up to 43% (Hunziker & Barr, 1986). Rocking can not only stop or prevent crying, but also regulate respiration (Elliot, Fisher & Ames, 1988). Elliot and colleagues further report ‘entrainment’ of breaths to rock rate, but it is worth noting that they observe is a directional change (more breaths for faster rocking than slower rocking), rather than entrainment in the strict musical sense. The results demonstrate that variability of respiration was lower during rocking and that infants rocked at a faster speed showed a greater rate of change than infants rocked slowly (Elliot et al., 1988). The direction of rocking (vertical, horizontal, or a see-saw motion) does not impact its efficacy (Pederson, 1975). The ‘touch’ element of baby carrying does not seem necessary for an impact on the infant: Rocking a baby within her cot without physical touch has been shown effective in neonates (Gordon & Foss, 1966), and swinging the baby in the arms or in a blanket is equally calming (Yilmaz & Arikan, 2015). However, the acceleration of vertical rocking is important; greater amplitude as well as frequency predicts efficacy in ceasing crying behaviours (Pederson & Ter Vrugt, 1973). Faster acceleration of movement has also been linked to infants being in a more bright-alert state, in contrast with drowsiness induced by slower, more continuous acceleration (Byrne & Horowitz, 1981). A more recent study of carrying shows the real-time impact of carrying on decreasing infant heart rate, compared to lying supine or being held in a stationary vertical position (Esposito et al., 2013).

Carrying may be beneficial for the infant due to the variability in posture that it exposes them to. The importance of variability, in order to learn new strategies of achieving gross and fine motor goals, is highlighted in a review paper by Dusing and Harbourne (2010), who describe how variability in the environment and caregiving, giving infants experience of a range of positions and movements, and allowing ‘errors’ in movement, is critical for healthy development, with upright carrying a core tool for stimulation. There is evidence that beyond an affective response, vestibular-proprioceptive stimulation (e.g. being moved from lying supine to sitting) improves visual tracking in neonates, compared to being stationary in the supine or upright position (Gregg, Haffner & Korner, 1976). Rocked and carried infants have been recorded as scoring higher than controls on the Bayley Scales of Infant Development, which measures cognitive and motor abilities, and show higher activity levels (Rice, 1975), and greater visual alertness (Korner & Thoman, 1972). In the absence of vestibular stimulation, infants engage in more rigid stereotypical behaviours, which may be compensatory self-stimulation (Thelen, 1981). Other forms of vestibular stimulation (e.g. rotary, obtained by spinning infants around on a chair in the dark), have also been shown to accelerate motor development (Clark & Chee, 1977). Infant monkeys raised on a waterbed that moved when they moved performed better on the Bayley Scales than infant monkeys raised on a stationary blanket (Schneider, Kraemer & Suomi, 1991). The proposed mechanism by which these improvements take place, at least in humans, is that vestibular stimulation trains the vestibuloccular reflex, which enables visual stability during head movements (Clark et al., 1977). Controlling eye-movements is critical for many motor activities, particularly because it is crucial for balance:

For example, children’s balance during independent standing is improved when they are making correct saccades as opposed to fixating the eyes (Arjezo, Wiener-Vacher & Bucci, 2013). In more complex dance behaviours, such as the pirouette in ballet, the control of the eyes is crucial for successfully balanced turns, with intentional 'spotting' the product of advanced training (Tokia, Aoki, Watanabe & Miyata, 1971).

1.3.5.3 The involvement of the infant whilst she is being carried

A benefit for control outline above may be adaptive because when infants are being carried, they need to compensate for the caregivers’ movement, both in terms of controlling their physical posture and controlling their saccades to maintain a stable view of the world. Maintaining posture was traditionally viewed as an automatic process, but over the last decades we have seen mounting evidence for an interaction between balance and cognitive processes (for a review see Maki & McIlroy, 2007), with evidence of cortical involvement in children’s postural control during standing (Blanchard et al., 2005; Schmid, Conforto, Lopez & D’Alessio, 2007; Olivier, Cuisiner, Vaugoyeau, Nougier & Assaiante, 2007; Laufer, Ashkenazi & Josman, 2008). In adults, galvanic vestibular stimulation to induce the feeling of instability during standing leads to increased commands from the motor cortex, as measured using motor evoked potentials (MEPS), to muscles involved in postural control, as measured through electromyography (EMG; Solopova, Kazennikov, Deniskina, Levik & Ivanenko, 2003). Electroencephalography (EEG) further demonstrates activation of the motor cortex during adult balance training, such as maintaining a standing position on a foam surface, with stronger activation to more complex stimulation (Tse et al., 2013). A recent review of neuroimaging data suggests activation of the supplementary motor area and premotor cortex during static balance control (standing), and activation of the supplementary motor area and sensorimotor cortex during dynamic balance tasks, (walking; Wittenberg, Thompson, Nam & Franz, 2017).

The processes underlying the stable posture of the child, adult, and atypical populations have been well researched. However, study of the earliest development has been limited, and we do not have a good understanding of what is happening when infants are being carried. Hadders-Algra (2005) documents the development of postural control through the first two years of life. She identifies a first critical change in infant postural control occurring at three months of age, when muscle activation becomes more specific rather than wide-spread, and a second critical change at six months when postural control can be adapted to changes in position, such as lying or sitting. At six months, infants are able to use trial-and-error to find the pattern of postural control that best stabilises their head in space. According to Hadders-Algra, throughout the first year infants are mainly engaging only in direction-specific adjustments, engaging the dorsal muscles during forward movements, and ventral muscles for backward movements: It is not considered that infants are making anticipatory postural adjustments until they are walking, in their second year of life. However, all of the above results are based on the study of infants moving independently, either static (seated or standing) or self-locomoting. More recently, it has been evidenced that from very early in development, infants make anticipatory postural adjustments to being picked up by the caregiver, during caregiver approach and point of contact (Reddy, Markova & Wallot, 2013). Infants seem to participate in being carried, using their arms or legs to grip their mother (Negayama, Kawai, Yamamoto, Tomiwa & Sakaihara, 2010). When infants are carried, in addition to a decrease in arousal as measured by heart rate, infants engage in active motor control (i.e. less flailing of limbs), with complementary evidence in mouse pups suggesting that an immobility response is separate from the cardiac arousal response, and functionally aids the mother's carrying (Esposito et al., 2013). This responsiveness to the mother's actions is seen as adaptive, supporting infant survival (Esposito, Setoh, Yoshida & Kuroda, 2015). Being unresponsive to the mother during carrying has even been characterised as a risk factor for developmental disorders such as Autistic Spectrum Disorders (ASD; Teitelbaum et al., 2004).

We do not know the details of how infants process the vestibular, proprioceptive, visual and auditory information they receive when carried; if the postural changes that make during carrying are compensatory or anticipatory; and how the timings of changes, at the least necessary to keep the head in a relatively stable position, may coincide with the timing of locomotion. However, whilst the caregiver may seemingly dictate the action, the evidence above at the least suggests that the infant is an active participant in carrying.

1.3.4 Summary

We argue that the human propensity to move to music, and the way in which we do so, may be linked to the fundamental behaviour of human locomotion. Specifically, we think that regular vestibular information, from self-produced locomotion and from being carried by the ambulating caregiver, may set rhythmic preferences, both in production and perception. Evidence considering the role of the vestibular system on rhythm perception, the upright human body structure, the common tempi of walking and music, and infant carrying have motivated our vestibular hypothesis. The current thesis aims to test several tenets of this idea using behavioural and neural measures with the developing human infant.

1.4 Statement of research questions

This thesis thus aims to explore the early development of infant musicality, testing how vestibular experience of locomotion may impact fundamental rhythm production skills of sensorimotor synchronisation and spontaneous motor tempo, in addition to how such experience may shape rhythm perception. The core research questions explored are as follows:

- Does infant SMS change with age over the first two years of life? Is infant performance related to the presence of a social partner, or, is the tempi of auditory stimulation, close or far from their natural rate of movement, important? (Chapter 2).
- Is infant SMS a function of their locomotive experience? Does novel bipedal walking experience improve SMS, and how is infant performance related to

existing locomotive experience? (Chapter 3).

- What is the SMT of young infants and how does this change with age? Are the rates of these rhythms that we naturally produce the product of our own biomachinery, or alternatively, can it be linked to the rate of walking cadence that we most experience? (Chapter 4).
- Can we experimentally manipulate infant SMT with novel walking experience? (Chapter 5) In addition to the effect on spontaneous behaviour, does this experience also effect the neural processing of auditory rhythm? (Chapter 6).

In the following chapter, we begin asking these questions with an experiment that attempts to scaffold infants' SMS abilities, and in doing so, documents for the first time, a transition from inflexibility to flexibility of rhythmic behaviour, in the first two years of life.

Chapter 2

The beginnings of sensorimotor synchronisation

2.1 Introduction

Tracking the development of movement to music in infancy provides a window into the perceptual and physical skills, experience and contexts necessary, for synchronizing movements to music. The current chapter will discuss the development over the first two years of life of two types of behavior commonly seen in response to music: (1) moving isochronously, or moving at a steady rate, and (2) moving synchronously, or moderating rhythmic behavior so that it coincides with an external auditory rhythm.

From an early age, infants hold many of the prerequisites for movement to music. They are able to detect violations of rhythms from birth (Winkler et al., 2009), and by seven-months-of-age they can process complicated variations in rhythmic structure (Trehub & Thorpe, 1989). A relationship between movement and music also appears around this age. For example, movement to a beat biases the perception of an ambiguous rhythm from seven-months-of-age (Phillips-Silver & Trainor, 2005), and cultural specificity in rhythm preference is accelerated if infants are subjected to movement training (Gerry, Faux & Trainor, 2010).

However, although the skills that underlie music (and especially rhythm) perception are in place very early on, infants do not seem to synchronize their movement to music spontaneously, despite spending up to 40% of their time performing repetitive movements (Thelen, 1979; 1981). Some evidence for very early sensorimotor synchronisation (SMS) comes from the study of non-nutritive sucking in neonates. Rhythmic sucking is observable in newborns at a rate of 1-

2 Hz (Wolff, 1968). Newborns and two-month-olds are able to accelerate sucking rate away from their spontaneous motor tempo (SMT) to better match a faster auditory rhythm, whilst only the two-month-olds tested were able to decelerate to match a slower auditory rhythm, with better overall synchronisation for acceleration than deceleration (Bobin-Begue et al., 2006). Whilst sucking is not directly perceivable by an observer, such synchrony may be perceivable by the mother during breast-feeding (Provasi et al., 2014). The closest evidence of infants' gross motor movements matching a beat comes from Zentner and Eerola (2010). Using motion capture technology these authors demonstrated that infants aged 5 to 24 months engage in more isochronous movement to music than to speech, and have a degree of tempo flexibility; i.e., infants spontaneously move faster to faster rhythms, and slower to slower rhythms. Zentner and Eerola’s work suggests a developmental progression from moving isochronously in response to music, as seen in their data, to moving synchronously with music, as commonly seen in adults.

Infants appear not to progress into moving truly synchronously with exogenous rhythms until the preschool years. In a tapping paradigm, children aged 3.5 years, but not 2.5 years, are able to move away from their spontaneous motor tempo (SMT) towards a track with 15 - 20% acceleration from baseline (though not towards a decceleration; Provasi & Bobin-Begue, 2008). However, there is evidence that 2.5 year-olds will modify their behavior to entrain a drumming movement with a significantly slower than natural inter-stimuli-interval (ISI), but *only* in the presence of a social partner (Kirschner & Tomasello, 2009).

This hints at how humans may transition from ‘feeling’ the beat of music, to moving to it: Moving to music might be inherently linked to moving together, or joint action, where individuals are motivated towards a higher-level process of reaching a common goal. The effect of a social partner is also in line with the idea of 'communicative musicality', or the idea that infants are sensitive to, and able to fine-tune, temporal responses of movement, affect and vocalisations, to engage in dialogue with the caregiver (Trevarthen, 2000). The interactions are bidrectional, used and prompted by both caregiver and infant, to create 'parent-infant synchrony', a sensitive, dyadic interaction shown to benefit social development (e.g. Feldman & Eidelman, 2007; Feldman 2007; Feldman et al., 2009; Feldman, 2012). This may extend to better interpersonal synchrony in childhood.

At the least, the facilitative effect of a social context seems intuitive. We move in synchrony with others unconsciously, even when it is not the most efficient action (Goodman et al., 2005). Adults (Chartrand & Bargh, 1999) and infants (Tuncgenc, Cohen & Fawcett, 2014) prefer those who mimic their movements. In the context of music, the desire to move together may go beyond physical mimicry, and may actually speak to the adaptive value of facilitating social cohesion; producing, hearing and performing to music may elicit a shared emotion in a group, which induces cooperation, a key skill for increased chance of survival (Trainor, 2010). Moving together, even when not initiated by the infant themselves, has been shown to increase pro-social behavior in 14-month-olds: Infants bounced to music in time with an experimenter were more helpful to that experimenter than if bounced out of time (Cirelli, Einarson & Trainor, 2014; Cirelli, Wan & Trainor, 2014).

However, an alternative explanation for how infants transition to moving synchronously with music to enhanced communication is that infants may ‘feel’ music in a qualitatively similar way to adults from very early on, but simply lack the motor skills to synchronize their movement (e.g. Zentner & Eerola, 2010). The finding that infant preference for rhythm is not culturally defined has led to the discussion of beat induction as a ‘spontaneously developing’ process, emphasizing a biological basis over a cultural, or learned basis (Honing, 2012). Furthermore, anthropometric features including height and leg length have been shown to correspond with preferred beat rate in adults, with longer limbs associated with a slower preferred beat (Mishima, 1965; Todd, Cousins & Lee, 2007; Dahl, Huron & Brod, 2014). Children have a faster SMT than adults; under-three-year-olds spontaneously tap at an inter-stimuli-interval (ISI) of around 400ms, whereas adults typically tap at an ISI of around 600ms (Provasi & Bobin-Begue, 2003). If rhythm production is tied into physical characteristics of the body, it is plausible to predict that infants’ natural rhythm is again faster than young children’s, and that infants will find it easier to synchronize when presented with musical stimuli of a faster than 400ms ISI.

The current study aims to test these two contrasting, though not mutually exclusive, accounts of the development of movement to music, through the adoption of a novel experimental procedure. Provasi and colleagues (2014) advise that a true understanding of the rhythmic capabilities of young infants can only be achieved if they are tested in the appropriate context, facilitating, rather than imposing adult testing constraints, on the infants' natural behaviour. In an attempt to do so, rather than measuring spontaneous gross motor movement, which has been shown to be asynchronous in infancy (Zentner & Eerola, 2009; Fujii et al., 2014), in the current study, infants are given small hand-held bells to ring. This provides auditory feedback from their movements, something essential for an ape synchronizing to a beat (Hattori et al., 2013). It also allows us to evaluate infant abilities on a movement that does not require advanced motor skill (unlike in the measurement of finger tapping, that requires a precise spatial location of the movement and fine motor control). Finally, it allows us to predict where on the body a movement will originate, enabling the accurate measurement of muscle activity in the arms using surface electromyography (EMG). By moving away from measurement of spontaneous movement to music, we are better able to see what infants are capable of doing when guided, in addition to the actions they spontaneously produce, when presented with music.

To evaluate the role a social partner in moving to the beat, infants take part in two conditions, a social condition in which they interact with a live social partner, and a non-social condition in which they are presented with a non-social visual animation. In accordance with Kirschner and Tomasello's (2009) finding with 2.5-year-olds, we hypothesize that infants' isochronous movements will be more accurate in the social condition than the non-social condition. To test if infants are better synchronisers at rates closer to their SMT, infants will be exposed to auditory tracks that vary by ISI from 300 ms (close to hypothesised infant SMT) to 600 ms (adult SMT), with the hypothesis that infant SMS will improve as it is closer to their SMT.

2.2 Method

2.2.1 Participants

Seventeen 10-month-olds (6 female; mean age= 302 days, range= 290 days to 317 days), and 27 18-month-olds (7 female; mean age= 555 days, range= 534 days to 615 days) took part in this study. Although we initially matched the infant groups by number of participants, 18-month-olds provided less data than 10-month-olds. We therefore recruited further 18-month-olds to match the number of data points across the groups. The results of our analyses are the same both with and without the additional 18-month-olds. All caregivers gave written, informed consent concerning the experimental procedure. Infants received a certificate and a t-shirt as a thank you for participation. Ten adults (8 female; mean age = 34 years, range = 22-60 years) also took part. Adults gave written, informed consent and received no recompense for participation.

2.2.2 Procedure

For infants, surface electromyography (EMG) was used to record the electrical activity of the right and left biceps brachii. Infants always experienced the familiarization trial first. The social and non-social conditions were then presented in a counter-balanced order.

Familiarization Trial. Infants were given two small hand-held sleigh bells and seated on a cushion on the floor adjacent to their caregiver. The experimenter sat opposite the infant, held a separate sleigh bell in each hand and demonstrated ringing the bells using a vertical up-and-down movement whilst singing. Infants were allowed to play freely with their bells for approximately 10 seconds. They were congratulated on playing, regardless of their behaviour during the trial. To familiarise the infants with the testing environment, a video screen approximately 100 cm from the infants was then switched on. Infants saw two cartoon stills alternating every 5 seconds for 45 seconds. Two speakers either side of the screen played the sound of running water concordantly. The sounds were intended to keep the infants' attention directed towards the screen (and away from the caregiver) during the trial, without providing an alternative rhythm.

Social Condition. Infants took part in four trials of 45 seconds each. Each trial used an abridged version of one of four naturalistic musical tracks, each of a different beat ISI (**300 ms**, Traffic Jam by Weird Al Yankovic; **350 ms**, Good Golly Miss Molly by Little Richard; **450 ms**, Let's Get Loud by Jennifer Lopez; and **600 ms**, Rock Your Body by Justin Timberlake), with the trial order randomised between infants and between conditions. In each trial, the experimenter played her sleigh bells using the vertical motion, in time with the underlying beat of the track being played through the speakers (i.e., at the corresponding ISI). Infants were engaged in eye contact and smiles by the experimenter, regardless of their behaviour, remaining unconstrained and allowed to move freely. Between each trial infants were given a short (approximately 10 second) break during which they were congratulated on taking part; if they dropped or rejected their bells during the trial these were returned before the beginning of the next trial. If infants stood up and/or moved around the room during the trial, they were returned to their seated position.

Non-social Condition. In the non-social condition infants heard the same four tracks across four trials, for 45 seconds per trial, in a randomized order. In this condition the experimenter moved out of sight, behind a curtain, and the video screen was turned on. For each trial, the infants saw an animation on the screen of two sleigh bells moving in a vertical up-and-down motion against a plain black background, in time with the track being played. Again, between trials infants were congratulated on taking part.

The adult protocol was identical to the infant protocol, without the familiarization condition. Adults were instead given the following instructions:
'You're going to hear two sets of four songs, and I'd like you to play your bells with the music. For one set of four, you will also see and hear me playing my bells with the song. For the other set, you will see and hear an animation of bells on the screen ahead of you.'

2.2.3 Apparatus

EMG data were collected using four bipolar pediatric surface electrodes (3M monitoring electrodes with micropore tape and solid gel) and the Myon 320 wireless EMG system, at a sampling rate of 4000 Hz. Animations for the baseline and non-social conditions were presented on a video screen using Matlab R2009b (Mathworks Ltd.). Simultaneous video recording of the testing session was conducted using a Logitech HD 1080p webcam positioned on top of the screen. See Figure 2.1 for a visual representation of testing set up.

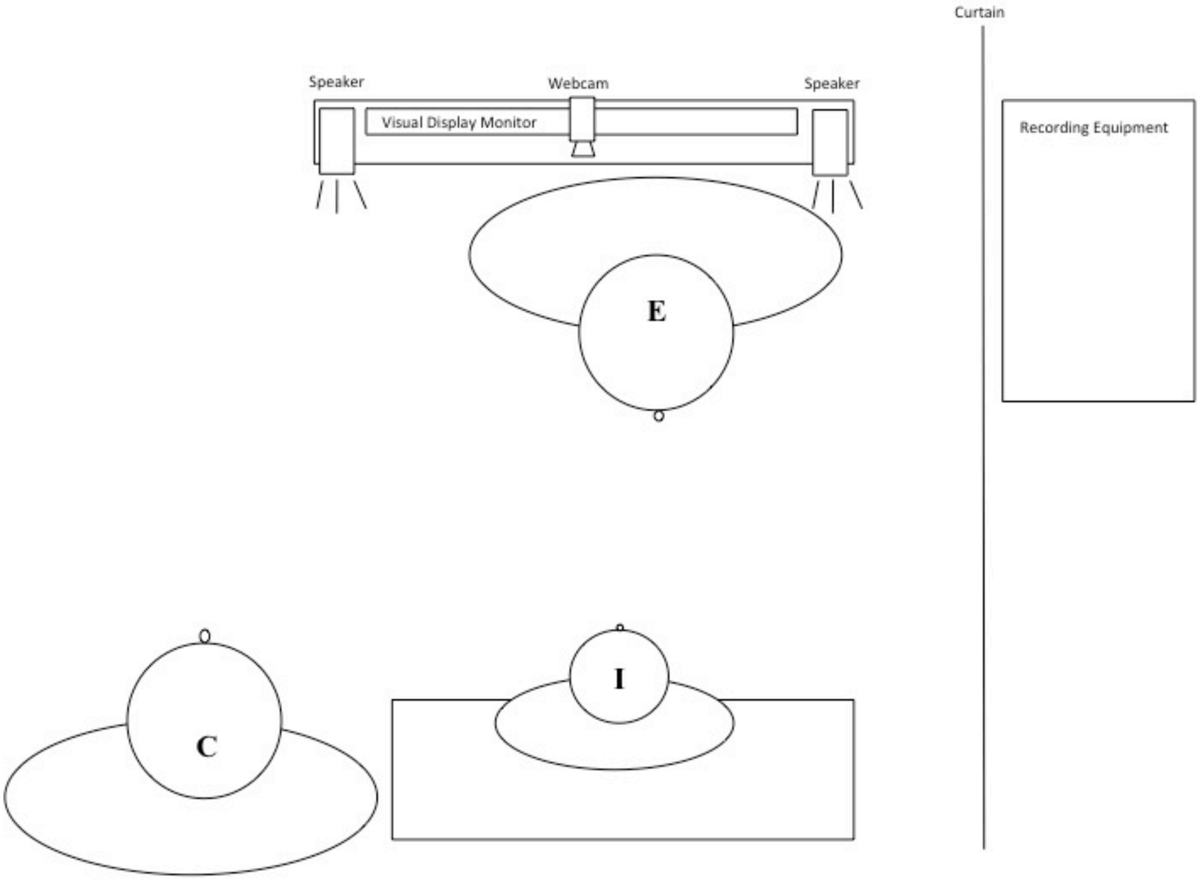

Figure 2.1 Schematic representation of the experimental scene in the social condition. E: Experimenter; C: Caregiver; I: Infant. The experimenter is not present in the non-social condition.

2.2.4 Data Processing

Video recordings of the testing session were coded for all incidences of infant motor activity (see Table 2.1 for a summary of behaviors included). To be categorized as potentially rhythmic, infants had to make two or more of each movement; i.e., we coded for repetitive movements. Incidences in which infants made only a single bounce or kick did not meet the criterion. Although we identified bouts of potentially rhythmic activity, no judgments about the relative timing of the movements were made at this stage of the analysis. Behaviors were excluded if the infant was in physical contact with the caregiver and the caregiver was moving, or if the infant performed repetitive movements in order to locomote (i.e. incidences of crawling and walking). An independent researcher double coded the video data for ten infants. The single measure ICC for duration of ringing behavior was .854, with a 95% confidence interval from .770 to .908, ($F(2,63)=12.658$, $p < .001$). For duration of other repetitive movements the ICC was .966, with a 95% confidence interval from .945 to .979, ($F(2,63)=57.826$, $p < .001$).

Table 2.1 Behavioral Coding Scheme

Behaviour	Criteria
Ringing	Vertical or horizontal arm movements on a single plane, with or without bells
Bouncing	***Either*** contracts and lengthens torso, ***or*** in standing position only, bounces up and down by bending and straightening knees
Kicking	Moves leg on a single plane in any direction, without placing or transferring weight
Rocking/Swaying	Moves torso left to right or forward and backward, does not include up and down motion
Nodding	Moves head on a single plane in any direction

The EMG data were analyzed using the stand-alone ProEMG software

(ProPhysics). Data were rectified and high-pass filtered at 400 Hz, low-pass filtered at 10 Hz and notch filtered at 50Hz. Infant EMG data were then segmented into corresponding periods of ‘shaking behavior’ as defined by the video coding. A researcher blind to trial type and the ISI of the track, hand-coded the onset of each burst of activity from the corresponding EMG channel traces for right or left biceps during the ‘ringing’ period by taking the first peak of each burst with processed amplitude at or above 1 volt (see Figure 2.2). If data were so noisy that no burst was visible, they were discarded. Distances between burst onsets were then calculated in milliseconds to give an inter-ring-interval (IRI). Adult data were processed in the same way, except that as adults rang their bells continuously through each trial, three-second periods (roughly the mean length of an infant segment) of clean data were pseudo-randomly selected from within the trial for analysis. The difference between the IRI for each bout of ringing and the target ISI of the track was calculated to give a tempo mismatch index for each trial. Accordingly, in the results described below, a lower score reflects less difference from the target ISI. A pseudo-randomly selected subset of 10 infants were double coded by an independent researcher. The single measure ICC was .899, with a 95% confidence interval from .793 to .953, (F(2,26)=18.621, p<.001).

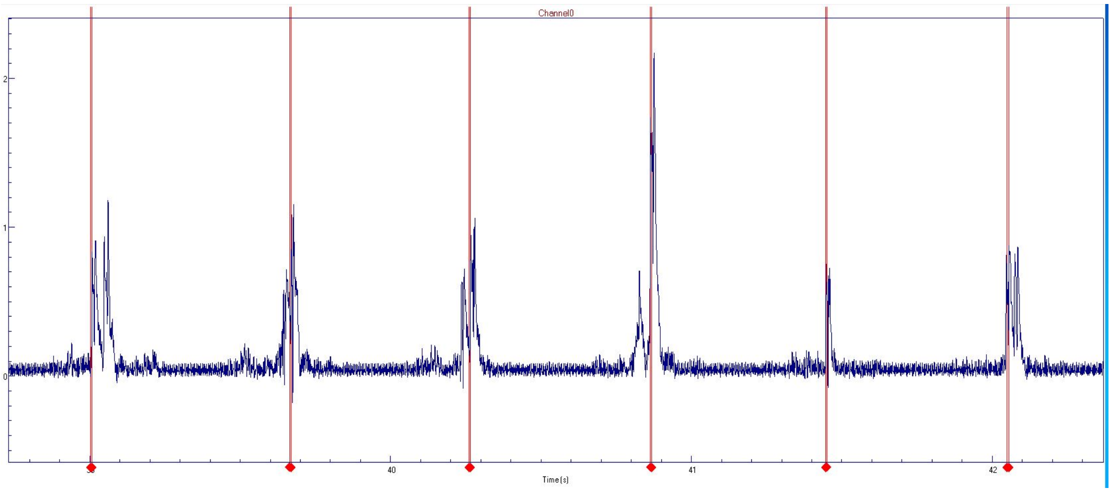

Figure 2.2 A typical trace of bicep electrode in an adult participant. The y-axis is in microvolts and the x-axis is in milliseconds. Vertical lines indicate the event markers for burst onset as hand-coded by the experimenter.

2.3 Results

2.3.1 EMG Data

A univariate ANOVA with Tempo-Mismatch as the dependent variable, and Age Group (10-months, 18-months, and adult), Social/Non-Social Condition and Target ISI (300, 350, 450 and 600ms) as fixed factors, revealed significant main effects of Age (10-months *M* = .206, *SE* =. 016 , 95% CI (.175, .237); 18-months *M* = .196, *SE* = .015, 95% CI (.166, .225); adult *M* = .024, *SE* = .013, 95% CI (.000, .049); (F(2,194)=55.973, *p* < .001)) and Target ISI (300ms *M* = .099, *SE* = .016, 95% CI (.085, .151); 350ms *M* = .118, *SE* = .017, 95% CI (.085, .151); 450ms *M* = .131, *SE* = .018, 95% CI (.096, .165), 600ms *M* = .220, *SE*=.017, 95% CI (.187, .252); (F(3,194) = 10.326, *p* < .001)), with a significant Age*Target ISI interaction (F(6,194) = 3.758, *p* < .001). We found no main effect of

Social/Non-Social Condition (Non-Social *M* = .148, *SE* = .013, 95% CI (.123, .173); Social *M* = .135, *SE* = .011, 95% CI (.114, .157); (F(1,194) = .597, *p* = .441)), and no other interactions. The mean ISI for each age group to each musical track is presented in Table 2.2.

Table 2.2 ISI of bell-ringing in seconds, for each age group at each target ISI

ISI	Age Group	N	ISI Mean (s)	ISI SD
300ms	10-months	26	.280	.155
	18-months	27	.389	.245
	Adults	20	.284	.037
350ms	10-months	32	.294	.107
	18-months	21	.371	.259
	Adults	20	.346	.027
450ms	10-months	20	.264	.141
	18-months	20	.383	.193
	Adults	20	.451	.055
600ms	10-months	26	.275	.227
	18-months	18	.418	.218
	Adults	20	.586	.040

Planned comparisons revealed that the main effect of Age was driven by the adult group being closer to target tempo than both infant groups (both *p* < .001), with no difference between the 10- and 18-month-olds (*p* = .647). The main effect of Target ISI was driven by significantly higher mismatch in the 600ms condition than the three faster tracks (all *p* < .001), with no other differences between tracks (all *p* > .192). Figure 2.3 illustrates the tempo-mismatch for each age group at each target ISI.

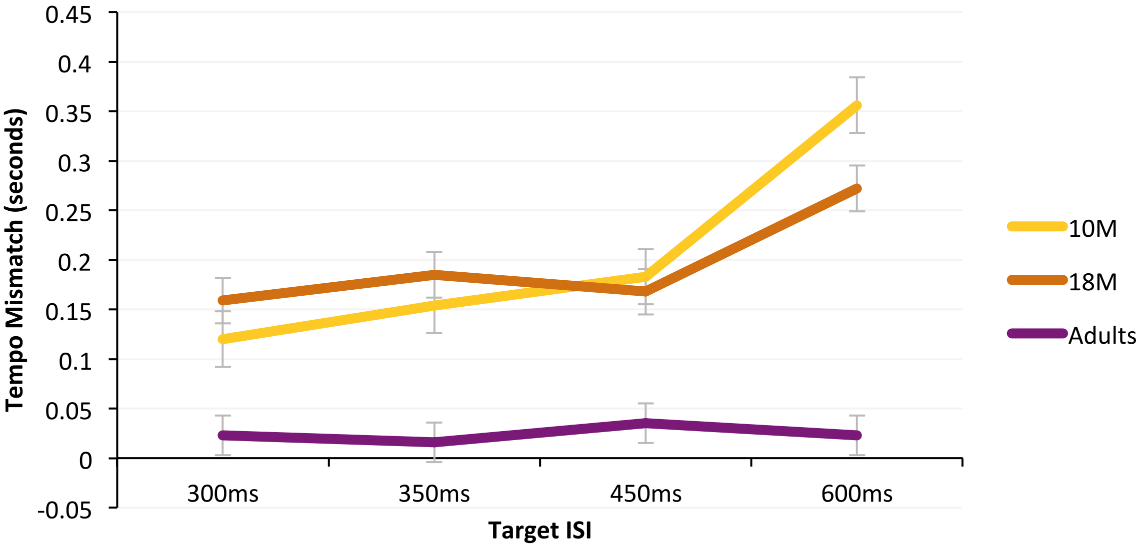

Figure 2.3 Mean tempo-mismatch scores in seconds for each age group at each of the target ISIs. 10- and 18-month-old performance is similar for all target ISIs except the slowest 600 ms condition.

The significant Age*Target ISI interaction was further explored using a one-way ANOVA with Tempo-Mismatch as the dependent variable and Age group as a factor, at each of the four target beat frequencies. All four ANOVAs confirmed the significant effect of Age (300ms, F(2,51) = 9.370, *p* < .001; 350ms, F(2,48) = 6.494, *p* = .003; 450 ms F(2,46) = 10.847, *p* < .001; 600 ms F(2,48) = 67.752, *p* <. 001; see Table 2.3 for full descriptive statistics). Planned pairwise comparisons revealed that adults were significantly better than the two infant groups at all target frequencies (all *p* < .01), but that the 10- and 18-month-olds did not differ from each other in the three fastest conditions (300 ms, *p* = .286; 350 ms, *p* = .572; 450 ms, *p* = .706). However, in the slowest 600 ms condition, the comparisons confirmed a developmental progression whereby the 18-month-olds were significantly closer to the target tempo than the 10-month-olds, (*p* = .014), and adults were significantly better than both infant groups (all *p* < .001).

Table 2.3 Tempo mismatch scores for each age group at each target ISI

ISI	Age Group	N	Tempo Mismatch Mean	Tempo Mismatch SE	95 % CI	
300ms	10-months	26	.115	.026	.063	.166
	18-months	27	.177	.025	.126	.228
	Adults	20	.023	.030	-.036	.082
350ms	10-months	32	.142	.023	.097	.187
	18-months	21	.146	.028	.090	.201
	Adults	20	.016	.029	-.041	.074
450ms	10-months	20	.201	.023	.154	.248
	18-months	20	.153	.023	.107	.200
	Adults	20	.035	.023	-.012	.082
600ms	10-months	26	.373	.020	.333	.412
	18-months	18	.261	.024	.213	.309
	Adults	20	.023	.023	-.022	.069

Note: Tempo mismatch scores refer to the difference between observed values and the target ISI. Each bout of ringing is treated independently. The number of bouts differs by age group. If bouts are pooled per subject, the results remain the same.

Despite the initial ANOVA showing no overall difference in tempo matching between the two infant groups, we were interested in whether the developmental shift in the slow 600ms condition reflects an overall ability to modulate movement to music in the 18-month-olds (and lack thereof in the 10-month-olds). We reasoned that if participants were modulating their movement, they should be equally accurate across the different beat frequencies. We conducted a univariate ANOVA at each age group, with Tempo-Mismatch as the dependent variable and Target ISI as a fixed factor. We did not find a main effect of ISI for the adults (F(3,80) = .990, *p* = . 402), who performed highly accurately across tracks, or the 18-month-olds (F(3,57) = 1.275, *p* = .292), who performed with the same degree of tempo-matching across tracks. However, in the 10-month-old age group, we found a significant main effect of Target ISI (F(3,55) = 16.997, *p* < .001). As shown in Table 2.3, the youngest infants were closer to the target in the faster tracks, which are closer to hypothesized infant SMT, and further from the targets in the slower tracks.

The results suggest that the 10-month-olds did not modulate their rate of bell ringing to the music. They were further from the target tempo when the music was slower than their hypothesized SMT. There was no impact of a social partner on their tempo-matching. The 18-month-olds did show some tempo-flexibility: they were equally proficient in all four ISI conditions. A developmental progression from 10- to 18-months of age is evidenced in a lower mismatch in the 18-month-olds in the slow 600 ms ISI condition, compared to the 10-month-olds. However, even these older infants were not synchronizing at an adult-like level. As with the younger age group, there was no impact of a social partner on the tempo-matching of the 18-month-olds.

2.3.2 Behavioral Data

Although we were only able to test the tempo-matching of one of our repetitive behaviors of interest (ringing), as piloting revealed infants would not reliably tolerate wearing more than two wireless EMG sensors, we also used the video data to calculate the amount of time infants spent in potentially rhythmic movement (see Table 2.1 for a full list).

At 10-months-of-age, a univariate ANOVA with time spent ringing bells as the dependent variable and Social/Non-social Condition and Target ISI as fixed factors revealed no difference in time spent ringing between the social condition (*M* = 7.729, *SE* = 1.187, 95% CI (5.360 10.097)) and the non-social condition (*M* = 9.886, *SE* = 1.385, 95% CI (7.123 12.648); F(1,76) = 1.399, *p* = .241), and no effect of target ISI (300 ms *M* = 10.446, *SE* = 1.766, 95% CI (6.922 13.969); 350 ms *M* = 10.972, *SE* = 1.900, 95% CI (7.182 14.762); 450 ms *M* = 7.585, *SE* = 1.869, 95% CI (3.857 11.313); 600 ms *M* = 6.226, *SE* = 1.757, 95% CI (2.721 9.732); F(3,76) = 1.580, *p* = .202). Similarly, a univariate ANOVA with time spent in non-ringing repetitive behaviors as the dependent variable also showed no difference between the social and non-social conditions (Social *M* = 9.086, *SE* =

2.871, 95% CI (3.251 14.920), Non-social *M* = 13.394, *SE* = 2.816, 95% CI (7.670 19.117); F(1,41) = 1.147, *p* = .292) or between target ISIs (300 ms *M* = 8.605, *SE* = 3.721, 95% CI (1.044 16.166); 350 ms *M* = 11.811, *SE* = 4.102, 95% CI (3.475 20.146); 450 ms *M* = 12.190, *SE* = 3.983, 95% CI (4.096 20.284); 600 ms *M* = 12.353, *SE* = 3.983, 95% CI (3.691 21.015); F(3,41) = .241, *p* = .886)

At 18-months-of-age we see a different pattern of behaviour. Though a univariate ANOVA with time spent ringing as the dependent variable and Condition and Target ISI as fixed factors also showed no difference between conditions (Social *M* = 5.600, *SE* = .986, 95% CI (3.640 7.559); Non-social *M* = 5.179, *SE* = 1.029, 95% CI (3.136 7.222); F(1,99) = .087, *p* = .786) or target ISI (300 ms *M* = 6.018, *SE* = 1.424, 95% CI (3.190 8.845); 350 ms *M* = 6.021, *SE* = 1.424, 95% CI (3.193 8.849); 450 ms *M* = 5.047, *SE* = 1.395, 95% CI (2.276 7.817); 600 ms *M* = 4.472, *SE* = 1.457, 95% CI (1.578 7.366); F(3,99) = .283, *p* = .838), a univariate ANOVA with time spent in other repetitive behaviours revealed that at 18 months of age, infants engaged in *non-ringing* repetitive actions for significantly longer in the absence (non-social *M* = 3.880, *SE* = .828, 95% CI (2.228 5.531)) than the presence (social *M* = .916, *SE* = .896, 95% CI (-.871 2.703)) of a social partner (F(1,79) = 5.896, *p* =.018). Again, there was no effect of track (300 ms *M* = 2.340, *SE* = 1.217, 95% CI (-.087 4.767); 350 ms *M* = 2.287, *SE* = 1.183, 95% CI (-.073 4.646); 450 ms *M* = 3.179, *SE* = 1.236, 95% CI (.714 5.643); 600 ms *M* = 1.785, *SE* = 1.244, 95% CI (-.695 4.266); F(3,79) = .217, *p* = .884)).

2.4 Discussion

Our results revealed a developmental progression in the ability to move in time with music. Whilst 10-month-olds did display ringing behaviour, they were not able to adapt this movement to the beat. At 18 months, infants demonstrated a degree of tempo-flexibility, modulating their movement: In contrast to the 10-month-olds, they matched the tempo equally across all four tracks. Though the 18-month-olds did not match better than the 10-month-olds overall, they performed significantly better in the slowest 600ms condition, the condition furthest from infants hypothesised SMT. This suggests that the 18-month-olds, but not the 10-month-olds, were able to move away from their natural rate of movement, and is consistent with independent findings of deceleration being harder than acceleration in the developing child (Provasi & Bobin-Begue, 2003; Bobin-Begue & Provasi, 2008). However, this ability clearly continues to develop past 18 months, as even when showing tempo-flexibility, infants were not matching their movement at an adult level. We should note that this progression is in contrast to Zentner & Eerola's (2010) finding, of no effect of age on tempo-flexibility in 5-24 month-olds. There are several possible explanations for this. For one, Zentner and Eerola measured infants' spontaneous movement. The current study effectively engaged infants in a task of bell ringing. It may be that the presence of a partner (social or not) impacted younger infants' timing abilities, perhaps acting as a distracter from the music played. However, Zentner and Eerola also studied isochronous movement across the whole body and across almost the entire period of infancy. It may therefore be possible that the enormous advance in motor control seen between five and 24 months of age led to high heterogeneous variability in their data set, which may have masked age interactions. In the current study, we investigated infant abilities in a bell-ringing task, requiring a shaking motion that is well within the motoric competencies of both infant age groups. Perhaps we were better able to detect developmental change because our task was more constrained.

Our choice of design was motivated by a desire to facilitate infant synchrony, through the provision of visual, auditory and social cues; in particular we anticipated that the presence of a social partner would be advantageous for synchrony, in light of Kirschner and Tomasello's (2009) findings with young children. However, contrary to our hypothesis, we found no difference in tempo matching in any age group between the social and non-social conditions. Kirschner and Tomasello referred to this advantage in their work as the product of joint action; they argue that when drumming with a human partner, young children are motivated by the relatively higher-level process of reaching a common goal. It may be that the infants in our experiment were too young to understand or act upon these motivations. However, studies show many of the prerequisites for joint action are apparent early in the first year of life (for a review see Carpenter, 2009), with active engagement in joint tasks appearing between 12 to 18 months (see Sebanz, Bekkering & Knoblich, 2006). If understanding of joint action were crucial for synchronous movement to music, and this understanding shows considerable advancement between 12 and 18 months, we could therefore expect an interaction between the social and non-social conditions of the study and the age of the 10-month-olds and 18-month-olds tested.

Although we are only able to test the temporal matching of one action, bell ringing to music, we also recorded the duration of other repetitive motor actions during the testing session. Both infant groups displayed spontaneous repetitive behaviours. Whilst 10-month-olds showed no difference in amount of non-ringing repetitive behaviour dependent on social/non-social condition, the 18-month-olds displayed significantly more spontaneous repetitive movement in the non-social condition. One possible explanation is that the 18-month-olds were more aware of a joint goal of ringing together, and inhibited other, perhaps more ecological movements, such as bouncing or nodding the head, when attempting to participate in joint ringing. According to this interpretation, the 18-month-olds understood the joint goal of ringing together, but this did not translate to better temporal matching of movement to music. Further, we cannot ignore the fact that tempo-matching did indeed improve from 10 months to 18 months, at least in the difficult 600ms condition. That this improvement seems independent of the presence or absence of a social partner suggests a distinction between '*moving together*' and '*moving to the beat'*, which may have separate underlying trajectories. Though they seem concurrent skills in the history of dance (Trainor, 2010) they may actually reflect separate developmental processes, with different historical adaptive advantages.

If we are thus wary of explaining the improvement in infant's temporal matching of movement to music as a product of better interpersonal coordination, it is interesting to consider what may explain the change between 10- and 18-

months-of-age. The lowest level explanation is that infants' motor skills will have seen a dramatic improvement over these eight months. Perhaps, the 18-month-olds are better able to modulate their movement to music simply because they have better control over their movement in general. Research with young children relates synchronisation to fine motor skill, speed of processing and inhibitory control (Provasi et al., 2014). However, the current data also fit with a more complex picture of movement to music interacting with rhythmic experiences of locomotion, as discussed in Chapter One.

Humans' optimal tempo to perceive is between 300-900ms, which is similar to the tempo of human gait (Trainor, 2007). Most music also falls within this category. When we consider individual differences, we see that limb length corresponds with preferred beat rate, both when perceiving a rhythm (Todd, Cousins & Lee, 2007) and when moving rhythmically (Dahl, Huron & Brod, 2014). Further, Trevarthen (2000) proposes that humans' ability to move in time to music is based in bipedal locomotion, in that our upright stance with flexibility of complex movements across the body provides our multi-jointed highly stacked bodies with the need to coordinate a multiplicity of rhythmic acts at any one time in order to locomote whilst also twisting, turning or isolating our free limbs. Anthropological data show that societies where infants are frequently held produce more music with a regular rhythm than those where infants are predominantly kept in baskets or cradles (Ayres, 1973). Most Western infants do not walk independently until after their first birthday (Storvold, Aarethun & Grete, 2013). It may be that the developmental progression seen in the current study reflects the infants’ experience of self-locomoting. Future studies should test the function of experience of bipedal locomotion directly.

2.5 Summary

In the current chapter, we show a developmental progression in infants’ ability to move with music when given a simple bell ringing to music task. Ten-month-olds are capable of ringing bells when presented with music, but are unable to modulate this movement to match the beat of the music played. Eighteen-month-olds are able to modulate their rhythmic movement, but not to an adult level of synchronisation. Further, we find that a social partner does not improve temporal coordination of movement to music, although in older infants it may impact the extent to which they deviate from the task. Rather, it seems that the tempo ISI of the auditory stimulus is critical in predicting infant performance over the first years of life, with locomotive experience hypothesised as a potential factor influencing infant ability. The following chapter tests this idea.

Chapter 3

How experience of locomotion influences sensorimotor synchronisation

3.1 Introduction

In the previous chapter (Chapter 2), we show that infant ability to match the beat of an external auditory rhythm improves between 10 and 18 months of age. Whilst 18-month-olds showed tempo flexibility, able to slow down their movement in the presence of slower ISI auditory tracks, the 10-month-olds were not able to modulate their rate of movement, ringing at a consistent tempo regardless of the auditory presentation. In Chapter 1, we put forward the hypothesis that bipedal locomotion, with its unique combination of sensory inputs, may be the particular human behaviour that facilitates our proclivity to move at the timing of music. One of the distinctive utilities of developmental work, especially with young infants, is the ability to introduce new but naturalistic behaviours to the participants' repertoire, and analyse the impact of this new experience on other functions. The current chapter therefore asks if giving novel locomotive experience to non-walking 10-month-olds results in the improved ability to shift away from natural tempo to match an auditory beat. First, we outline the normal developmental course of locomotion, highlighting how even early experience of locomotion may be altering processes relevant to sensorimotor synchronisation, before more broadly considering how the onset of locomotion may engender the further development of rhythmic skill, as an epigenetic event.

3.1.1 The normal trajectory of infant walking

In the following section we consider the developmental time course of human walking from primitive stepping to mature bipedal locomotion, arguing that the critical change in infant ability lies in their control of sensory inputs, which may lead to better SMS. The developmental time course through the first years of life is particularly interesting because of its ‘U-shaped’ curve. It has been well documented that very early in post-natal development, infants display a stepping reflex (McGraw, 1940). When their weight is supported by an adult, newborns will ‘step’, alternating legs, both when making contact with a surface or when held in the air. Training infants to preserve the newborn stepping reflex is possible through repeated, short, parent-led interventions (Zelazo, Zelazo & Kolb, 1972). Administering supported stepping exercises to infants from two to eight weeks old results in a higher stepping rate at week eight than in active and passive control groups; quality as well as quantity of walking is rated as higher, and earlier onset of independent walking is later reported by the caregiver, compared to both control groups and population norms (Zelazo et al., 1972). These findings led Zelazo and colleagues to suggest that newborn reflexive walking is one of a set of abilities that contribute to later independent walking. In the absence of early training, neonatal stepping is not normally observed after eight weeks of age (Zelazo et al., 1972).

Work by Esther Thelen may shed insight into the disappearance of reflexive stepping early in development and the much later onset of independent walking. Thelen & Fisher (1982) used EMG to measure muscle activation during young infants’ stepping and kicking, and found activation of the same muscle groups for the two actions. The authors speculate that kicking may replace early stepping due to increased body mass and postural changes, in a theory often described as the ‘heavy legs’ hypothesis. This view was supported by later studies that show that infants demonstrate more walking when they are submerged in water, which alleviates some of the pull of gravity, and less if they are weighed down (Thelen, Fisher & Ridley-Johnson, 2002). Supporting the weight of older, seven month old infants over a motorised treadmill will also elicit alternating steps (Thelen, 1986). Other work suggests that infant stepping disappears not because the legs become too heavy to lift, but because of a tendency to collapse the legs when making contact with a surface, due to a lack of strength to support the body from the legs (Barbu-Roth et al., 2015; Anderson et al., 2016). Under both accounts the basic motorics of locomotion are in place early, and when truly independent walking occurs months later in development, it is not only due to the increased strength and changed body proportions of the infant (to less chubby; see also Adolph, Bertenthal, Boker, Goldfield & Gibson, 1997), but also the ability to *integrate* the rhythmic walking with the control of posture and balance (Thelen, 1983; Anderson et al., 2016).

The ontogeny of human locomotion does not seem to be a special case, but follows the pattern seen in other complex human behaviours, such as language, with some skills in place early, even prenatally, but a protracted developmental course to gain adult-like skill. Time from conception to independent walking is linearly related to brain mass across mammals, with the implication that the more complex demands of our distinctive bipedalism - balance, coordination and orientation - in addition to locomotion, require the more mature human brain (Garwicz, Christensson & Psouni, 2009).

Independent locomotion in humans occurs from around one year of age (Storvold et al., 2013). Infant's independent walking is highly variable (Lacquaniti, Ivaneko & Zago, 2012). Infants have to learn the adult pendulum gait, and at first step with a wide stance, taking short steps with a high foot lift (Ivanenko, Dominici & Lacquaniti, 2007). Once the infant overcomes problems in posture and balance, the muscle activity during toddlers' independent walking is considered widely similar to adult walking (Okamoto, Okamoto & Andrew, 2003), and induced treadmill stepping in pre-walking infants shows the same gross motor activity as in adult walking (Yang, Stephens & Vishram, 1998). Critically, whilst other species may have a greater reliance on spinal pattern generators, the motor cortex involvement seen in adults is likely similar in infants from early onset, as measured by similar responses to perturbations (Yang & Gorassini, 2006). As the child grows taller, step length increases and step cadence decreases, from the rapid 176 BPM mean rate of one-year-old walking infants to the adult rate of approximately 120 BPM (Sutherland, 1997).

Improvements in walking are generally fastest in the time immediately after walking onset than in subsequent months (Adolph, Vereijken & Shrout, 2003). For example, vestibular stimulation from head movements produced by walking needs to be minimised for smooth locomotion, and in healthy adults, the head is therefore stabilised in space through compensatory movement in phase with stepping (Pozzo, Berthoz, Lefort & Vitte, 1991). In infants, the sensitivity of otolith responses change rapidly at the same time as the onset of the first steps (Weiner- Vacher, Ledebt & Bril, 1996), and head and trunk stabilisation changes dramatically in the first 15 weeks of walking (Ledebt, Bril & Wiener-Vacher, 1995), though months of experience are necessary for full compensation of the head (Bril & Ledebt, 1998). Walking practice is the largest indicator of walking skill, above the effects of body dimensions or chronological age (Adolph et al., 2003). Bipedal locomotion is not fully matured until around the age of seven years (Bril & Brenière, 1992). Importantly, when taken together the above research highlights that the maturation of walking is not concerned with the basic stepping mechanism, but rather, with the complexity of dealing with sensory inputs and balance control. It is this process of development that we believe may be related to infant rhythmic abilities.

3.1.2 The importance of learning to walk

Beyond the direct neural and motoric consequences of acquiring locomotion, Bertenthal, Campos & Kermoian (1994) emphasise how the early, self-produced experiences of infants, particularly locomotion, can lead to more mature performance on diverse tasks, such as spatial search or wariness of heights. According to the authors, behaviours such as locomotion are not only products of development but also the process by which further development occurs. Self-produced locomotion (especially the onset of crawling) is viewed as particularly important as a 'setting event', or point of epigenesis (Gottlieb, 1983). Above and beyond the development of the skill itself are the new experiences it provides, and the resultant impact on related systems (Bertenthal, Campos & Barrett, 1984). In a review of the impact of locomotion on other aspects of development, Anderson and colleagues stress that the effect of locomotion can be threefold: to induce completely dependent changes; to facilitate changes that would happen anyway, and to maintain changes that have already taken place (Anderson et al., 2013). We ask if bipedal locomotion may set up the human infant for more complex behaviours relevant to sensorimotor synchronisation, inducing or facilitating rhythmic skill.

It certainly seems that the experience of independent walking may engender skills requisite for rhythm production. Improvement in postural control, even the transition to sitting unsupported, helps provide a stable base of support that is critical to the efficacy of motivated manual actions, such as reaching (Bertenthal & von Hofsten, 1998). The balance required for maintaining posture during locomotion may similarly support more complex volitional musical action: Before infants attempt their first steps, they have no need for the control required for dynamic bipedal movements necessary for walking, and this necessitates a dramatic learning period (Bril & Brenière, 1992). The initial three to six months from onset of locomotion are spent mastering the control of different independent elements of walking (Bril & Brenière, 1992), and this ability to integrate motor, visual, and vestibular information in a dynamic way may be necessary for sensorimotor synchronisation. In particular, the large periods of time spent on only one leg during the act of walking may lead to an enhanced ability to utilise sensory feedback during bipedal locomotion compared to quadrupedal locomotion (Nielsen, 2003), which may translate to sensorimotor efficacy across domains.

Trevarthen (2000) conceptualises human's unique rhythm skills as reflective of our unique bipedal locomotion, with multiple degrees of freedom. Whilst early postural control over the many degrees of freedom involved in bipedal standing can be achieved by 'freezing', attained through sustained muscle contractions (e.g. Sveistrup & Woollacott, 1996), to successfully navigate the environment, infants need to be able to adapt and utilise these degrees of freedom (Metcalfe & Clark, 2000). Metcalfe and Clark (2000) argue that experience of walking allows exploration of the body and environment, which strengthen perception-action relationships, in order to facilitate the integration of external sensory inputs and internal bodily functions. Accordingly, experience of bipedal locomotion may in such a way be a ’setting event’ for the complex task of sensorimotor synchronisation.

3.1.3 Aims and Hypotheses

The current study aims to assess whether direct experience of walking improves infants’ abilities to move in time with music. We ask if the special combination of information that we receive from walking upright, and the multisensory integration that it requires, lays the foundation for SMS. Pre-walking infants were tested on their ability to ring bells in time with music, pre and post walking training on an infant treadmill. Parent-report measures of infant gross motor skill and time spent in motoric activities were collected. We predict improved tempo matching to music in infants at post-test, especially to songs with a slow inter-stimuli-interval (ISI), because slow songs require greater modulation from an infant’s hypothesised natural rate of movement. Though the infants tested cannot walk independently, we further ask if existing experience of locomotion at time of testing, both self-driven (through crawling or cruising) and other-driven (through carrying), predict infant tempo-matching.

3.2 Method

3.2.1 Participants

Thirty-five pre-walking 10-month-olds (22 female, mean age = 302 days, range = 276 - 329 days) took part in this study. Of these, seven infants were excluded due to refusal to be positioned over the treadmill (*N* = 3) or not providing any EMG data (*N* = 4). All parents gave written, informed consent concerning the experimental procedure. Infants received a certificate and a t-shirt as a thank you for participation.

3.2.2 Procedure

Infant tempo-matching was tested through the recording of the electrical activity of the infant's right and left biceps brachii. Infants experienced a pre- and post-test bell ringing to music task, always experiencing the familiarisation condition first, and then a counterbalanced presentation of tracks that vary by ISI. Between pre- and post-test, infants took part in a five-minute training session of supported walking on an infant treadmill. Conditions are detailed below, and pre- and post-test measures match the Social Condition documented in Chapter 2. Parents completed a questionnaire at the end of testing.

Familiarisation Condition. Infants were given two small hand-held sleigh bells and seated on a cushion on the floor adjacent to their caregiver. The experimenter sat opposite the infant, held a separate sleigh bell in each hand and demonstrated ringing the bells using a vertical up-and-down movement whilst singing. Infants were allowed to play freely with their bells for approximately 10 seconds. They were congratulated on playing, regardless of their behavior during the trial. To familiarise the infants with the testing environment, a video screen approximately 100cm from the infants was then switched on. Infants saw two cartoon stills alternating every 5 seconds for 45 seconds. Two speakers either side of the screen played the sound of running water concordantly. The sounds were intended to keep the infants' attention directed towards the screen (and away from the caregiver) during the trial, without providing an alternative rhythm.

Pre- and Post-test. Infants took part in four trials of 45 seconds each. In each trial the experimenter played her sleigh bells using a vertical motion, in time with the underlying beat of the track being played through the speakers (i.e. at the corresponding ISI). Infants were engaged in eye contact and smiles by the experimenter, regardless of their behaviour, remaining unconstrained and allowed to move freely. Between each trial infants were given a short (approximately 10 second) break where they were congratulated on taking part; if they dropped or rejected their bells during the trial these were returned before the beginning of the next trial. If infants stood up and/or moved around the room during the trial, they were returned to their seated position.

Each trial used an abridged version of one of four naturalistic musical tracks, each of a different beat ISI (**300 ms**, Traffic Jam by Weird Al Yankovic; **350 ms**, Good Golly Miss Molly by Little Richard; **450 ms**, Let's Get Loud by Jennifer Lopez; and **600 ms**, Rock Your Body by Justin Timberlake). The order of the songs was counterbalanced across participants and across pre- and post-test presentations.

Walking on a fixed speed treadmill. Infants spent five minutes being supported by the experimenter whilst using an infant treadmill (Figure 3.1). The experimenter knelt behind the infant, supporting the infants weight from their torso/ under the arms. If infants happily supported their own weight, the experimenter remained in this position but may have held the infant by their hands, from above. The caregiver and an assistant spoke to the infant, blew bubbles, and otherwise ensured that the infant was happy to continue.

Figure 3.1 Participant walking on the infant treadmill with support from the experimenter

Questionnaire measure. Caregivers completed a questionnaire method detailing infants' gross motor milestone achievements (age of sitting unsupported, crawling, cruising and walking), and the amount of awake time the infant spends in motor positions/activities on an average day (carried in a sling; sat upright; lying on back, lying on stomach, crawling).

3.2.3 Apparatus

EMG data were collected using two bipolar paediatric surface electrodes (3M monitoring electrodes with micropore tape and solid gel) and the Myon 320 wireless EMG system, at a sampling rate of 1000 Hz. Animations for the familiarisation condition were presented on a video screen using Matlab R2009b (Mathworks Ltd.). Simultaneous video recording of the testing session was conducted using a webcam positioned on top of the screen. For walking experience, we used a miniature infant treadmill (Carlin's Creations L.L.C., Sturgis, Michigan). Video recording of the treadmill use was recorded using a webcam with a frontal view of the infant.

3.2.4 Data Processing

Pre-and post-test infant behavioural data. Video recordings of the testing session were coded for all incidences where infants made a ringing action. Ringing is defined as vertical or horizontal arm movements on a single plane, with or without bells. Infants had to make at least two such movements in succession with no more than a two-second interval between movements for ringing to be counted. We therefore coded repetitive movements, with the timing of the movements within the two-second threshold not extracted at this stage.

Pre- and post-test infant EMG data. To analyse the timing of infant movements, EMG data were examined using the stand-alone ProEMG program (ProPhysics). Data was rectified and high-pass filtered at 400 Hz, low-pass filtered at 10 Hz and notch filtered at 50Hz. Infant EMG data were then segmented into corresponding periods of ‘ringing behaviour’ as defined by the video coding. A researcher hand-coded the onset of each burst of activity from the corresponding EMG channels for right and left biceps during the ‘ringing’ period by taking the first peak of each burst. Distances between burst onsets were then calculated to output the distance between bursts in milliseconds. The difference between the average distance between bursts and the target ISI of the track was calculated to give a tempo mismatch score. Accordingly, in the results described below, a lower score reflects less difference from the target ISI.

Treadmill analysis. Video recordings of the training activity were coded for number of alternating steps, and how many steps the infant took in each unbroken ‘run’ of alternating steps. Number of steps in a 'run' is considered a more sensitive measure of locomotive ability when measuring infant treadmill walking (Groenen, Krijsen, Mulvey & Ulrich, 2010).

3.3 Results

Our primary hypothesis was that infants would show improved tempo-matching in the bell-ringing task following walking training. A paired samples t-test comparing Tempo-Mismatch at Pre-Test and Post-Test reveals a non-significant increase mismatch following the treadmill training (Pre-Test M = .119, SE = .051; Post-Test M = .131, SE = .070; *t*(25) = -.749, *p* = .461). Infants also contributed to significantly less trials following the treadmill training (Four maximum; Pre-Test M

= 2.64, SE = .257, Post-Test M = 1.96, SE = .220; *t*(25) = 2.125, *p* = .044).

During treadmill training, infant weight was fully supported by the experimenter. As a result, the amount of active training the participants received was dependent on their own willingness to step: If they so chose, they could spend the full five minutes with their legs suspended in mid-air. The mean number of steps taken was 110 (*SD* = 76, range = 268), and the mean highest run length was 33 (*SD* = 39, range = 133). We reasoned that infants who participated more in the walking training may show better tempo matching. However, Pearson correlations only show non-significant relationships between the number of steps infants took during the treadmill training and their mismatch at Post-Test (*r*(26) = -.288, *p* = .145), and similarly between Post-Test mismatch and maximum number of steps performed in a 'run' of steps; *r*(26) = -.145, *p* = .470).

In the previous chapter we evidenced that 10-month-old’s performance is significantly worse in the slowest, 600 ms ISI condition, than in the other conditions. The current data replicate these findings. A univariate ANOVA with Tempo-Mismatch as the dependent variable, and Target ISI (300, 350, 450 and 600 ms) as a fixed factor, reveals a significant main effect of Target ISI (300 ms *M* = .091, *SE* = .014, 95% CI (.064, .119); 350 ms *M* = .080, *SE* = .014, 95% CI (.053, .108); 450 ms *M* = .090, *SE* = .014, 95% CI (.063, .117), 600 ms *M* = .225, *SE* = .014, 95% CI (.197, .253); F(3,140) = 23.536, *p* < .001). Planned comparisons confirm this effect is driven by significantly higher mismatch in the 600 ms condition than in the three faster tracks (all *p* < .001), with no other differences between tracks (all *p* > .588). It is possible that the non-significant effect of treadmill training could be due to a flat effect across the three faster ISI tracks, and that improvement may be visible in the 600 ms condition. Eleven of the infants provided data in the 600 ms condition at both time points. A paired samples t-test comparing 600 ms Target ISI Tempo-Mismatch at Pre-Test and Post-Test again reveals a non-significant increase in mismatch following the treadmill training (Pre-Test M = .167, SE = .098; Post-Test M = .243, SE = .097; *t*(10) = -.1.678, *p* = .124). Performance in the 600 ms Target ISI Post-Test trial was not correlated with Total Steps (*r*(13) = -.321, *p* = .284) or Highest Run Length (*r*(13) = -.129, *p* = .673) during treadmill training.

Whilst the current data does not reveal an impact of the five-minute training session on temporal matching of movement to music, we were interested to see if overall motor skill and experience at the time of testing was related to infant sensorimotor synchronisation. All infants were able to sit unsupported, and no infants were able to walk unaided, at time of testing. We created dichotomous variables of whether infants could crawl, cruise (walk with assistance/walk whilst holding onto furniture), and whether they were sling users (i.e. the caregiver reported carrying their infant in a sling for more than thirty minutes on an average day). As infant tempo-matching did not demonstrably change from pre- to post-test, infant data from both time points were collapsed to look at overall impact on sensorimotor synchronisation. Table 3.1 shows the descriptive statistics for all measures, demonstrating an advantage for all types of motor activity measured on tempo-matching of bell ringing to music.

Table 3.1 Overall infant tempo mismatch by motoric experience.

	Tempo Mismatch (s)			
	M	SE	95% CI	95% CI
Non-Crawlers	.248	.022	.202	.293
Crawlers	.113	.017	.077	.148
Non-Cruiser	.172	.019	.133	.210
Cruisers	.130	.017	.095	.164
Non-Sling Users	.199	.024	.149	.249
Sling Users	.117	.012	.091	.142

A linear regression was executed with overall Tempo Mismatch as the dependent variable and Crawling Ability, Cruising Ability and Sling Experience entered as predictors. The resulting model was significant, (F(3,24) = 5.864, *p* = .004, R^2 = .650), explaining 65% of variance of the dependent variable. Crawling Ability (*β* = -.584, t(24) = -2.887, *p* = .008) and Sling Experience (*β* = -.418, t(24) = -2.675, *p* = .013) were significant predictors of infant temporal matching. Cruising Ability was not a significant predictor (*β* = .142, t(24) = .696, *p* = .493) .

3.4 Discussion

We hypothesised that experience of bipedal locomotion would facilitate infants' movement to music. Non-walking ten-month-old infants were tested on their ability to ring bells in time with auditory tracks, before and after experience of walking on an infant treadmill. Contrary to our hypothesis, we did not find improvement in infant tempo matching from pre- to post-test. However, we did find that infant's naturalistic experience of different forms of locomotion prior to testing was related to their ability to match movement to the tempo of music. Specifically, infants who could crawl at time of testing were better than infants who could not crawl at time of testing, and infants reported to be carried in a sling by their caregiver were better than infants who were not regularly carried.

3.4.1 The impact of existing locomotive experience

Though our laboratory intervention did not work, we do find evidence that infants with greater locomotive experience were better matched to the tempo of the music in the bell-ringing task. Further, we show an effect for both self-produced locomotion (crawling), and other-produced locomotion (being carried).

The effect of crawling on SMS is ostensibly consistent with the idea of self-produced crawling as a point of epigenesis, or a springboard, creating experiences that facilitate the attainment of skills in other domains (Gottlieb, 1983). Research has shown the impact of onset of crawling on infants' spatial abilities (e.g. Kermoian & Campos, 1988), perceptual development (e.g. Higgins, Campos & Kermoian, 1996) and emotional development (e.g. Campos, Bertenthal & Kermoian, 1992). The wealth of findings for which crawling is beneficial suggest that there are likely unanticipated and untested effects of this major life transition: Crawling results in changes of neural processing and social interaction, and the effects this can have may not be immediate or obvious

(Campos et al., 2000). Is the impact of crawling on rhythm production a result of the changed world of the infant following this life event?

Our results certainly fit with the finding that crawling infants perform better in tests of postural stability than non-crawling infants (Higgins et al., 1996). Campos and colleagues (2000) suggest that this is advantage is due to crawling infants experiencing a stronger degree of correspondence between visual, vestibular and somatosensory systems. Self-locomoting, as opposed to carried infants, may have a higher need for visual information in order to navigate the environment (Higgins et al., 1996), and therefore make more use of external perceptual cues, such as of direction, for better motor control. Though our study was only able to measure tempo-matching, it may be that crawling infants are also better at using auditory cues and aligning their own movement with the external perceptual information, as required for full sensorimotor synchronisation.

However, that infant experience of other-produced locomotion, through sling use, impacts rhythm production, is an extremely novel finding. Though sling use was only measured at ten months of age, it is likely an experience present throughout the infants' development, and so would be difficult to reconcile as an epigenetic 'event'. Rather, we interpret these findings as reflecting similar benefits to those found in neonatal carrying and rocking interventions; improving attentiveness, perceptual tracking and motor coordination (e.g. Korner & Thoman, 1972; Rice, 1975; Gregg, Haffner & Korner, 1976; Clark, Kreutzberg & Chee, 1977). Infants engage in anticipatory postural changes (Reddy et al., 2013) and adaptive motor activity (Esposito et al., 2013; 2015) when being carried. Carrying, with active motor engagement from the infant and enhanced variability of postural experience, may lead to improvement in motor function (cf. Dusing & Harbourne, 2010). Sling use may be giving infants experience of rhythmic vestibular stimulation equal to that of self-produced locomotion.

If it is the case that sling use and crawling both impact sensorimotor synchronisation in the developing infant, potentially through the same kind of vestibular experience, we do not believe it parsimonious to label crawling, and not sling use, an epigenetic event. In the first chapter of this thesis we put forward a detailed argument for how the input from, and control required for, bipedal locomotion, may have made us the highly rhythmic creatures that we are. The idea of locomotion onset as an epigenetic 'event' - a sudden turning point in development whereby new experiences, whether cognitive, physical or social, are available - belittles the complexity of infant participation in the world prior to self-locomotion, at least in the sensorimotor domain. Whilst onset of own locomotion may be where these skills are most critical, and perhaps rate of change is most dramatic and observable in infant testing, we know that early caregiver intervention can prolong the newborn stepping reflex, and that infants with such training have earlier onset of independent walking (Zelazo et al., 1972). Experience matters. Our own results demonstrate for the first time that both infants' self-driven and 'passive' experience of locomotion impact upon their early sensorimotor synchronisation skills.

3.4.2 Limitations

We do not find a significant effect of whether infants were cruising on infant tempo-matching. We would have predicted that experience of cruising, with its new need for bipedal postural control, would have shown some benefit. It should be noted that in our sample all cruising infants could crawl, whilst not all crawlers could cruise, so that all infants were following a traditional trajectory of development whereby crawling precedes bipedal locomotion. In the infants who could crawl, median age of crawling onset was 8 months, compared to 9 months for cruising onset. It may be that the ten-month-old infants who could cruise had not been cruising for long enough to see an effect of this new form of locomotion. Further, the ability to cruise does not mean it is an individuals' most used locomotive strategy. Cruising infants still engage in crawling (for an average of over 90 minutes a day in the current sample), and thus whether or not infants could crawl may have captured the key variance due to infants' primary experience of self-produced locomotion.

The treadmill intervention was similarly unsuccessful in improving tempo-matching. Though the amount of training infants experienced in the laboratory was variable and constrained to a maximum of five minutes, it is unlikely that increasing the length of the training session, or using a minimum number of steps from each infant for inclusion, would be beneficial. Infant performance decreased from pre- to post-test, which likely reflects that infants found the treadmill training tiring. In naturalistic observation of infants over the first year of life, Thelen (1981) reports that infants exhibit most rigid movement stereotypies when they are in a fussy state. Infants took part in less trials at post-test, so it may be that performance was worse simply because the infants had less chance to be accurate, but it is also possible that they were more stereotyped or less engaged by the task following the effortful active walking training. Upon reflection, measuring infants over multiple, short training sessions (e.g. two minute sessions every day for five days) may allow for more experience to be given with less overwhelming physical exertion for the infant.

That we find an impact of naturalistic, but not laboratory induced, locomotive experience, suggests that studying the natural onset of bipedal locomotion may have produced different results. Future longitudinal work assessing infants on the cusp of locomotion would be highly informative. Further, a treadmill was chosen over using an infant walker because we did not have room within the laboratory for the infants to locomote through space. The intervention could be therefore be fairly described as 'stepping' training rather than 'walking' training. In studies that describe locomotion as an epigenetic event, walker assisted locomotive infants have been found equally adept at search tasks as hands-and-knees crawlers, outperforming pre-locomotive and slow 'belly crawling' infants, suggesting that efficacy of locomotion, rather than type of locomotion, is important (Kermoian & Campos, 1988). Allowing infants to self-pace and direct their own movement would have been more naturalistic. For example, the onset of bipedal walking allows more object exploration and sharing with the caregiver (Karasik, Tamis-LeMonda, & Adolph, 2011), which was not possible on the treadmill. Walker assisted experience could have allowed more of these social interactions, and peripheral optic flow, suggested as mechanisms of change in other domains

(Campos et al., 2000). Alternatively, our own hypothesis is that it is vestibular information, postural stability, and dynamic coordination over multiple degrees of freedom that may be of particular importance to sensorimotor synchronisation. The treadmill training also did not allow for true experience of locomotion in these regards, as the infants' balance was always maintained by the experimenter to ensure the baby was safe from harm. A way to tease apart if it is the use of (predominantly vertical, otolith) rhythmic vestibular information that is important or simply the ability to efficiently move around, would be to compare pre-locomotor infants trained with a traditional infant walker (i.e. the infant steps themself with some body weight support), infants in a jumperoo bouncer (i.e. experiencing vertical movements only), and infants trained to use an motorised infant go-kart via a joystick (i.e. enjoying a relatively smooth ride; see Figure 3.2).

Figure 3.2 Alternative training methods to the motorised treadmill, for novice infant walkers. A) Traditional baby walker. B) Static Jumperoo. C) Powered Mobility Device (Picture C retrieved from Andersen et al., 2013).

3.5 Summary

We hypothesised that infant temporal matching of movement to music would be dependent on locomotive experience. We tested non-walking ten-month-olds on a bell ringing to music task, before and after five minutes of treadmill walking training. Infant SMS ability did not improve from pre- to post-test, but we did find an association between natural locomotive experience and level of mismatch. Infants who were crawling at the time of testing had a lower level of mismatch than pre-crawling infants, and infants who were reported as carried in a sling by their caregiver had a lower level of mismatch than infants who were not reported carried. Together, our results suggest that not only is locomotive experience related to infant's rhythm production skill, but that this experience is just as important when it is other-driven as when it is self-propelled. The following chapter aims to tease apart how own and caregiver locomotion might impact the rhythms that infants spontaneously produce.

Chapter 4

Infant spontaneous motor tempo

4.1 Introduction

In the previous chapter (Chapter 3), we evidence that infants' experience of locomotion, both self-propelled and when carried by the caregiver, is related to performance in a sensorimotor synchronisation task. Ten-month-olds who could crawl and who were reported as carried in a sling were more accurate synchronisers to music than infants without those locomotive experiences. In the current chapter we aim to test the impact self- and other-driven locomotion over a much larger period of development. In order to do so, and having corroborated reports of asynchronous movement to music in infancy (Chapter 2; Chapter 3; Zentner & Eerola, 2009; Fuji et al., 2014) we attempt to level the playing field and measure a type of rhythm production evidenced to be in place from the neonatal period, spontaneous motor tempo (SMT).

One of the simplest rhythmic capacities is the ability to produce a regular beat. Understanding the development of SMT, or our natural rate of rhythmic movement (Fraisse, 1982), provides the opportunity to better understand the roots of our rhythmic predispositions. SMT is often measured as the inter-onset-interval (IOI) between a person’s self-paced finger taps (Fraisse, 1982). Adult SMT is highly stable, showing little intra-individual variability across testing sessions spanning several days (Vanneste, Pouthas & Wearden, 2001). However, across the lifespan, SMT is known to change. Children’s SMT is faster than adults, who are in turn faster than older people, with a cubic relationship suggesting that SMT slows with age during childhood and late adulthood, but remains consistent through mid-adulthood (aged 18-38 years, *M* = 630ms IOI; McAuley et al., 2006). The earliest equivalent measure of SMT comes from Provasi and Bobin-Begue (2008), who demonstrated that spontaneous tapping data can be obtained from eighteen-month-olds, with toddlers tapping at close to 450 ms ISI. Infant SMT has been recorded as close to this rate from 1.5 to 4.5 years of age, significantly faster than adults, with inter-individual variability starting narrow and broadening through the early years (Provasi & Bobin-Begue, 2003; 2008). The SMT of other, infant centric behaviours, including crying and sucking, have been recorded from birth, but these measures are difficult to reconcile with the lifespan, predominantly tapping, literature (see Provasi et al., 2014 for a review of neonatal SMT work).

It has been widely reported that both adult SMT and adult walking cadence lie in the range of 600ms IOI, or around 120 beats per minute (BPM; Fraisse, 1982). One possibility is that this relationship is causal, with walking cadence being the origin of our preferred tempo at which to move, and perhaps even to listen. Studies revealing correlations between anthropometrics (measures of body size) and SMT have been used to argue for this possibility, following the logic that body size may be used as a proxy for walking cadence, as rate of locomotion should be set by the mechanics of the human body (see Repp, 2007, and Todd & Lee, 2007, for debate on this subject). Anthropometrics correlate with SMT (Mishima, 1965), naturalistic full body dancing (Dahl, Huron, Brod & Altenmüller, 2014), and preferred tempo in a perceptual task (Todd, Cousins & Lee, 2007). A critical issue with this argument is that within-subject correlational studies cannot show a causal impact of walking cadence on SMT: results correlating body size with the tempo of motor tasks (Mishima, 1965; Dahl et al., 2014) may rather support a broader concept of biomechanical resonance, or a natural frequency of movement across the body. Crucially, however, the correlation with preferred *auditory* tempo (Todd et al., 2007) suggests that some experience must be necessary for rhythmic bias, as there is unlikely to be a genetic mechanism that directly matches body size to auditory preferences (Trainor, 2007). Locomotion is a sensible, pervasive, candidate experience for such a transfer (Todd et al., 2007, Trainor, 2007).

Infants present a unique opportunity for understanding the impact of walking cadence, removed from the context of one's own body size. Before an infant is able to efficiently locomote herself, she experiences months of being carried by a caregiver. There is therefore a clear dissociation between an infant's body size, and the rate of her predominant locomotive experience, which may be reflected in her parents' body size. The current study aims to exploit this dissociation to test the hypothesis that locomotion experience drives our basic rhythmic preferences.

Though infant SMT has not previously been measured, infants are known to spend up to 40% of their time performing repetitive movements (Thelen, 1979, 1981). Infants from as young as 4 months of age have been shown to spontaneously move rhythmically in the context of music (Zentner & Eerola, 2010; Fuji et al., 2014; Ilari, 2015). In Chapter 2 we demonstrate that ten- and 18-month-olds engage in rhythmic movement with small instruments. Thus whilst traditional tapping tasks may lie outside the range of infant motor control, it seems plausible to measure infant SMT using a gross motor rhythmic movement. The current study does so using a drumming paradigm that is similar to tapping, and so can be synthesised with the adult literature, but which allows for i) a large surface area for infants to strike ii) a unimanual or bimanual whole hand action and iii) rewarding auditory feedback from hits, motivating infants to make repeated movements.

4.1.1 Aims and Hypotheses

The current study therefore aims to uncover the rate of spontaneous rhythmic movements in infants, who have little to no experience of locomoting themselves, but rich experience of being carried by a locomoting adult. Concomitant with findings from across the lifespan, we predict that infant SMT will slow with age. There are two hypotheses for the relationship between infant SMT and anthropometric measures. If infant SMT is related to own body size, this would support a biomechanical resonance explanation, as infants' own walking experience is unlikely to be regular, or pervasive, enough to provide a tempo for other actions. However, if infant SMT is related to parental body size, this would instead suggest that information gained from the passive experience of locomotion drives SMT.

4.2 Method

4.2.1 Participants

An opportunity sample of 170 infants (74 female, mean age = 12.3 months, SD = 6.5 months, range = 4.1 to 37.8 months) took part in this study. An additional 11 infants were recruited but excluded for not providing any drumming data. Infants were recruited to take part in the study conducted at Polka Theatre, Wimbledon, as part of a neuroscience festival. All parents gave written, informed consent concerning the experimental procedure. Infants received a certificate as a thank you for participation.

4.2.2 Procedure

Testing took place inside a blackout tent located in the foyer of Polka Theatre. Infants were sat on their caregiver's lap or on the floor in front of their caregiver, within easy reach of the drum table. The experimenter sat adjacent to the drum table and opposite the infant. The experimenter demonstrated that the drum made a sound by hitting the drum with the flat of her hand once, and prompting the infant to drum using verbal cues such as 'Shall we play with the drum?', 'Can you hit the drum?' or 'What noise does the drum make?'. This prompt was repeated as necessary throughout the session, but with a minimum interval of two seconds between prompts to ensure the experimenter did not provide a rhythmic example. Infants were allowed to move freely and engage with the drum as they wished, but were kept engaged by the experimenter through eye-contact and smiles, and were verbally encouraged to hit the drum if they were not doing so spontaneously. Between bouts of drumming, the experimenter interacted with the child by saying 'Well done, you're doing a great job!', and encouraged them to continue (‘Shall we play some more with the drum? What does it do?’), regardless of their behaviour during the trial. Infants interacted with the drum for an average of 2 minutes 20 seconds (*SD* = 1 minute, 1 second), with the trial terminated if the infant became bored or fussy, or the infant had drummed for more than two minutes continuously.

Either before or after infant participation, caregivers completed a short questionnaire about their infant’s gross motor skills and milestones and experience of being carried. To ascertain infant and parent anthropometrics, a second experimenter administered the questionnaire and took measurements of infant and caregiver limb length (arm length, leg length), and asked the caregiver to self-report her height. Arm length was calculated by adding measurements from the spine to the shoulder to measurements from the shoulder to the wrist. Leg length was measured from the hipbone protrusion to the ankle. All adults were measured in a standing position. Infants were measured when standing (if able to hold themselves in a standing position), lying supine on the floor, or whilst being held by the caregiver.

4.2.3 Apparatus

The drum was a 12-inch tunable wood shell and natural skin head drum, secured to a height and angle adjustable mini-table. Sound was recorded from the drum via a Piezo contact microphone pickup attached with adhesive tape to the underside of the drum shell, and connected to a Focusrite Scarlett 2i2 (American Music and Sound, MS, USA), a hardware interface connecting the microphone audio signal to the computer (MacBook Pro; Retina, 15-inch, Mid 2014). The Scarlett 2i2 was selected as the audio input and the sound recording was taken using Audacity®, version 2.1.2 (2015). ScreenFlow (Telestream, Inc., CA, USA) was used to create a simultaneous screen capture of the Audacity recording and video footage of the infant using the forward facing built-in webcam.

4.2.4 Data Processing

The Screenflow captures of the testing sessions were used to code all incidences where infants hit the drum with one or both of their hands. The corresponding time point of the audio signal was then identified and the experimenter hand marked the onset of each hit (as defined by the first peak in the sound stream, see Figure 4.1 for example). For each ‘bout’ of drumming (i.e. series of hits) the time stamp of each hit onset was recorded, along with how many hits were in the bout, and whether the bout was produced by one hand drumming, both hands drumming simultaneously, or both hands in an alternating sequence. An independent researcher blind to the aims of the study double-coded the video data for 30 infants. The single-measure ICC for the Inter-Onset-Interval (IOI) was .924, with a 95% confidence interval from .790 to .968, ($F(29, 29) = 33.353$, $p < .001$).

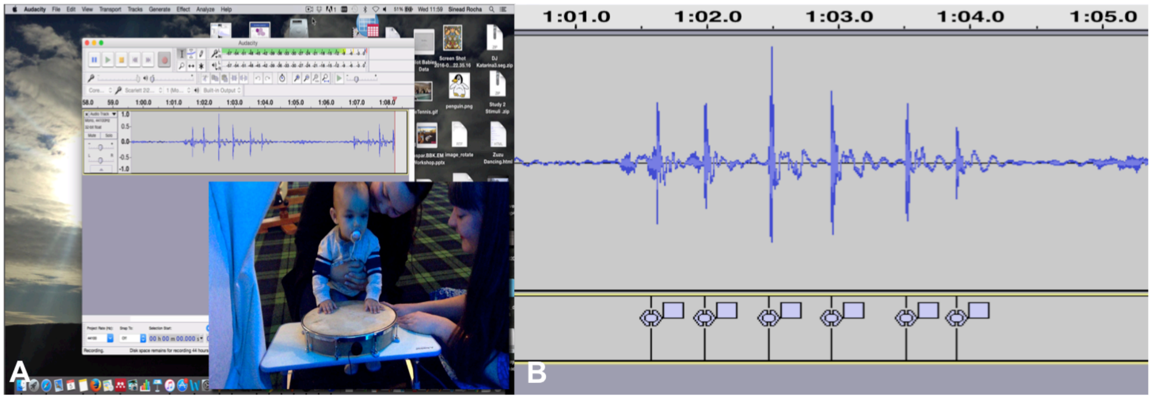

Figure 4.1 Visualisation of data coding. A) Video and sound data are aligned. B) Corresponding sound data to infant hitting is time stamped in Audacity ®.

To best match the adult literature on unimanual tapping, the following analyses were performed on the IOI of unimanual hits, or on the IOI of the first hand to strike during bimanual hits, with alternating sequences excluded. Data where the onset of the hit was ambiguous (i.e. because of wire noise, very low amplitude hitting, etc.) were also discarded. To be included as a ‘bout’, infants had to perform four sequential hits with no more than a two second IOI between hits. Infants who did not have at least one such ‘bout’ were excluded from further analyses. This reduced the sample of infants from 170 to 115. The 115 infants with sufficient data comprised of 67 males and 48 females, with an average age of 12.2 months (SD = 6.8 months, range = 4.9 months to 37.8 months).

Matlab (MATLAB R2015b, The MathWorks Inc., MA, USA) was used to calculate the IOI. The mean IOI was calculated for each participant and taken as a measure of SMT. The relative standard deviation (also known as the coefficient of variation; the ratio of the standard deviation to the mean, expressed as a percentage) of the IOI was also calculated for each participant and taken as a measure of regularity, i.e., a low relative standard deviation indicated more consistent drumming.

4.3 Results

We hypothesised that infant SMT would slow with age. Across all participants, the mean SMT was 542ms, with a standard deviation of 16ms. Contrary to our hypothesis, a two-tailed Pearson correlation shows that infant SMT is negatively correlated with age, such that older infants are faster ($r(114) = -.279$, $p = .003$). This is likely to be because younger infants are still learning how to control their limbs to make continuous and targeted movements. Indeed, we find that older infants' SMT also had a lower relative standard deviation ($r(114) = -.217$, $p = .021$), and that regularity and tempo were correlated independently of age ($r(114) = .509$, $p < .001$). We did not find differences in tempo (Table 4.1) or regularity (Table 4.2) due to experience of motoric activities.

Table 4.1 Linear Regression Coefficients for effects of daily awake time spent in motoric activities on infant SMT

	Standardized Beta	*t*	*p*
Infant Age	-.0292	-2.375	.019
Sling use	-.062	-.601	.549
Sitting	-.106	-1.142	.256
Lying on back	1.311	1.311	.193
Lying on stomach	.049	.434	.665
Crawling	-.218	-1.965	.053
Cruising	.064	.655	.514
Walking	.027	.211	.833

Table 4.2 Linear Regression Coefficients for effects of daily awake time spent in motoric activities on infant regularity (relative standard deviation)

	Standardized Beta	*t*	*p*
Infant Age	-.264	-2.022	.046
Sling use	-.037	-.337	.737
Sitting	-.109	-1.109	.270
Lying on back	.196	1.501	.136
Lying on stomach	-.110	-.917	.361
Crawling	.005	.469	.640
Cruising	-.005	-.051	.959
Walking	.085	.626	.532

Our primary interest was in whether infant SMT might correlate with own body size, suggesting biomechanical resonance; or whether infant SMT would correlate with parental body size, suggesting a role of passive experience. The level of variance in infant SMT is large (Mean RSD = 23.13, *SD* = 11.56) and such large variance may mask a relationship between anthropometric measures and infant SMT: A consistent pattern is improbable if infants are not providing a regular tempo. Infants with a relative standard deviation of more than one standard deviation above the mean were therefore excluded, leaving 94 infants in the final sample[2]. A linear regression with SMT as the dependent variable was performed on the remaining infants, with Infant Age, Arm Length and Leg Length, Parent Height, Arm Length and Leg Length entered as predictors. Degrees of freedom in the following analyses reflect the number of infants for whom all infant and parent measures were taken. The resulting model was significant, (F(6,55) = 3.321, p = .007, R^2 = .266), explaining 26.6% of variance of the dependent variable. Infant Age (β = -.459, t(55) = -2.596, p = .012) and Parent Height (β = .413, t(55) = 2.577, p = .013) were significant predictors of SMT. In order to further ascertain whether the predictors provided evidence for either the alternative hypothesis, a contribution of anthropometrics to infant SMT, or for the null hypothesis, no contribution of the measurements to SMT, we used JASP (JASP Team 2017; Version 0.8.1.2) to calculate the Bayes Factors for each predictor, using the default priors. Table 4.3 contains the standardized

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[2] Whilst it is more common to use 2 SD above the mean as a cut-off criterion, the variation in infants was so large that only three infants met this criterion. 1 SD above the mean was therefore selected as efficient in removing infants with irregular drumming, whilst maintaining a large sample size.

coefficients and Bayes Factors for all predictors.

Table 4.3 Linear Regression Coefficients for effects of infant age and infant and parent anthropometrics on infant SMT

	Standardized Beta	*t*	*p*	BF_{10}
Infant Age	-.459	-2.596	.012	10.061
Infant Leg Length	.003	.016	.988	0.839
Infant Arm Length	.238	1.303	.198	0.474
Parent Height	.413	2.577	.013	6.179
Parent Leg Length	-.081	-.519	.606	0.580
Parent Arm Length	-.168	-1.305	.197	0.290

Bayes Factors over 3 or under 1/3 represent substantial evidence for the alternative/null respectively, with values close to 1 representing weak or anecdotal evidence (Dienes, 2014). We find strong evidence for the contribution of Infant Age (BF_{10} = 10.061), suggesting that these data are more than ten times more likely to be observed under the hypothesis than the null; and Parent Height (BF_{10} = 6.179), showing over six times the evidence for an effect of parental height on infant SMT. The relationship between Parent Height and Infant SMT is illustrated in Figure 4.2

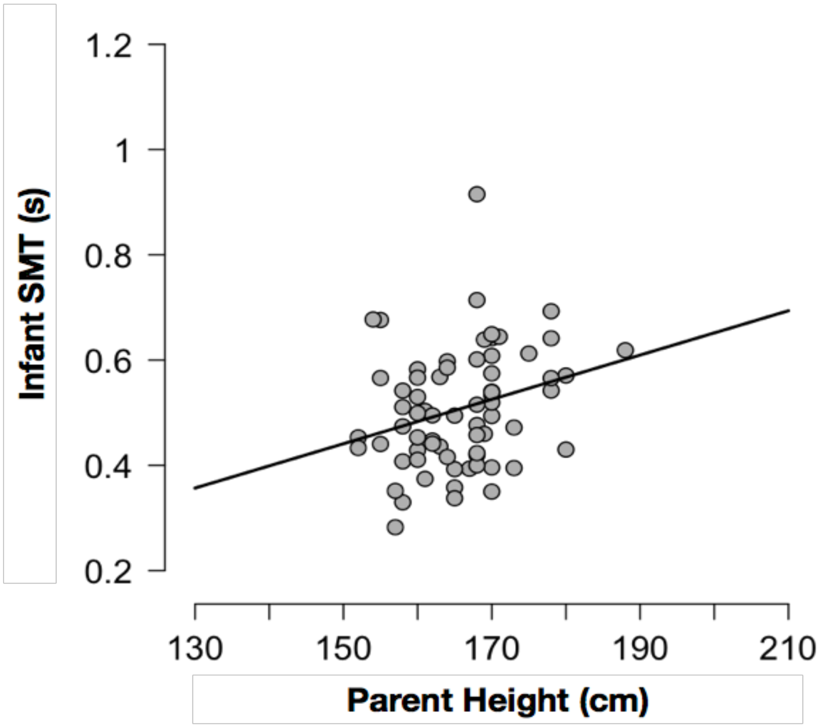

Figure 4.2 Relationship between Parent Height and Infant SMT.

For all other measures, the Bayes Factors suggest our data is more likely to be observed under the null (no contribution to infant SMT), although this evidence is weak for all measures except Parent Arm Length, where we see more than three times the evidence for the null hypothesis (Parent Arm Length BF_{10} = 0.290). Parent height was correlated with parent leg and arm length (two-tailed Pearson correlations for Parent Height and Parent Leg, *r*(65) = .666, *p* <.001; Parent Height and Parent Arm *r*(64) = .298, *p* = .017). Infant anthropometrics and age were correlated (two-tailed Pearson correlations for Infant Leg and Infant Age, *r*(68) = .729, *p* <.001; Infant Arm and Infant Age *r*(68) = .668, *p* <.001), but Parent Height was not correlated with Infant Age (two-tailed

Pearson correlation, (*r*(68) = -.075, *p* = .544), Infant Arm Length (two-tailed Pearson correlation, (*r*(65) = -.068, *p* = .593), or Infant Leg Length (*r*(66) = .031, *p* = .804).

4.4 Discussion

Overall we provide clear evidence that infant SMT is predicted both by infant age, and parental height, and anecdotal evidence that infants' own body size does not influence SMT. Taken together, our results suggest that infant SMT is related to both the infants' own ability to make repeated, targeted, movements, and critically, the cadence of the parent's walking, which they experience passively whilst being carried.

That infant SMT negatively correlates with age is at first glance at odds with the existing developmental literature. From childhood to late adulthood, SMT is known to slow with age (McAuley et al., 2006). However, though studies have not previously investigated the timing of spontaneous repetitive movements across infancy, our results are consistent with the fact that infants become better at controlling their movements over the first two years of life (Goldfield, 1995). Increased regularity of SMT is observed in 1.5 to 4.5 year old children (Provasi & Bobin-Begue, 2003; 2008). That speed and regularity of infant SMT both correlate with age, and independently with each other when controlling for age, supports our interpretation that through the first years of life, infant SMT at least in part reflects the infant's level of motor coordination, with movements becoming faster as motor control increases.

Our finding that infant SMT gets faster with age sheds new light on the relationship between SMT and age across the lifespan. The current data suggest a U-shaped curve, such that SMT decreases with age until the pre-school years, followed by an increase from childhood to late adulthood. Considering the diverse methods that have been employed to test SMT across early life (e.g. Provasi & Bobin-Begue, 2003), it is difficult to pin point exactly when in development the bottom of the U-shaped curve is hit. However, the free drumming procedure employed in the current study is an age appropriate method of measuring SMT across both infancy and early childhood, and it would be interesting for future studies to document when the change of direction from increasing to decreasing tempo occurs, and explore the motor or cognitive skills, or experience, that motivate this change.

Our findings strongly suggest a contribution of carrying experience to infant SMT. We find that tempo correlates with parent height, such that infants of taller parents show a slower SMT. Adult studies relating anthropometry to preferred tempo at which to move (Mishima, 1965; Dahl et al., 2014) could suggest that the link with body size is mediated by walking pace, with walking cadence providing a resonant tempo. However, the correlations found in prior studies could simply be a product of our own machinery, in that in a consistently proportioned body, a comfortable rate to move at likely correlates across different motor actions. The current study is better suited to consider whether walking, as a predominant rhythmic action, primes the rate of other rhythmic movements. Infants receive information, particularly vestibular information, at the rate of their mother's walking cadence, both in the womb and for months post-natally. The fetus and newborn responds to vestibular-tactile-somatosensory rhythms, (see review by Provasi et al., 2014), and vestibular information is known to impact rhythm perception, from infancy (Phillips-Silver and Trainor, 2005, 2008; Trainor et al., 2009). We argue that the relationship we find between parent height and infant SMT is the product of the vestibular experience infants receive whilst being carried.

Though we do not have strong evidence for the null, the lack of relationship between infant SMT and own body size is also consistent with the idea that it is experience of locomotion that is crucial. Aside from the fact that there was variability in the amount of self-locomotive experience *between* infants tested in the current study, the rapid physical growth and development of motoric skill *within* each infant would presumably provide each subject highly variable (a)rhythmic self-generated experience to draw upon. Infant walking does not show the regularity of adult walking, and regularity needs to be learned; above infant age or body size, amount of experience of walking is the best predictor of walking competency (Adolph, Vereijken & Shrout, 2003). Todd et al. (2007) suggest even small changes in body size at the tail end of adolescence may prevent a stable relationship between preferred beat rate and anthropometry. It is thus plausible that the relationship between own body size and SMT may not appear until mid-adulthood, which is the point in the lifespan at which SMT seems to plateau (McAuley et al., 2006). Due to the limited time and testing space we had with participants in this opportunity sample, we were unable to directly test whether parent cadence is indeed the factor underlying the relationship between parent height and infant SMT. Future studies should directly test this interpretation.

4.5 Summary

Our study is the first to measure SMT across the first years of life. We developed a simple drumming task allowing data collection from infants as young as four months of age. We find that infant SMT becomes faster and more regular with age, and reveal a relationship between infant SMT and parental height, that we interpret as indicative of a contribution of the experience of being carried by the caregiver. In the following chapter, we test this interpretation directly with an experimental manipulation of infant carrying rate.

Chapter 5

The effect of novel carrying experience on infant spontaneous motor tempo

5.1 Introduction

In Chapter 4, we developed a simple free drumming task that allowed us to collect data on the spontaneous motor tempo (SMT) of infants across the first years of life, and found that infant SMT was predicted by parental body size, but not infant's own body size. Specifically, parent height predicted infant SMT such that infants with taller parents showed a slower SMT than infants with shorter parents. Whilst the dependent variables in the previous study were anthropometric indices, the goal of the experiment was not to see if height, arm length or leg length were predictors of SMT per se, but rather, we took the opportunity to collect large-scale data on the impact of own body size versus parental body size, allowing us to gain some insight into the role of biomechanics (own body size) versus experience (dictated by parental body size). We interpret our finding as reflective of the vast amounts of information gained by infants when they are carried by their caregiver, at the caregiver's walking cadence. In Section 1.3.5 we discuss in detail how infants experience this highly rhythmic information, with a strong vestibular signal, and how it may change motor and cognitive abilities in the developing child (Korner & Thoman, 1972; Rice, 1975; Gregg et al., 1976). Particularly before infants are able to locomote independently, such exposure may bias ones' own rhythmic preferences, in production, and potentially in perception, as hypothesised by Ayres (1973).

The interpretation of our data therefore relies on two assumptions that we were unable to measure in Chapter 3, due to our correlational design, and the fact that the study was conducted in a non-laboratory environment. First, we assume that parental height can be used as a proxy for parental walking cadence, and second, we assume that it is specifically the experience of the *tempo* of walking during carrying that explains the link between parent height and infant SMT. We attempt to test these two assumptions experimentally in the current chapter.

5.1.1 Assumption A: Body size and walking cadence

Whilst the link between body size and walking cadence is theoretically well established (e.g. Whittle, 1990, cf. Todd et al., 2007), the empirical evidence is not straight forward, and definitions of terms and relevant findings are expanded below.

Walking cadence is the number of steps in a given time, and often refers to steps per minute, which is particularly useful for the current research programme as it allows easy equivalence with beats per minute (BPM). In the gait literature, however, ‘cycle time’ or ‘stride time’ is often the preferred measure, as there are two steps in a gait cycle and thus cadence measures half-cycles, which is less parsimonious (Whittle, 1990). Cycle time is calculated with the following formula, where cadence is steps per minute:

Equation 1: *Cycle time (s) = 120 / cadence*

and is thus the inverse of cadence (Equation 1). Accordingly, either cycle time or cadence will be used interchangeably in the following section, as it is measured in the literature presented. Speed of walking depends on both cadence and stride length, and is thus calculated with the following formula (Equation 2):

Equation 2: *Speed (m/s) = stride length (m) / cycle time (s)*

Whilst speed could therefore be changed by only changing stride length or cadence, normal walking across different tempi tends to conserve a walking ratio, so that a shorter stride length is associated with a shorter cycle time, changing both elements to adjust speed (Whittle, 1990). It is critical to note that if a taller person has a longer stride length but the same cadence as a shorter person, they would be faster, in that they would cover ground more quickly. Speed and cadence can therefore be dissociated.

Gait researchers often work on the assumption that shorter people walk with smaller steps and a faster cadence, and when assessing for clinical gait problems it is recommended to scale walking measures by individual stature to ensure fair comparisons (Hof, 1996). Scaling by height and weight is effective at reducing inter-subject variation (Pierrynowski & Galea, 2001). However, there is not a clear consensus on the relationship between height and cadence or walking speed.

Findings in favour of the intuitive observation that shorter people walk with faster cadence include that in middle aged adults (Himann, Cunningham, Rechnitzer & Paterson, 1988) and in children (Beck, Andriacchi, Kuo, Fermier & Galante, 1981; Sutherland, 1997; Dixon, Bowtell & Stebbins, 2014) height and leg length are related to walking cadence, such that taller people exhibit fewer steps per minute. The shorter Korean population shows shorter stride lengths than European population norms (Ryu, Choi, Choi & Chung, 2006). Computations of an individuals' gait is more accurate when knowing height and stride parameters than just stride parameters (BenAbdelkader, Cutler & Davis, 2002). If two individuals walk side-by-side, and do not synchronise steps, the walker who is taller has the slower cadence (Zivotofsky, Gruendlinger & Hausdorff, 2012).

There is evidence for an inverse relationship, such that taller adults are faster, though in a study measuring speed, not cadence, which suggests only an impact on stride length (Bohannon, 1997). That said; null or confounded results are more commonly reported than an inverse relationship. In a study of the elderly, the relationship between height and walking speed was not independent of gender, and gender was the better predictor (Bohannon, Andrews & Thomas, 1996), though studies have also shown the opposite effect, with gender differences on walking speed disappearing when adjusted for height (Ryu et al., 2006). Whilst studies of children reported above show a taller-slower height-cadence relationship (Beck et al., 1981; Sutherland, 1997; Dixon et al., 2014), one study found the relationship in children only up to a height of 130 cm, after which the relationship plateaued (Thevenon et al., 2015). In a further study of 20 adults' natural walking rate, MacDougall & Moore (2005) show a mean rate of 2 Hz (120 BPM) that was not correlated to individual differences in age, gender, or body size. The authors argue for a resonant frequency of movement unrelated to biomechanics (MacDougall & Moore, 2005). A larger study of 239 adults showed no associations between body height, weight or age and walking cadence, but associations with stride length (Samson et al., 2001). The authors did however note a substantial difference between genders (Samson et al., 2001). Not all measures are equal: Cadence can be more sensitive to anthropometrics than speed (Dixon et al., 2014), and the fact that men are normatively taller than women means results are susceptible to different strategies of controlling for non-independent variables.

In the absence of a consensus on the extent to which body size can be considered a proxy for walking cadence, the following study acknowledges that our assumption is intuitive, and has received some support in the literature, but does not necessarily reflect a robust effect. Many of the studies above acknowledge that walking cadence is a difficult measure as it can change dependent on cultural expectations or task constraints, such as the length of the runway, and whether treadmill or over-ground, or indoor or outdoor walking is measured (e.g. Oberg, Karsznia & Oberg, 1993). We hope to clarify our assumptions in the current study by measuring parent walking cadence and measuring height and limb lengths, such that findings of a taller-slower height-cadence relationship in our current sample could add explanatory power to our previous study. However, our study will be limited as all the above studies are, to the precise measure of cadence that we take, and may be impacted by other individual differences that are not independent, such as gender and body mass.

5.1.2 Assumption B: It is specifically the *tempo* of caregiver walking that influences infant SMT

As elaborated in Section 1.3.5, much of the literature on the impact of infant carrying has focused on the effect of vestibular stimulation on infant arousal, with studies showing a calming effect (Gordon & Foss, 1966; Pederson & Ter Vrugt, 1973; Pederson, 1975; Hunziker & Barr, 1986; Elliot et al., 1988; Esposito et al., 2013; Yilmaz & Arikan, 2015), as has been physiologically documented by measuring respiration (Elliot et al., 1988) and heart rate (Esposito et al., 2013). In the current study, we therefore need to be cautious in the interpretation of our results if we find that SMT is changed by carrying experience; it is possible that more energetic carrying increases arousal and less energetic locomotive experience decreases arousal. If so, results fitting our hypothesis that SMT is influenced by the tempo of carrying could alternatively be explained by a generic change of state in the infant, such that any arousing experience should influence SMT.

5.1.3 The present study

In order to test whether walking cadence biases infant SMT, the current study employs a pre-test, training, post-test design. Infant SMT was measured at pre- and post-test using the free drumming task employed in the previous chapter. During the training period, non-walking, ten month-old infants were carried in a forward facing baby carrier and walked by the experimenter at either a Fast (138 BPM) or Slow (98 BPM) pace, for ten minutes. The age and gross motor development of infants in the current study are therefore consistent with the population studied in Chapter 2, in order that we can later draw parallels between active and passive locomotive experience, and consistent with the population in Chapter 3, such that we can further our understanding of infant SMS with more precise knowledge of the SMT of this age group than following the mean SMT reported in Chapter 4, which captured SMT over the first years of life.

The range of cadence of free-speed walking females aged 18-49 years is 98 BPM to 138 BPM (Whittle, 1990). The range for equivalently aged men is the slightly slower 91 - 135 BPM. In the present study, the extreme values of the normal female range, 98 BPM and 138 BPM, were chosen as the Slow and Fast rates of carrying. In doing so we hoped to give the infants experience that was likely novel, in that we were not carrying infants at the population mean cadence, but still ecological, in that we were not walking at a non-naturalistic pace.

5.1.4 Aims and Hypotheses

To date nobody has directly tested whether the experience of being carried during locomotion impacts infant rhythm. In the current chapter we aim to fill this gap in the literature, and offer explanation of the results in the previous chapter, by giving infants experience of locomotion at a novel tempo, thus attempting to experimentally manipulate infant SMT with a short lab based carrying intervention.

To contextualise the results of the impact of carrying practice within the findings of the previous chapter, the anthropometrics of both infant and parent were also taken here. In the literature on body size and rhythm, weight has also been measured (Todd et al., 2007; Dahl et al., 2014), but in the previous study in a public setting it was deemed potentially too sensitive to measure. We quantified weight of infant and parent in the current, laboratory study. Additionally, parent SMT was measured via free drumming, free tapping and a free treadmill walking measure. We predict that parental body size will predict infant SMT, such that infants with a larger parent will drum more slowly at pre-test than infants with a smaller parent, as seen in the previous chapter, and further hypothesise that parent body size will similarly predict parent's own SMT, both in typical rhythm tasks and as measured by walking cadence.

Our primary hypothesis centers on the experimental manipulation, and predicts that infants in the Fast condition will drum faster at post-test than pre-test, and that infants in the Slow condition will drum more slowly at post-test than pre-test. Finally, to ensure that changes in SMT in the current study are not the product of a general state of higher or lower arousal, we measure infant heart rate whilst at rest, immediately before and after carrying, and predict no change from pre- to post-test.

5.2 Method

5.2.1 Participants

Forty-four ten-month-olds took part in the study, in a between-subjects design (22 female; mean age = 10 months (M = 305 days, range = 290 to 332 days)). Twenty-three infants (M = 304 days, range = 291 to 323 days)) were randomly allocated to the Fast condition, and 21 infants (M = 305 days, range = 290 to 332 days) to the Slow condition. Only non-walking infants were recruited for the study. All caregivers gave written, informed consent concerning the experimental procedure for themself and their infant. Infants received a certificate and a t-shirt as a thank you for participation.

5.2.2 Procedure

We employed a pre-test, training, post-test design. Infants participated in a free drumming measure of SMT pre and post experience of the Fast (138 BPM) or Slow (98 BPM) walking conditions. Caregivers were subsequently asked to complete additional parental measures.

*Pre- and Post-Test Measure of Spontaneous Motor Tempo***.** Infants were seated on a cushion adjacent to the caregiver or on the caregiver's lap. A 12-inch drum supported on an adjustable height table was placed over the infant's lap. To familiarise the infant with the instrument, the experimenter demonstrated that the drum produces noise, telling the infant "Look!" and then hitting the drum once. If the infant did not spontaneously try to drum herself, the experimenter repeated the demonstration, leaving at least two seconds between each demonstration. In this way infants were not primed with a rate at which to hit the drum.

The trial started when the experimenter commenced the demonstration, and lasted for five minutes. Infants were congratulated when they hit or interacted with the drum. If infants moved away from the drum the caregiver returned the infant to their seated position. At the end of the trial infants were congratulated again, regardless of their behaviour during the trial.

Carrying experience – Fast condition. The caregiver placed the infant in a forward facing infant sling worn by the experimenter. The sling supported the infants weight so that the experimenter had both hands free. The experimenter, with infant, stepped onto the treadmill. A display monitor facing the infant from a distance of 50cm was turned on and displayed an infant cartoon. The experimenter remained stationary for one minute, and infant and experimenter heart rate was recorded using surface electromyography (EMG). Following the heart rate recording, the experimenter started the treadmill and gradually increased the speed for up to one minute until it reached a comfortable speed at which to walk at 138 BPM (434 ms between steps). In order to keep pace whilst walking the experimenter listened to a metronome recording at 138 BPM through one in-ear headphone. The experimenter walked with both hands holding the handlebars and with easy access to the speed controls and emergency stop. The experimenter walked on the treadmill for 10 minutes. During the training, the caregiver was seated adjacent to the treadmill. Both experimenter and caregiver spoke to the infant in the first instance if the infant was not engaged with the video presented to them. An assistant also blew bubbles and provided toys if the infant became unsettled. At the end of the walking the experimenter reduced the speed of the treadmill to a stop over the course of one minute, and then remained stationary on the treadmill for a further minute, whilst heart rate was again recorded. A digital camera recorded the training from the side such that the experimenter’s feet were in shot throughout.

Carrying experience – Slow condition. The procedure for the Slow condition was identical to the Fast condition except that the treadmill speed facilitated walking at 98 BPM (612 ms between steps), and the experimenter could hear a corresponding metronome recording of 98 BPM.

Caregiver Measures. Following completion of infant testing, caregivers were asked to complete the following measures. Infants remained in the same room as the caregiver and were entertained by the experimenter’s assistant.

Caregiver SMT measures. Caregivers took part in an abbreviated version of the infant drumming SMT task, where they were asked to sit within easy reach of the drum and drum consistently with one hand for one minute, with a smooth gesture, and at a comfortable, regular rate. They also took part in a tapping task, where they tapped the surface of the drum with their index finger, also for one minute and following the same instructions as when drumming.

Caregiver walking cadence measure. Caregivers were asked to step on to the stationary treadmill and were familiarized with the emergency stop. The caregiver then started the treadmill and the experimenter gradually increased and decreased the speed using a two-up two-down stair casing procedure (prompted: “Is this rate better, or worse, than before?”), until the caregiver reported that they were walking at their most comfortable pace. The caregivers walked at this pace for one minute. A video of the caregiver’s footsteps was recorded in profile.

Questionnaire measure. Caregivers completed a questionnaire method detailing infants' gross motor milestones and the amount of time their infant typically spends in different gross motor activities.

Infant and Caregiver anthropometric measurements. We took measurements of parent and infant height, leg length, arm length, and weight. The experimenter took all measurements. Height was measured from the top of the head to the floor. Arm length was calculated by adding measurements from the spine to the shoulder to measurements from the shoulder to the wrist. Leg length was measured from the hipbone protrusion to the ankle. Adults were measured in a standing position. Infant arm and leg lengths were measured when standing (if able to hold themselves in a standing position), lying supine on the floor, or whilst being held by the caregiver, and height was always measured whilst lying supine on the floor. To calculate infant weight the caregiver or experimenter stood on scales with and without the infant and the experimenter calculated the difference.

5.2.3 Apparatus

Measures of Spontaneous Motor Tempo. Data were recorded using a Piezo contact microphone pickup fixed with adhesive tape to the underside of a 12-inch wood shell and natural skin head drum, attached to a height and angle adjustable mini-table. The pickup was connected to a Focusrite Scarlett 2i2 (American Music and Sound, MS, USA), a hardware interface connecting the microphone audio signal to the computer (MacBook Pro; Retina, 15-inch, Mid 2014). The Scarlett 2i2 was selected as the audio input and the sound recording was taken using Audacity®, version 2.1.2 (2015). ScreenFlow (Telestream, Inc., CA, USA) was used to create a simultaneous screen capture of the Audacity recording and video footage of the infant/caregiver using the forward facing built-in webcam.

Carrying experience. Walking experience was given on a Domyos Comfort Run treadmill, with 0% incline. Animations during the carrying experience were presented on a 12-inch video screen. Video recordings of the carrying session and parental cadence measure were conducted using a Logitech HD 1080p webcam positioned one meter to the left of and facing the treadmill, allowing profile view of the experimenter and infant.

Anthropometric measures. For all measures except height and weight a standard soft textile tape measure was used. Caregiver height was measured against a line-measured wall. Infant height was measured by laying the infants on an infant height chart. Weights were taken on digital bathroom scales.

Heart rate data. Infant heart rate data were collected using a bipolar pediatric surface electrode (3M monitoring electrodes with micropore tape and solid gel) placed on the infants' back over the heart, recorded via the Myon 320 wireless electromyography (EMG) system, at a sampling rate of 4000 Hz. The experimenter's heart rate was recorded in the same way but with the electrode placed over the pectoralis major.

5.2.4 Data Processing

Measures of Spontaneous Motor Tempo. For infants, the ScreenFlow video recordings of the drumming sessions were used to identify periods of drumming and determine the corresponding time point in the original Audacity sound file. The experimenter hand marked the onset of each hit (as defined by the first peak in the sound stream, see Figure 5.1 for example). For each ‘bout’ of drumming (i.e. series of hits) the time stamp of each hit onset was recorded, along with how many hits were in the bout, and whether the bout was produced by one hand drumming, both hands drumming simultaneously, or both hands in an alternating sequence. If data were so noisy that the onset of the drum hit was not distinguishable (i.e. because of wire noise, very low amplitude hitting, etc.), they were discarded. Each bout of drumming was considered separately, with a pause of more than two seconds between hits considered a break in drumming. To best match the adult literature on unimanual tapping, the following analyses were performed on the rate of unimanual hits, or on the first hand to strike during bimanual hits, with alternating sequences excluded.

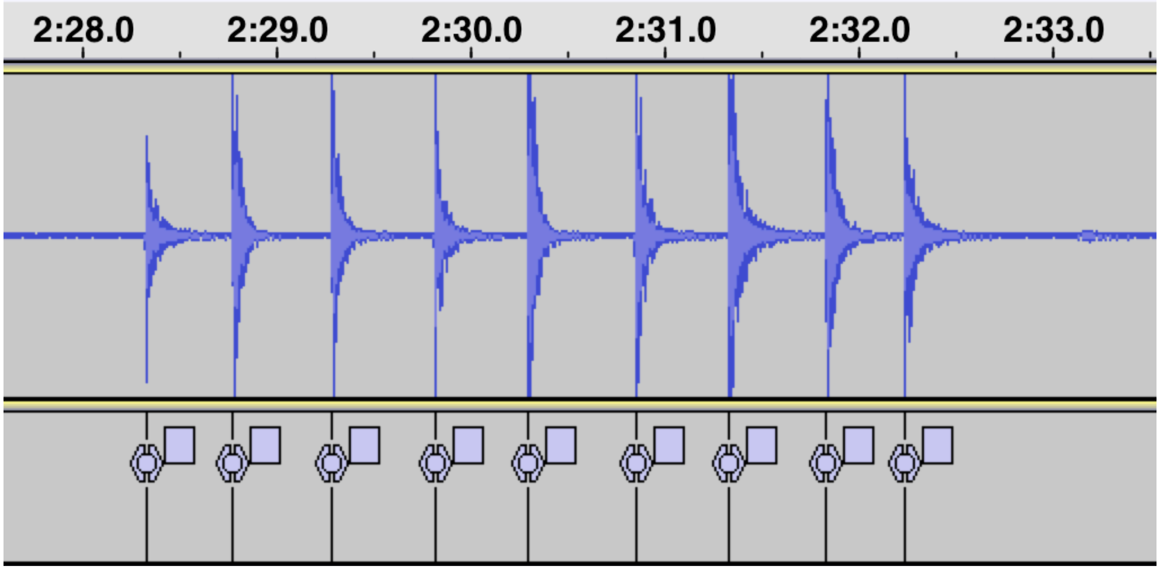

Figure 5.1 Example of manually event marked sound stream of infant drumming.

Matlab (MATLAB R2015b, The MathWorks Inc., MA, USA) was used to calculate the IOI. The mean IOI was calculated for each participant and taken as a measure of SMT. The relative standard deviation (also known as the coefficient of variation; the ratio of the standard deviation to the mean, expressed as a percentage) of the Inter-Onset-Interval (IOI) was also calculated for each participant and taken as a measure of regularity, i.e., a low relative standard deviation indicated more consistent drumming. To be included as a ‘bout’, infants had to perform four sequential hits with no more than a two second IOI between hits. Infants who did not have at least one such ‘bout’ were excluded from further analyses. This reduced the sample with data at pre- and post-test to 15 infants in the Fast condition and 16 infants in the Slow condition. As a very high RSD would indicate that the infant was drumming with very little regularity and therefore the IOI would not be a good measure of SMT, two outliers with an RSD of over 45% were further excluded from analyses. This leaves a final sample of infants with sufficient data at pre- and post-test of 15 infants in the Fast condition and 14 infants in the Slow condition.

For caregiver drumming and caregiver tapping, the inbuilt Audacity ‘Beat Finder’ analysis tool was used to automatically detect and mark the onset of beats produced by the caregiver, by identifying each instance the signal went past a set decibel. This criterion was modified for each individual participant to account for individual variations in the strength of the hit/tap. The experimenter visually inspected the marked file and ensured all beats had been represented faithfully (see Figure 5.2 for example).

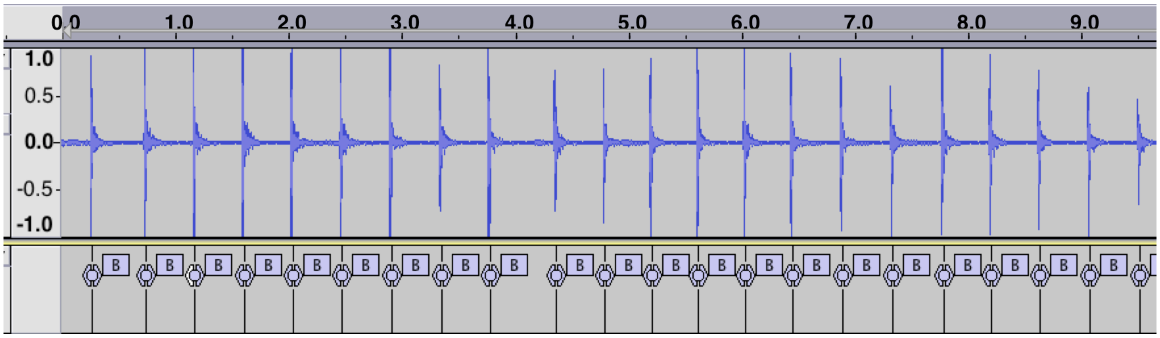

Figure 5.2 Example of the event marking of an adult drumming, conducted with the Audacity ® automatic beat finder function.

Caregiver Cadence. The number of steps that each caregiver took in one minute was coded from the profile view videotape. Steps per minute were translated to an Inter-Onset-Interval, giving milliseconds between steps as the independent variable, allowing easy comparison with the drumming and tapping data.

Heart rate. The infant EMG signal for the stationary period prior to walking and the stationary period immediately after walking were analysed using a custom built ProEMG pipeline, marking the onset of each heartbeat. Data where the heartbeat was not evident due to wire noise or signal dropout were discarded. This left pre- and post-test data for 20 infants; 10 in the Fast condition and 10 in the slow condition. The IOI of heartbeats were calculated using Matlab (MATLAB R2015b, The MathWorks Inc., MA, USA).

5.3 Results

Our primary hypothesis was that infant SMT would be influenced by experience of being carried at a novel rate; with infant SMT becoming faster from pre- to post-test if walked at the Fast speed of 138 BPM, and slower if walked at the Slow speed of 98 BPM. This was confirmed with a repeated measures ANOVA with infant SMT as the dependent variable, Time (Pre-Test or Post-Test) as a within subject factor and Condition (Fast or Slow) as a between subjects factor, revealing no main effects of Time ($F(1,27) = .081$, $p = .778$) or Condition ($F(1,27) = 1.390$, $p = .249$) but a significant Time*Condition interaction ($F(1,27) = 6.799$, $p = .015$, $\eta p^2 = .201$), such that infant SMT in the Fast condition became faster from pre- to post-test, and infant SMT in the Slow condition became slower from pre- to post-test (Fast Pre-Test $M = .495$, $SE = .025$, 95% CI (.445, .546); Fast Post-Test $M = .467$, $SE = .027$, 95% CI (.412, .521); Slow Pre-Test $M = .504$, $SE = .026$, 95% CI (.452, .557); Slow Post-Test $M = .540$, $SE = .028$, 95% CI (.484, .596); Figure 5.3).

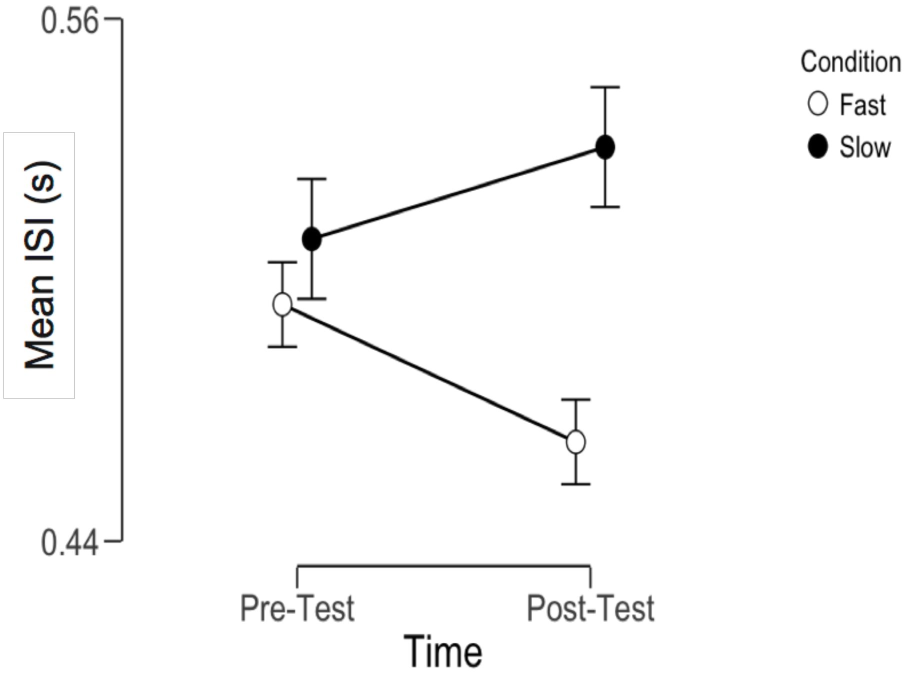

Figure 5.3 Graph to show interaction between Walking Condition (Fast or Slow) and Pre- and Post-Test measurement on infant SMT. Note: A faster SMT has a shorter ISI.

We further asked whether the differences in performance following the carrying experience could be explained by a differing state of arousal following the Fast walking compared to the Slow walking. If this were the case, we would expect an increase in heart rate where we see the faster drumming post-test in the Fast condition, and a decrease in heart rate in the Slow condition post-test. Figure 5.4 displays the mean heart rate IOI for infants in each condition; it is evident that the direction of change is the opposite of this prediction.

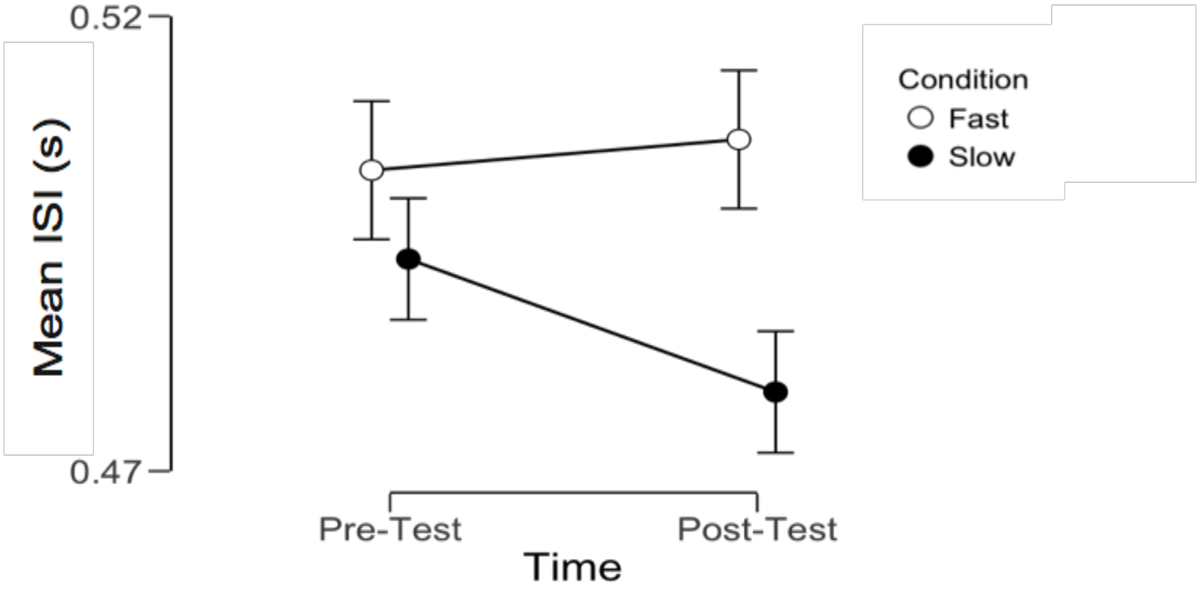

Figure 5.4 Graph to show interaction between Walking Condition (Fast or Slow) and Pre- and Post-Test measurement on infant heart rate. Note: A faster heart rate has a shorter ISI.

Though these results are the opposite from what one would predict if change in infant SMT were driven by higher arousal, or more physical exertion (faster heartbeat) in the Fast condition, and lower arousal in the Slow condition, the change is not statistically significant. A repeated measures ANOVA with infant heart rate (IOI of heartbeats) as the dependent variable, Time (Pre-Test or Post-Test) as a within subject factor, and Condition (Fast or Slow) as a between subjects factor, confirms no significant effect of Time (F(1,18) = .612, *p* = .442) or Condition (F(1,18) = .898, *p* = .356), and no evidence of a Time*Condition interaction (F(1,18)= 1.585, *p* = .224).

In order to confirm that our data support the null hypothesis (no effect of carrying experience on infant heart rate), and is not the result of insufficient power, we used JASP (JASP Team 2017; Version 0.8.1.2) to calculate the Bayes Factors for the interaction, using the default priors. It is assumed that $BF_{10}<.33$ provide good evidence to support the null (Jeffreys, 1939; Lee & Wagenmakers, 2014). The equivalent Bayesian repeated measures ANOVA revealed evidence for the null (Time*Condition $BF_{10} = .263$), showing that there is over three times the evidence in our data that there is no effect of carrying rate on change in heart rate. We can therefore confirm that our SMT results are not explained by a change in arousal, as measured by heart rate.

5.3.1 Parent measures

In addition to our experimental manipulation, we were further interested in whether parents' rhythm as measured in the laboratory via drumming, tapping and crucially by walking cadence, would predict infant SMT. A linear regression with infant SMT at pre-test as the dependent variable and caregiver drumming rate, tapping rate, and stepping rate IOIs as predictors did not provide a significant model ($F(3,28) = 1.255$, $p = .309$, $R^2 = .119$), and none of the predictors were significant (Parent Drum $\beta = .406$, $t(28) = 1.897$, $p = .068$; Parent Tap $\beta = -.173$, $t(28) = -.805$, $p = .421$; Parent Walking Cadence $\beta = -.025$, $t(28) = -.139$, $p = .891$).

Similarly, linear regressions reveal that both infant and parent anthropometrics fail to predict infant SMT, and that parental anthropometrics fail to predict parent drumming and tapping. Table 5.1 displays the standardised coefficients, *t* and *p* values for all body measurements, both infant and parent, when predicting the dependent variable of infant pre-test SMT (infant measurements, F(4,30) = 1.840, p = .147, R^2 = .197; parent measurements F(4,27) = .220, p = .925, R^2 = .032); and for parent measurements predicting parent drumming (F(4,36) = .613, p = .656, R^2 = .064), and parent tapping (F(4,36) = 1.491, p = .225, R^2 = .142).

Table 5.1 Linear Regression Coefficients for effects of infant and parent anthropometrics on measures of infant and parent SMT

	Infant Drum			Parent Drum			Parent Tap			Parent Walk		
	β	*t*	*p*	**β**	*t*	*p*	**β**	*t*	*p*	**β**	*t*	*p*
Infant Arm	.255	1.388	.175	/	/	/	/	/	/	/	/	/
Infant Leg	.142	.752	.458	/	/	/	/	/	/	/	/	/
Infant Height	.284	1.313	.199	/	/	/	/	/	/	/	/	/
Infant Weight	-.137	-.634	.531	/	/	/	/	/	/	/	/	/
Parent Arm	-.133	-.486	.631	-.086	-.386	.702	.034	.159	.875	.367	1.756	.089
Parent Leg	-.019	-.060	.953	-.286	-.990	.329	-.253	-.916	.366	-.100	-.337	.738
Parent Height	-.025	-.083	.935	.137	.483	.632	-.196	.722	.475	-.244	-.837	.409
Parent Weight	.097	.426	.674	.157	.824	.415	.268	1.466	.151	.500	2.804	.009*

However, we do see a significant contribution of parent body size to parent walking cadence (F(4,30) = 3.832, p = .012, R^2 = .338). This is driven by a highly significant contribution of parent weight, such that heavier adults have a slower walking cadence than lighter adults (Parent Weight β = .500, t(30) = 2.804, p = .009). Parent weight is positively correlated with the other parent anthropometrics (all p <.01), and all parent anthropometrics are positively correlated with walking cadence, such that larger measurements correlate with slower walking, though only weight and arm length reach significance (for correlations see Table 5.2). As the anthropometrics were highly correlated, it is possible that overall stature is the best predictor of walking cadence. We therefore calculated a height*weight composite score ('Stature') and entered this as a predictor for parental cadence in a simple linear regression. The new Parent Stature variable predicts walking cadence (F(4,34) = 10.092, p = .003, R^2 = .229).

Table 5.2 Correlations between parent anthropometrics

	Parent Arm	Parent Leg	Parent Height	Parent Weight	Walking Cadence
Parent Arm		.642***	.581***	.454**	.319^
Parent Leg			.788***	.380*	.137
Parent Height				.455**	.146
Parent Weight					.478**

* $p > .05$, ** $p > .01$, *** $p > .001$, ^ $p = .051$

That we do not find that parental height predicts infant SMT within this sample seemingly contradicts the findings of the previous chapter. This is likely due to the smaller sample size in the current study. A Bayesian linear regression with the same factorial design as in Chapter 3 confirms that this model has inconclusive Bayes Factors (around 1) for all predictors (Parent Height BF10 = .621), showing that there is not evidence for an absence of an effect. Adding the 10-month-old data from the current study to the sample collected in the previous study, our previous finding of a significant model and parental height predicting infant SMT stands ((F(6,85) = 3.576, *p* = .003, R^2 = .202; Parent Height *β* = .364, t(85) = 2.509, *p* = .014).

5.3.2 Infant motor activity

Finally, we were interested in whether the rate or regularity of infant SMT was related to the types of experience of own locomotion and caregiver locomotion the infant participates in, during her daily life. Two linear regressions with infant SMT and the RSD of infant SMT as dependent variables, and whether parents reported infants were carried for more than 30 minutes a day, could crawl or could cruise entered as predictors, revealed that although motor activity did not predict the rate at which infants drummed (infant SMT, F(3,31) = .887, *p* = .459, R^2 = .079), we find a significant model for the contribution of these activities to the variability in infant data (infant Relative Standard Deviation (RSD), F(3, 31) = 4.037 *p* = .016, R^2 = .281), explain 28% of the variance in the data. This result is driven by a highly significant effect of whether infants could cruise on infant RSD, such that infants who were cruising at the time of testing were more variable in their drumming (Cruising *β* = .532, t(31) = 3.349, *p* = .002). Full results are displayed in Table 5.3.

Table 5.3 Linear Regression Coefficients for effects of motoric experience on infant SMT and infant RSD

	Infant SMT			Infant RSD		
	β	*t*	*p*	**β**	*t*	*p*
Crawl	-.199	-1.120	.271	-.231	-1.472	.151
Cruise	.234	1.305	.201	.532	3.349	.002
Sling Use	-.053	-.305	.763	-.013	-.086	.932

5.4 Discussion

We predicted that the experience of being carried at either a faster (138 BPM) or slower (98 BPM) than average walking pace would directly influence the SMT of 10 month old non-walking infants. Our results reveal that infants in both the Fast and Slow conditions showed change in SMT from pre- to post-test in the hypothesised directions, with a mean rate of change of 20-30 ms. We are thus the first to provide direct evidence that carrying infants can bias the rhythms that they spontaneous produce. Further, by monitoring infant heart rate before and after the walking training, we provide evidence that this rate of change is not related to an increase or decrease in physiological arousal caused by the different paces of walking. We took additional correlational measures of infant and parent body size, and parent rhythm, including parent cadence. Parental body size predicted parent walking cadence, which corroborates our interpretation of the results of the previous chapter, that parental body size predicts infant SMT as parent body size sets the tempo of parent walking. However, perhaps due to the low power for correlational measures in the current sample, we did not find that parent body size or parent rhythm predicted infant rhythm in the current sample. Finally, we find that in our ten-month-old age group, infants who were cruising at the point of test displayed more variable drumming. Our results therefore confirm the two assumptions carried over from the previous chapter: parental body size predicts parental cadence, and ten minutes of training at a new cadence is enough to impact SMT, with this effect independent of arousal.

5.4.1 Anthropometric measures

As predicted, we see a significant model for the impact of parent anthropometrics on parental cadence. However, it was not the hypothesised height measurement that drove this result. Although the parental anthropometrics were all highly correlated, when measurements were entered into a multiple regression weight was the strongest predictor, with arm length also marginally significant. That arm length was a predictor may reflect that it is a composite score, consisting of breadth (spine to shoulder) plus length (shoulder to wrist). Measuring cadence, indicators of overall stature may be more important than length measurements alone. Prior research on body size and walking cadence do show an impact of both weight and height, and both are normally used to standardise gait measurements (e.g. Pierrynowski & Galea, 2001). Findings that gender may be a more sensitive measure than limb length (e.g. Bohannon, et al., 1996) may also reflect the overall different statures of males and females. This interpretation is corroborated by the significant predictive power of a composite Parent Stature measure.

We fail to replicate our prior finding that parent height predicts infant SMT, and this is likely due to a lack of statistical power, as Bayesian analyses reveal that we are not finding evidence that supports the null. When the 30 infants with pre-test data from the current study were added to the sample with equivalent data from the prior chapter (Chapter 4; Prior N with all measures = 55 infants, New N = 85), parental height remains a significant predictor of infant SMT, suggesting this was not a spurious effect.

Whilst body size predicted parental cadence, we did not find an impact of parental walking cadence on parent's own SMT as measured by drumming or tapping, or on infant SMT as measured through drumming. As such, we are unable to claim from our correlational measures that infant SMT is related to experience of locomotion at their caregiver's walking cadence. Though the caregiver tested was the primary caregiver at time of the appointment, the recent introduction of equal maternity and paternity rights meant that we saw a mix of mothers and fathers.[3] We did not collect data on time spent with different adults,

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[3] Note: When fathers were removed from analyses, all results are the same, and parental gender was not a significant predictor of any dependent variable.

and multiple caregiver families may weaken the effect we predicted to see. However, it is important to note that in the controlled laboratory environment our experimental manipulation worked, with novel experience changing infant SMT in the hypothesised directions, after only a ten-minute intervention. It would be of great interest to directly record parents' behaviour, perhaps using accelerometers worn by the infant and caregiver, and explore how the natural rhythms experienced in daily life impact infant SMT.

5.4.2 Infant motor experience

We find that infants who were cruising at the point of testing were more variable in their drumming than infants who were not cruising. In section 1.3.5 we detailed how increased vestibular experience may benefit cognitive and motor functions (Korner & Thoman, 1972; Rice, 1975; Gregg et al., 1976; Clark et al., 1977; Schneider et al., 1991), likely through increased variability of experience (Dusing & Hardbourne, 2010). Our findings are in line with Thelen's documentation of rigid, rhythmic stereotypies disappearing after the onset of more mature, volitional action; flexible and complex behaviour supersedes the regularity of initial motor outputs (Thelen, 1981). In Chapter 2, we demonstrate in a separate sample of same-aged infants that those who are cruising are better sensorimotor synchronisers. Speculatively, the mechanism that makes infants better synchronisers could potentially be more variable rhythmic behaviour, which may be achieved through greater motor control gained from own, diverse, locomotive experience.

5.5 Summary

In the current chapter, we sought to confirm that our previous finding of parent height predicting infant SMT was due to experience of the caregiver's walking cadence. Through a pre-test, training, post-test design, we successfully manipulated infant SMT with a ten-minute novel walking pace carrying intervention. This is the first direct evidence that carrying infants can change the rhythms that infants naturally produce. In the following chapter, we ask if the same experience of being carried influences infant rhythm perception at a neural level.

Chapter 6

The effect of novel carrying experience on sensorimotor alpha suppression

6.1 Introduction

Across Chapters 3 and 5, and to some extent in Chapter 4, we see evidence that experience of locomotion, whether active, through crawling, cruising, or walking, or passive, when being carried by the caregiver, impacts infants' rhythm production. We see an advantage for both the more motorically advanced and the more frequently carried infants in sensorimotor synchronisation skill (Chapter 3), and that being walked at a novel tempo can change the tempo an infant spontaneously produces (Chapter 5). There are of course two components to successful SMS; i) accurately predicting when the next beat will occur, and ii) timing one’s movements to coincide with the following beat, which involves initiating movement before the beat is present. The current chapter asks if part of the advantage of locomotive experience on SMS results from greater sensorimotor neural activation, utilised to *predict* the beat, during the perception of rhythmic auditory stimuli. In this way we are investigating whether improved rhythm production following experience of being carried is the result of improved rhythm perception.

First, we briefly outline why measuring sensorimotor alpha suppression, as an index of both action execution and action observation (and correspondingly, production and perception), is a good candidate for assessing the contribution of carrying experience to rhythm perception. Second, as this approach is more commonly used to measure perception of visual events, the relevant literature on sensorimotor alpha suppression for auditory observation and temporal information is explored. Finally, the evidence for experience-dependent change in sensorimotor alpha suppression in infant populations is considered. Data are then presented that test the idea of greater recruitment of the sensorimotor system during the presentation of rhythms previously experienced via carried walking, through EEG measurement of five-month-old infants.

6.1.1 Sensorimotor event prediction

Music elicits movement from early infancy (e.g. Zentner & Eerola, 2010), and in adulthood, the tempi of music influences the tempi of movement even when we are explicitly told to ignore it (e.g. Peckel, Pozzo & Bigand, 2014). The current chapter asks whether sensorimotor involvement during rhythm perception could be responsible for this relationship. Specifically, we ask whether an enhanced sensorimotor response to an auditory beat can be seen after a relatively short period of locomotive experience. In the previous chapter, we evidence that motor training at a novel tempo (via carrying) can influence the tempo of other self-produced actions (i.e. spontaneous drumming). This chapter asks if infants are using the information gained during this experience, when they hear the auditory presentation of the same tempo, triggering a stronger sensorimotor response. In such a way, better performance in SMS tasks might be contributed to by a sensorimotor perceptual benefit.

There is overwhelming empirical evidence that perceptual stimuli (visual and auditory), that do not require a motor response, and are perceived without overt engagement in a motor task, can elicit sensorimotor activation, as is outlined later (see Fox et al., 2016, for a review). Since the discovery of 'mirror neurons' from single-cell recordings in macaques, which fire in response to both performing and observing simple actions (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Rizzolatti, Fadiga, Gallese & Fogassi, 1996), motor activation in response to even-related perceptual information is often conceptualised as part of a mirror system. Csibra (2007) argues that sensorimotor activation recorded during observation of action may not be 'mirroring', but anticipating; that the response does not follow but precedes observation, and that this is a predictive mechanism. The benefit of motor activation during observation would thus be to better prepare us for what is coming next. Evidence for this view comes from findings that mirror neurons fire in anticipation of actions (Maranesi, Livi, Fogassi, Rizzolatti & Bonini, 2014). Csibra argues that such predictive ‘mirroring’ may be advantageous, allowing us to deal with unexpected events, and undertake coordinated interaction. "Even the simplest task, like taking a walk with someone or handing over an object to someone, requires precise adjustment of the timing of movements to the other party" (ibid., p.19).

A predictive mechanism account has also been conceptualised as an online forward model. Wilson and Knoblich (2005) propose that a well-calibrated and accurate action simulator can provide information about the current state of the world before actual sensory input arrives. Rather than processing all the incoming information during actions in real time, we perceive more fluently if we are generating expectations and then simply verifying whether our expectations have been met. Crucially, Wilson and Knoblich suggest that motor activation during (or preceding) *observation* may also be used to generate such predictions. Such a model may well explain the benefit to infants of learning the tempi of caregiver locomotion at a sensorimotor level. Whilst carried by the caregiver, the infant experiences the action of the carrier, with changing visual stimulation, likely congruent auditory feedback from steps, and critically, engaging in regular vestibular-motor action, as highlighted in Section 1.3.5. Accurate predictions may benefit the infants' own participation during carrying.

Further, Schubotz (2007) expands on how such online forward models may be used to create expectations, and use sensory feedback to check for discrepancies, even when there is not a direct motor representation on which to map the observed action; rather than a one-to-one mapping, Schubotz argues for somatotopic organisation, such that the *most relevant* effectors within the motor system for the *properties* of the action may be engaged, i.e. processing of the pitch of a non-executable sound may make use of premotor loops for vocal and articulatory actions, whereas observing an abstract shape rotating may make use of a motor loop for reaching actions, with shared spatial precision. In such a way, premotor areas respond to the prediction of sensory patterns in an efficient, body-centered manner, such that both top-down and bottom-up information result in a sensorimotor representation (Schubotz, von Cramon & Lohmann, 2003). These feed-forward models proposed by Wilson and Knoblich (2005) and Schubotz (2007) are of course largely in line with the Action Simulation for Auditory Prediction hypothesis (ASAP; Patel, 2006), outlined in Section 1.2. The ASAP hypothesis argues that human rhythmic skill is so refined because of the complexity of sensorimotor learning necessary to be a good vocal learner, with rhythmic skill utilising sensorimotor representations already in place for speech. There is certainly evidence for use of speech areas of the premotor cortex during auditory processing (e.g. Schubotz et al., 2003). In the current chapter, we hope to extend this body of literature and ask whether we may also be building strong and relevant sensorimotor representations when we are being carried. Are infants using the motor-temporal information they gain when carried for more accurate prediction during auditory perception? In the following section we outline how we can attempt to answer these questions using EEG to record sensorimotor alpha suppression.

6.1.2 Sensorimotor alpha suppression

A popular and practical approach to measure sensorimotor activation in humans has been the measurement of sensorimotor alpha suppression during action execution and action observation, using surface EEG. Whilst other methods, including use of fMRI and TMS, have been employed, EEG benefits from the relative ease of data collection, the passive nature of the recording and the high temporal accuracy afforded in the data. It is particularly useful in the current circumstances as it a reliable method for use with infants.

Sensorimotor alpha suppression describes the desynchronisation of neuronal activity over the sensorimotor cortex of the brain, in the alpha range: In adults, this corresponds to the 8-13 Hz frequency band. Sensorimotor alpha (also described as mu) is distinguishable from the classic (occipital) alpha signal, with differences evident in signal source, sensitivity to sensory events, bilateral coherence, and the frequency and power of observations (see Pineda, 2005, for a summary). As during resting state, highly synchronised neuronal activity is observed, desynchronisation, or suppression, can be used as an index of greater processing. Sensorimotor alpha suppression, measured as the reduction of the alpha power band relative to a baseline measure over central sites, has been recorded during action execution and action observation, across multiple studies, with both adult and infant populations (see Fox et al., 2016, for a meta-analyses of 85 studies). During execution, sensorimotor alpha suppression can be seen during both voluntary (controlled) and involuntary (reflexive or passive) actions (Chatrian, Petersen & Lazarte, 1959).

Much of the literature measuring sensorimotor alpha suppression has focused on visual observations, demonstrating that watching another person perform an action, such as reaching for an object, induces sensorimotor alpha suppression (e.g. Cochin, Barthelemy, Roux & Marineau, 1999; Muthukumaraswamy & Johnson, 2004a; Muthukumaraswamy & Johnson, 2004b). There is similarly convincing evidence of sensorimotor alpha suppression in infants when they are predicting the action of others, as presented visually (e.g. Southgate, Johnson, Osborne & Csibra, 2009; Southgate, Johnson, El Karoui & Csibra, 2010; Southgate & Begus, 2013; Southgate & Vernetti, 2014). In the following section we therefore present evidence for a similar representation of auditory events.

6.1.3 Auditory events

Novembre and Keller (2014) review how audiomotor experiences may be particularly important in group music making, with increased experience of audiomotor actions fine-tuning internal forward models, such that one has more detailed predictions and becomes better able to detect temporal properties of the actions of others. To illustrate, when a pianist presses on a key (a movement), which produces a tone (an auditory consequence); she experiences sensorimotor training. More training leads to strengthened action-perception couplings, such that the pianist hearing a piece she is familiar with will show greater motor activation than for an unfamiliar piece as measured by TMS (D'Ausilio, Altenmuller, Olivetti, Berlardinelli & Lotze, 2006), and greater auditory activation when pressing piano keys in silence, than a non-musician, as measured by fMRI (Bangert et al., 2006). According to Novembre and Keller (2014), in a musical framework, these experiences not only make us better at predicting the 'what' and 'when' of upcoming events, but also allow us to better represent the actions of others, and integrate these actions with our own.

It is in a similar vein that we ask if infants may be using information gained from walking experience to provide expectations of auditory rhythms. The open question is whether infants are experiencing some form of sensorimotor training when their caregiver carries them at a steady rate. Being held whilst the caregiver walks provides the infant with movement information (what) and temporal information (when). In the current chapter, we ask whether infants may be using a motor programme with those temporal dynamics when the same predictable tempo from that carrying experience is presented as an auditory rhythm.

Hearing auditory events should provoke the same response as in traditional, visual, action observation. In single-cell monkey recordings, the same excitation response is seen for hearing action sounds, as for seeing and hearing action sounds (Kohler et al., 2002). In Kohler's study, more excitation was seen for commonly produced action sounds, such as breaking open a peanut, than less common sounds, such as tearing paper. Whilst Kohler suggests this may be a goal oriented response, due to the functional significance of the nut breaking sound as an indicator that the task was successful, it is also possible that it is an effect of familiarity, such that the sound that monkeys have more experience of elicits the strongest response.

When adult human expert pianists hear familiar piano pieces for which they have a strong sensorimotor representation, they show increased neural activity over the M1 compared to novice listeners: Further, when pianists are anticipating musical notes, it is even possible to detect distinct activation over the coordinates for the thumb versus the little finger, depending on which would typically be used to produce that sound (Haueisen & Knosche, 2001). Indeed, whilst MEG measured responses in the 10 Hz (alpha) range are unsurprisingly clearer for executed actions that involve movement (finger tapping), than observed actions, Caetano, Jousmaki and Hari (2007) show similar neural modulations for auditory observation (hearing taps) as for visual observation (watching a finger tap a drum).

Whilst in studies that directly compare the influence of auditory, visual, and audio-visual (AV) events on sensorimotor alpha suppression (e.g. McGarry, Russo, Schalles & Pineda, 2012), the pattern tends to be that AV stimuli elicit the greatest desynchronisation, followed by visual stimuli, with auditory stimuli having the least impact; it is noteworthy that the complexity, and even duration, of audio stimuli in the above study were not controlled for, and the action observed was the simple act of ripping paper. Considering the argument that a core function of sensorimotor alpha suppression is to facilitate understanding of goal-directed action (e.g. Rizzolatti, Fogassi & Gallese, 2001), it is perhaps not surprising that auditory stimuli, which in such transitive actions may not be as informative about the goal, provides the smallest contribution. Alternatively, as stated above, sounds that are more clearly action related could show a response closer to that seen for visual stimuli. In the following section we consider evidence for a sensorimotor response to regularly timed events, as seen in the auditory presentation of a beat.

6.1.4 The importance of the timing of actions

Rhythm is the product of predictable timing; by definition it is a regular repeated pattern such that we can predict the onset of the next beat. Knowledge of the nature and onset time of a predictable action is enough to activate the motor system, even prior to the observation of said action (Kilner, Vargas, Duval, Blakemore & Sirigu, 2004). Consistent with these findings is evidence that (only) once infants have been familiarised to see a repetitive reaching action, infants show sensorimotor alpha suppression *in anticipation* of seeing the reach

(Southgate et al., 2009).

Motor activation has further been recorded during observation of rhythmic, intransitive actions. During visual observation of the rhythmic flexion and extension of a wrist, excitation as measured by motor evoked potentials (MEPs) was apparent, was *timelocked to the tempi* of the stimuli, and further, anticipated the action, as is seen during action execution (Borroni, Montagna, Cerri & Baldissera, 2005).

Neural excitability to timings can also be altered with rhythmic experience. Avanzino and colleagues (2015) recorded participant's SMT with a finger tapping task, before using TMS to record MEPs during visual presentations of motion at 1 Hz, 2 Hz, or 3 Hz, with the 2 Hz condition most closely matching participant SMT. Observation of a video of a metronome moving at SMT was not associated with increased motor excitability at any tempo. However, observation of a video of a finger tapping (a human action), was accompanied by increased M1 excitability in the 2 Hz condition, which corresponds to when the tapping was closer to the participants' own natural rate of movement. When participants undertook a series of visual training sessions with multiple viewings of 3 Hz finger tapping (Lagravinese, Biso, Ruggeri, Bove & Avanzino, 2017), cortical excitability was higher when observing 3 Hz than 2 Hz. Together, these studies argue that a) there is some specificity of the neural response to human motor actions, and b) that observational experience of a familiar action at a new tempo can alter the motor excitability to observation of that action. Thus temporal information is being utilised in ones' own representation of an observed action, and training can change the extent to which differently timed movements are treated as part of one's motor repertoire.

It is however important to note that despite the emphasis in individual studies on a special role for human, transitive actions for sensorimotor alpha suppression, a recent meta-analysis revealed no overall effect of whether stimuli observed were biological/non-biological, or whether they were object directed or not (Fox et al., 2015). This is in line with the hypothesis of Schubotz (2007), that we recruit our sensorimotor system even for events not possible to replicate on the body. Due to the small sample sizes of individual experiments, such results should perhaps be interpreted as reflecting *increased* processing for such actions, but should not limit exploration to *only* human transitive actions.

6.1.5 Sensorimotor alpha suppression to auditory features and intransitive actions in infancy

We therefore see evidence in adults that sensorimotor alpha suppression can be seen when we are trained with actions at novel tempos and that suppression is evident to auditory, as well as visual, stimulation. As in the adult literature, the majority of studies with infants have used sensorimotor alpha suppression to measure sensorimotor activation to visual stimuli. However, two studies have shown that infants show a similar response to auditory stimuli. In the first, infants were both given a rattle to play with, which made a distinctive, novel, sound when shaken, and were played another novel sound, that was not associated with an action, for an average of one week (Paulus, Hunnius, van Elk & Bekkering, 2012). Following training, infants displayed more sensorimotor alpha suppression when hearing the action sound than the control sound (novel and action sounds were counterbalanced across participants). In addition, the amount of sensorimotor alpha suppression recorded correlated with the amount of training infants undertook. In a study that trained infants on novel, two-part actions, Gerson, Bekkering and Hunnius (2015) demonstrated that infants show sensorimotor alpha suppression when presented with the sound associated with the motor actions only following motor-sound training, and not following observational visual-sound training.

As with adults, the focus of the literature also tends to be on transitive actions. However, some studies have explored the sensorimotor response to actions that are independent of object manipulation, including locomotion. More experience of crawling is associated with greater sensorimotor alpha suppression whilst watching crawling in 14- to 16-month-olds (van Elk, Schie, Hunnius, Vesper & Bekkering, 2008). De Klerk, Johnson, Heyes and Southgate (2015) experimentally manipulated locomotive experience by training non-walking infants to step on an infant treadmill. The amount of sensorimotor alpha suppression when watching videos of infant stepping was correlated with the quantity of infant stepping during the preceding training.

During infant action execution, sensorimotor alpha suppression is somatotopically organised, such that reaching shows greater suppression over the hand areas, and kicking over the leg areas (de Klerk, Johnson & Southgate, 2015). Adults, and even older infants (Saby, Meltzoff & Marshall, 2013), also show a somatotopic organisation for action observation. However, in younger 12-month-olds, this distinction is not yet present during observation: Watching a video of legs kicking or arms reaching resulted in a similar pattern of increased sensorimotor alpha suppression, which was not differentially organised over the areas shown in execution (de Klerk et al., 2015). This may reflect immaturities in recognising the effector performing the action during video presentation, or is alternatively consistent with the idea that in the face of less common actions (movement of an object via kicking), infants may be activating the parts of the motor system related to how they would achieve the same goal (movement of an object most commonly occurs with the arms). However, it is interesting that sensorimotor alpha suppression was shown over regions associated with both arm and leg movements, during observation, regardless of the visible action effector. This is also in line with the generalised event-prediction forward models that motivate the current work.

6.1.6 Aims and Hypotheses

The current study therefore aims to test if infants show greater sensorimotor alpha suppression when they are presented with sounds that match the tempo of walking they have experienced than when they hear sounds at another tempo. Five-month-old infants were securely held by the experimenter in a Baby Bjorn sling and walked on a treadmill at either a Fast (138 BPM) or Slow (98 BPM) tempo for ten minutes. The range of cadence of free-speed walking females aged 18-49 years is 98 BPM to 138 BPM (Whittle, 1990), and thus the extremes of the normal range were chosen to give the infants experience that was likely novel, in that carrying did not occur at the population mean cadence, but still ecological, in that it was not an unsafe or non-naturalistic pace. Following this carrying experience, infants were presented with counter-balanced blocks of metronome recordings at both the Fast and Slow tempi. We hypothesise that if infants rhythmic skill is related to greater utilisation of a corresponding motor programme following experience of being walked at that tempo, infants should show greater motor activation as indexed by sensorimotor alpha suppression when listening to the sound condition *congruent* to their walking training than the incongruent tempo.

6.2 Method

6.2.1 Participants

Fifty-two five-month-old infants took part in the study in a between-subjects design (23 female; M = 157 days, range = 136 to 180 days). Twenty-six infants (13 female; M = 159 days, range = 137 to 179 days) were randomly allocated to the Fast condition, and 26 infants (10 female; M = 154 days, range = 136 to 180 days) to the Slow condition. All caregivers gave written, informed consent concerning the experimental procedure for themself and their infant. Infants received a certificate and a t-shirt as a thank you for participation.

6.2.2 Procedure

Infants first experienced the treadmill training before the EEG auditory test.

Treadmill training. The carrying experience that the infants received was identical in protocol reported in Chapter 5. Infants were walked for 10 minutes at either the Fast (138 BPM, 434 ms between steps) or Slow (98 BPM, 612 ms between steps) pace.

EEG auditory test. Infants were seated on their parents lap facing an 102cm (width) x 58 cm (height) TV screen with two stereo speakers located behind a black cloth, underneath and to either side of the screen. The auditory stimuli consisted of Fast and Slow blocks that were presented in a pseudo-randomised order. The first 20 infants tested heard a Fast block first, and the rest a Slow block first; as block order was independent of walking condition, infants were equally likely to hear a congruent or incongruent tempo first. Each block consisted of four trials. Trials were a metronome recording of 12 beats at either 138 BPM or 98 BPM depending on condition, immediately preceded by a jittered 1500 - 3000 ms baseline period of white noise. The trials were matched by number of metronome beats, rather than by absolute time, to give infants equal experience of each type of stimuli across the testing session, resulting in trial lengths of 5000 ms in the Fast condition and 7000 ms in the Slow condition.

Within blocks, but consistent over each trial, the pitch of the metronome alternated between four possible pitches, in order to maintain infant interest. Throughout the trials, infants concurrently saw still colour photographs (houses, infant faces, landscapes) that changed roughly every two to three seconds, using a crossfade transition. These videos were designed to keep the infants still and facing the speakers. In infants were unhappy, the experimenter sat next to and slightly behind the infant and provided a continuous stream of bubbles for the infant to look at. Stimuli were created in Audacity and Apple Final Cut Pro and presented with MATLAB (The MathWorks, Natick, MA) using the Psychophysics Toolbox extension. Infants were exposed to up to 16 blocks (8 Fast, 8 Slow), so that each participant heard a maximum of 64 trials, 32 at the tempo congruent to their treadmill experience, and 32 incongruent. Testing continued for as long as the infants were not fussy, and if infants were compliant for all blocks, lasted just over eleven minutes.

6.2.3 Apparatus

Carrying experience. Walking experience was given on a Domyos Comfort Run treadmill, with 0% incline. Animations during the carrying experience were presented on a 12-inch video screen. Video recordings of the carrying session and parental cadence measure were conducted using a Logitech HD 1080p webcam positioned one meter to the left of and facing the treadmill, allowing profile view of the experimenter and infant.

EEG*.* EEG was recorded using a 128-channel Geodesic Sensor Net (GSN; EGI Inc, Eugene, Oregon), with respect to the vertex electrode. Due to a technical issue, half of the participants were sampled at a rate of 500 Hz, and half at a sampling rate of 250 Hz. Infants recorded at 500 Hz were therefore down-sampled within WTools (see below), so that every other data point was considered and results could be directly compared.

6.2.4 Data Processing

Video Coding. Video footage of each trial for each infant was examined by the experimenter for visible gross motor movements. In order to ensure that sensorimotor alpha suppression was related to the auditory perception of the beat, and not execution of movement, trials where infants made an overt action (waved arms, reached, kicked, or overall fussed), were excluded from analyses.

EEG Cleaning. Data were first filtered in NetStation version 4.5.4 (EGI, Inc., Eugene, Oregon), with a 0.3 Hz to 30 Hz bandpass filter. Data were then segmented into epochs around the beginning of each event. An extra 400 ms were added prior to the start of the baseline period and 400 ms added at the end of each trial, in preparation for the wavelet transformation to be performed later, which adds distortion to the data. For the five second long Fast trials, this resulted in a segment of 6800 ms, (-1400 ms to +5400 ms), and for seven second Slow trials, 8800 ms (-1400 to +7400 ms).

Each trial for which video coding had indicated the infant was still was then visually inspected for artifacts in the EEG signal. Common sources of noise in the signal included head and eye movements, which were not excluded in the video coding. In trials where data were generally clean and artifacts were apparent in less than approximately 20% of channels, those bad channels were marked for replacement. If more than this amount of channels were bad, the entire trial was excluded. For included trials, the NetStation bad channel replacement tool was utillised to interpolate data from surrounding channels in order that a maximal amount of trials could be used, without noise impacting the data. Cleaned data were exported to Matlab for further analysis. Only infants that following video coding and EEG cleaning had at least four clean trials per condition were included. This left a final sample of 13 infants in the Fast condition and 12 infants in the Slow condition, an attrition rate in line with the infant EEG literature (e.g. Stapel et al., 2010; Southgate et al., 2008; Southgate & Begus, 2013).

EEG Time-Frequency Analyses. The following analyses used Matlab toolbox WTools (Parise & Csibra, 2013). First, data were imported and re-referenced to the average reference. Morlet wavelets were then computed at 1 Hz intervals between 1 and 25 Hz. Average activation for each participant in each condition was computed across the valid trials. As mentioned, the morlet transform creates distortion at the beginning and end of the trial, so the 400 ms buffers were cut from the trial. Whilst 1000 ms of the preceding baseline to each trial were left, a 400 ms long section from 400 ms to 0 ms prior to the start of each trial was selected as a baseline period. Activity in the target alpha frequency range for this age of infants (5 – 7 Hz; Marshall, Bar-Haim & Fox, 2002; Berchicci et al., 2011; Southgate & Vernetti, 2014), during this baseline period was subtracted from activity in the 5 - 7 Hz range during the trial period. Whilst the stimulus presentation had a total duration of 5000 ms in the Fast trials and 7000 ms in the Slow trials, such that over the course of the experiment infants had equal exposure to the same number of beats in each condition, the first 4600 ms of each trial was selected for analyses in order to a) allow direct comparison of the two conditions, and b) capture the onset of the trial in order to best ensure infant attention to the auditory stimuli. Analyses used the channel average activation over 4 left sensorimotor channels, which have previously been identified as reflecting infant sensorimotor alpha suppression during observation/prediction (electrode numbers 30, 36, 37 and 42; Southgate & Begus, 2013; Southgate et al., 2009; Southgate et al., 2010; Southgate & Vernetti, 2014). Considering our exploratory hypothesis on a sensorimotor effect not constrained by a specific effector, and evidence of a non-somatotopic pattern of activation shown in young infants even in visual tasks denoting a specific effector (de Klerk et al, 2015), the consistency of activation in these channels during sensorimotor alpha suppression across a variety of tasks, rather than their somatotopic designation, motivated their selection. Figure 6.1 shows a map of channel locations.

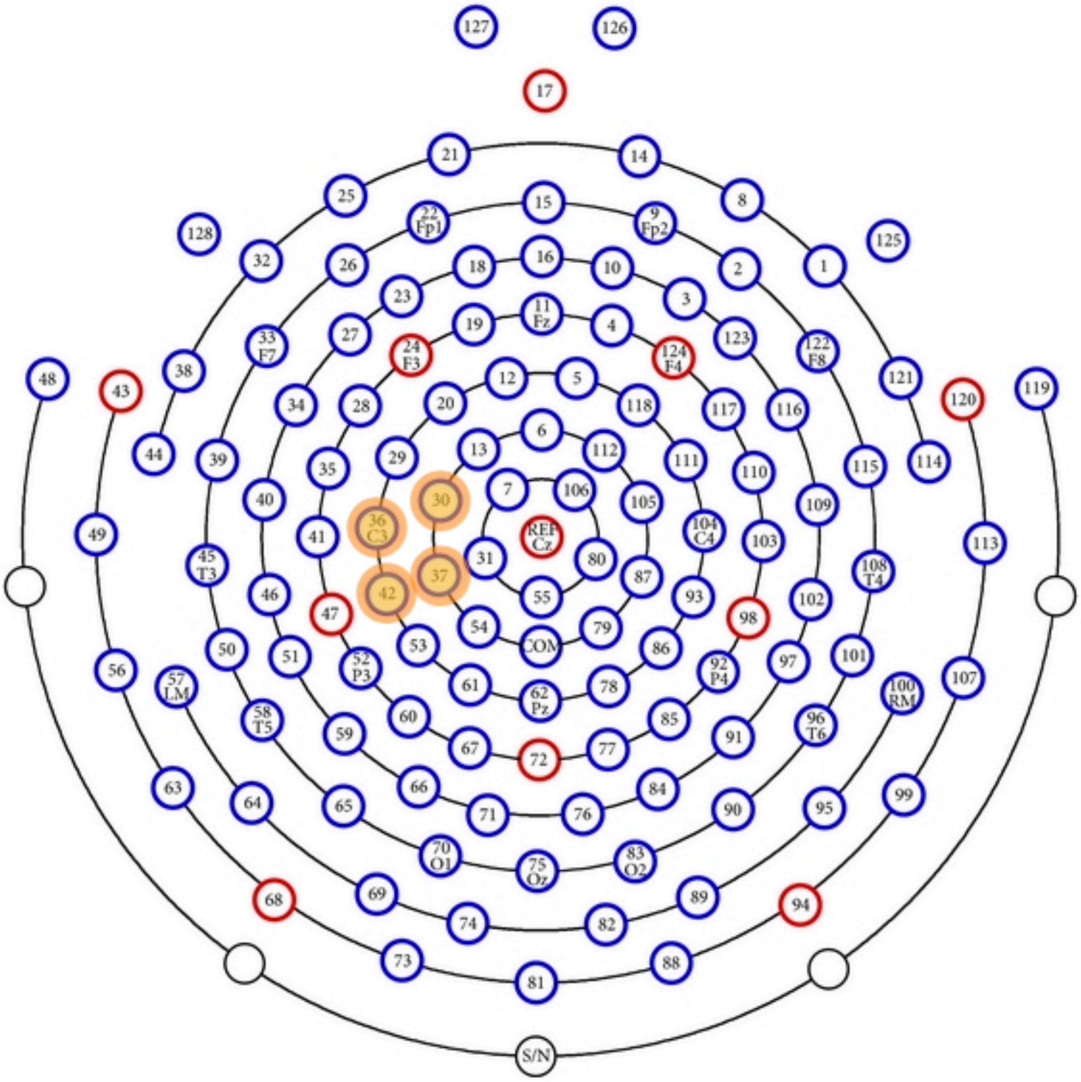


Figure 6.1 EEG electrode map, with group of electrodes from which sensorimotor alpha suppression data were extracted marked in yellow.

6.3 Results

We conducted a repeated measures ANOVA with sensorimotor alpha suppression during the Fast Sound trials and Slow Sound trials entered as within-subjects factors, and walking condition (Fast Walked or Slow Walked) entered as a between subjects factor. The predicted result was an interaction, such that infants would show greater suppression during the congruent trials (Fast Sound if Fast Walked, Slow Sound if Slow Walked) than during the incongruent trials (Slow Sound if Fast Walked, Fast Sound if Slow Walked). We do not find a main effect of Sound (F(1,25) = .183, $p = .672$, $\eta^2 = .007$) or Walking condition (F(1,25) = .767, $p = .390$, $\eta^2 = .030$). Critically, we do not see a Sound*Walking condition interaction (F(1,25) = 1.834, $p = .188$, $\eta^2 = .068$), see Figure 6.2.

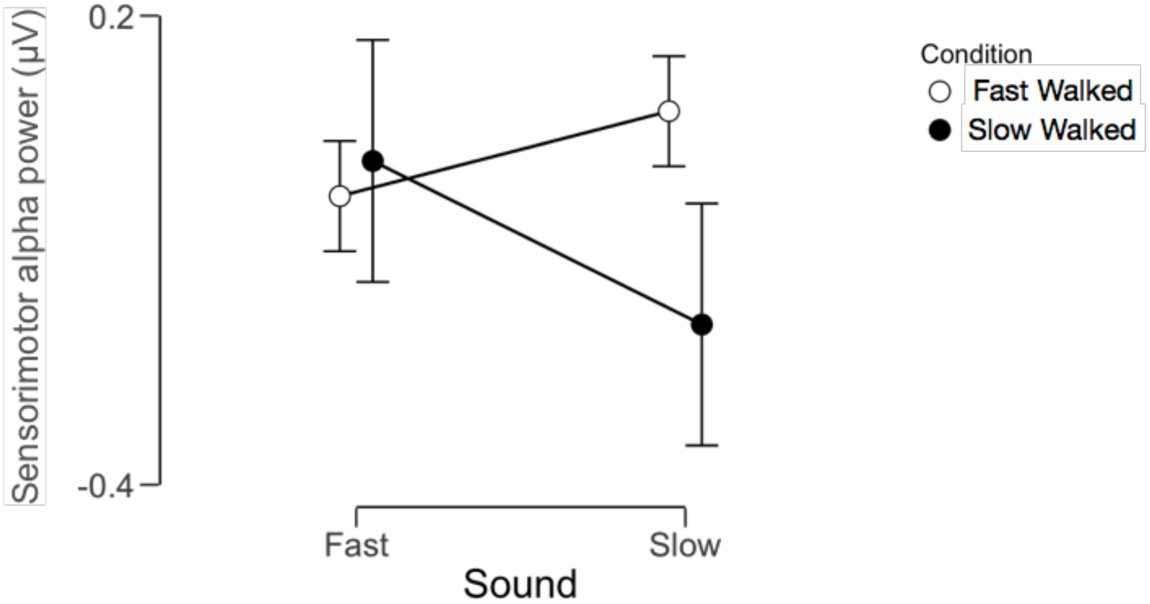


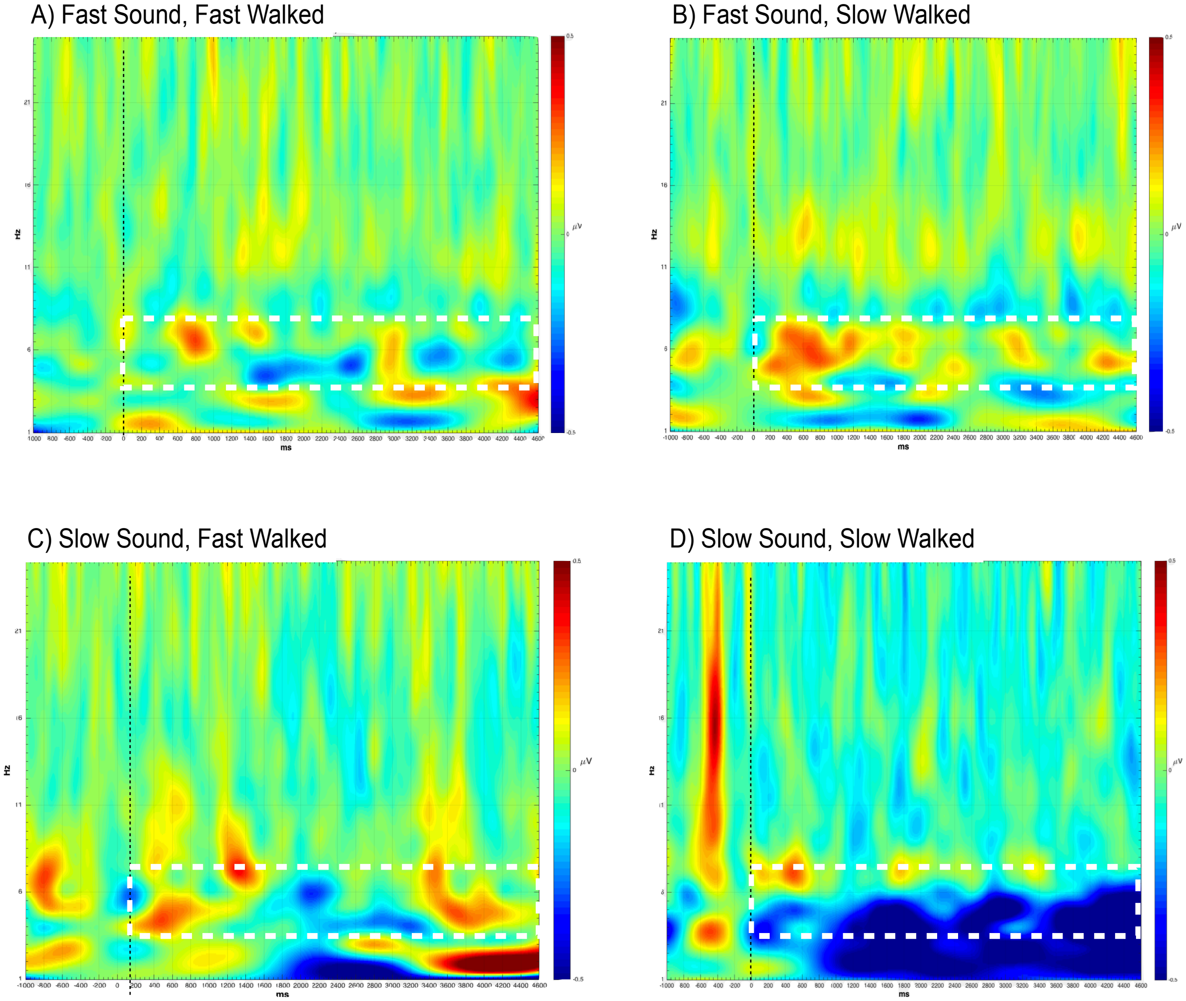
Figure 6.2 Graph to show the interaction between Walking Condition (Fast or Slow) and auditory presentation (Fast or Slow) on baseline corrected power in microvolts in the 5-7 Hz range, over the selected left sensorimotor channels (the infant sensorimotor alpha response). Lower power reflects greater suppression.

Whilst we do not find a significant interaction, the direction of responses in each condition is in the hypothesised direction (i.e., suppression in the congruent condition, activation in the incongruent condition; Fast Walk Fast Sound M = -

.031, SE = .068, 95% CI (-.171, .110); Fast Walk Slow Sound M = .078, SE = .158, 95% CI (-.247, .403); Slow Walk Fast Sound M = .014, SE = .071, 95% CI (-.132, .160); Slow Walk Slow Sound M = -.195, SE = .164, 95% CI (-.532, .142)). JASP (JASP Team 2017; Version 0.8.1.2) was therefore used to calculate the Bayes Factors for the interaction, using the default priors, to test if the lack of a significant interaction is reflective of evidence for the null, or is the result of insufficient power. It is assumed that $BF_{10} < .33$ provide good evidence to support the null, and a $BF_{10} > 3$ good evidence for the hypothesis (Jeffreys, 1939; Lee & Wagenmakers, 2014). A Bayesian repeated measures ANOVA with the same factorial design as above revealed evidence for the null (Walk*Sound BF_{10} = .328).

Figure 6.3 shows time frequency plots for the selected channels over the baseline and trial period. It seems possible that the absence of the predicted interaction may be due to an absence of any effect in the Fast Walk condition. We therefore decided to analyse the Slow Walk condition alone to see if we see sensorimotor alpha suppression when hearing the congruent Slow Sound compared to the incongruent Fast Sound. A paired sample t-test comparing the Slow Walked infants' activation during Slow Sound and Fast Sound finds no significant difference, with anecdotal evidence for the null (Slow Sound Mean = -.195, SE = .225, Fast Sound Mean = .014, SE = .079; $t(12) = .956$, $p = .358$, BF_{10} = .660). Further, when hearing the Slow Sound, Slow Walked and Fast Walked infants did not significantly differ from each other, but with anecdotal evidence for the hypothesis (Slow Walked M = -.195, SE = .225; Fast Walked M = .0779, SE =

.068. 95% CI; $t(25) = 1.162$, $p = .264$, $BF_{10} = 1.027$).


A) Fast Sound, Fast Walked

B) Fast Sound, Slow Walked

C) Slow Sound, Fast Walked

D) Slow Sound, Slow Walked

Figure 6.3 Time-Frequency heat map plots for the Fast and Slow sound conditions, plotted separately for the Fast and Slow walking conditions. A and D show congruent conditions, B and C show incongruent conditions. Trial onset is marked with black dashed lines. Analysis period and frequency band is marked with white dashed lines. The x-axes reflect time in miliseconds. The y-axes reflect the frequency of oscillations present in the EEG. Lower power is denoted with cooler colours.

Finally, the most basic criterion that could be applied asks if the decrease in activation seen in the Slow Walk Slow Sound condition truly reflects sensorimotor alpha *suppression*. As we have taken a baseline corrected, rather than raw measure of sensorimotor alpha suppression, what we are viewing in Figure 6.3 is whether there is more suppression during the analysis period (marked in white lines), compared to the period immediately before test when there was no auditory stimulation. If there is no effect of the rhythmic stimuli, we would expect a flat level of activation (as indicated by the green colour; activation around zero microvolts), If however, the auditory stimuli has led to increased suppression as compared to baseline, we expect activation to have decreased (indicated in Figure 6.3 as the blue colour, activation of less than zero microvolts). However, a one-sample t-test against zero reveals no significant suppression in the Slow Walked infants when hearing the Slow Sound, in relation to baseline, with anecdotal evidence for the null ($t(12) = -.868$, $p = .402$, $BF_{10} = .601$).

The equivalent analyses for the Fast conditions also show non-significant results, and also do not clearly support the null (see Table 6.1 for all comparisons with Bayes Factors). Had our results shown significant differences between congruent and incongruent conditions, further analyses to test the specificity of the effect to the sensorimotor regions would have been necessary. This is normally achieved through comparison of alpha power in the sensorimotor (central) area to a group of electrodes in the occipital area that show the ‘classic’ alpha response, with increased suppression during, for example, sustained attention (e.g. Southgate & Begus, 2013; Southgate et al., 2009; Southgate et al., 2010; Southgate & Vernetti, 2014). These analyses were not undertaken given our null results.

Table 6.1 Table of results for all comparisons performed between conditions, including Bayes Factors.

	Hearing Slow vs Hearing Fast			Congruent Condition vs Zero			Slow Walked vs Fast Walked		
	t	*p*	BF^{10}	*t*	*p*	BF^{10}	*t*	*p*	BF^{10}
Slow Walked	.956	.358	-.868	.402	.601	.660	/	/	/
Fast Walked	-1.090	.296	-.513	.308	.412	.446	/	/	/
Hearing Slow	/	/	/	/	/	/	1.162	.264	1.027
Hearing Fast	/	/	/	/	/	/	-.485	.651	.504

6.4 Discussion

Our results do not support our hypothesis that infants will show greater sensorimotor alpha suppression when they hear an auditory beat that matches the cadence of walking they were exposed to via a ten-minute carrying session. In Chapter 5, we demonstrated that a short carrying training session can influence the rhythm that infants spontaneously produce, and in Chapter 3 demonstrated that experience of being carried is beneficial to SMS. The current chapter was unable to elucidate a possible neural mechanism behind this behavioural change, in that infants do not seem to be preferentially exploiting a sensorimotor representation when hearing an auditory tempo that matches the rate at which they were carried.

Traditional inferential statistics showed the hypothesised direction of results, with non-significant *p*-values. Bayesian statistics were therefore employed to see if the found non-significant probability of sensorimotor alpha suppression dependent on carrying experience was the result of noise in the data, or reflects a true null. A Bayesian repeated measures ANOVA revealed that for the hypothesised interaction, the data convincingly supports the null. However, when we ran separate comparisons, to see if we saw sensorimotor alpha suppression in either of our Sound conditions (either, comparing congruent to incongruent Walking conditions, or in relation to baseline), we see mixed anecdotal evidence for the null or the hypothesis, with Bayes Factors close to 1, interpretable as near equal probability of results being observed under they hypothesis or the null.

It is therefore unwise to solidly conclude that carrying does not impact sensorimotor alpha suppression during listening, and better to more cautiously consider why the predicted results were not found with this test.

It is possible that infant recruitment of their sensorimotor system during the auditory presentation of a beat is not different following exposure to motor activation at the same tempo, at least as is reflected by desynchronisation of neural activity in the sensorimotor alpha band. However, it is also possible that the training given was not long enough, especially if infant participation in the act of being carried was not 'active' enough to form a strong motor representation. Alternatively, generally weaker effects for intransitive over transitive, goal-based actions, and auditory perception compared to visual perception, may explain our results. These possibilities are briefly discussed below.

6.4.1 Insufficient training

Other sensorimotor alpha suppression studies that give infants novel motor experience have multiple testing sessions over multiple days (van Elk et al., 2008; de Klerk et al., 2015; Gerson et al., 2015). Although in the previous chapter ten minutes of carrying experience was enough to change infant SMT, it may be that this amount of experience was not enough to result in visible changes in sensorimotor alpha suppression during a perceptual task.

Further, the training undertaken in the above mentioned infant sensorimotor alpha suppression studies (van Elk et al., 2008; de Klerk et al., 2015; Gerson et al., 2015), involved gross motor activities, including locomotion. In the current study, the action that infants were trained on was being carried, and our results may therefore reflect insufficient activation of the motor cortex during training, suggesting less *active* experience, in addition to less experience. We discussed in detail in section 1.3.5 how being carried is not purely passive, but requires the infant to adjust in order to aid the carrier, and to maintain head and postural control to keep a smooth visual representation of the world, requiring motor cortex activation on the part of the infant (cf. Solopova et al., 2003; Blanchard et al., 2005; Schmid et al., 2007; Olivier et al., 2007; Laufer et al., 2008; Negayama et al., 2010; Esposito et al., 2013; Reddy et al., 2013; Tse et al., 2013; Esposito et al., 2015; Wittenberg et al., 2017). However, the level of motor cortex involvement in being carried has not been directly measured, nor compared to activation for other actions. This necessary step is difficult to achieve because of the susceptibility to noise artifacts during EEG recording of locomotive movement, which necessitates movement of the head, and the need for wireless technologies to safely measure EEG whilst changing position. However, this technology is being rapidly developed at the time of writing, and should hopefully allow further investigation in the near future.

6.4.2 Intransitive action and auditory perception

Though a recent meta-analysis reveals no effect of whether actions were transitive or intransitive on sensorimotor alpha suppression (Fox et al., 2015), not enough studies had examined non-goal oriented actions for this to be included in the meta-analysis. The importance of goal-directedness remains highly debated (e.g. Cook & Bird, 2013; Cook, Bird, Catmur, Press & Heyes, 2014), but many authors subscribe to goal-directedness as central tenet of the human mirror system (e.g. Gallese & Sinigaglia, 2011), and if so, it is possible that the lack of a clear goal[4] in the auditory stimuli may contribute to our null results.

Whilst prior studies have shown sensorimotor alpha suppression during perception of auditory stimuli, the two comprehensive studies with infant response to auditory stimuli used a weeks worth of daily training sessions, with response magnitude correlating to the amount of training received (van Elk et al., 2008; Gerson et al., 2015). Similarly, in examining neural responses to intransitive actions, a study of infant locomotive experience did not show a significant difference in activation during observation of locomotion compared to baseline, but rather, a correlation between activation and walking experience (de Klerk et al., 2015). Our fixed level of training (the result of an experimenter, rather than infant controlled, training paradigm) may therefore have cost us variability that may have shed light on a relationship: Future studies would benefit from not only increasing training time, but doing so differentially amongst participants, or even better, examining infants longitudinally following multiple training sessions, such that a relationship between amount of experience and magnitude of sensorimotor alpha suppression could be measured.

It is also noteworthy that the infants in the current study were five-month-olds, younger than in other sensorimotor alpha suppression studies. The youngest study employing this measure to date used six-month-old infants

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[4] Although walking may be goal directed (i.e. to move through the world), the auditory representation of steps does not give information on movement; stepping could be in place.

(Southgate & Vernetti, 2014). Considering changes in strength of response and somatotopic organisation (de Klerk et al., 2015) during the first years of life, it is possible that older infants may show a different response to the ones tested here. Originally, we had planned that ten-month-olds, reported in the previous study in Chapter 5, would participate in this study following a second training session. Piloting revealed that ten-month-olds would not tolerate the passive listening task for long enough to get a meaningful amount of data, but that five-month-olds would be well entertained by the task. Therefore if this work were to be extended to older infants in the future, a more engaging task, still stripped of motor responses, would need to be designed. Such a task could involve a silent movie instead of still images, should it be deemed that any sensorimotor activation resultant from seeing a video containing actions would be sufficiently removed following the baselining procedure.

6.4.3 Future work

The current study was ambitious. Considering the impact of infant carrying on our prior measures of infants' own rhythm production (cf. Chapters 3, 4 & 5), we chose to investigate how the same experience would impact perception. In this way, we hoped to explore the perception-production relationship, hypothesising that improved SMS may be the result of enhanced sensorimotor processing of the auditory stimuli. Whilst there was support in the literature for various aspects of the design, the current study took a large leap from its predecessors, combining some of the less obvious aspects of both action and perception.

In adults, or even in young children, it is possible to investigate the impact of own walking rather than carrying. This may be a more fruitful exercise in that there would likely be greater motor activation, during action execution and possibly therefore also during perception. In addition, more motor experience can be given, and more perceptual trials recorded, giving enhanced power to statistical analyses and potentially elucidating if it is possible to capture the effect we predicted. However, this was not deemed the most interesting course of action: those learning to walk would by definition not produce a regular adult-like gait, and thus cadence would be difficult to reliably set, and those who already competently walk will have already have much experience of locomoting at altering tempi, questioning the novelty of training. It would be likely that giving experience of walking at a novel cadence in those who can walk would work similarly to the finger tapping studies reported earlier (e.g. Avanzino et al., 2015; Lagravinese et al., 2017); when the action is already in the motor repertoire, we might not necessarily expect huge differences from walking as from any other repetitive action. Infant carrying was chosen because it could be a true reflection of the ontogeny of this behaviour: the broader underlying question was whether these early experiences shape later, more complicated and abstracted, musical behaviour. Nonetheless, future work considering whether walking is 'special' would be welcome.

Adult work could also illustrate whether the component parts of the reported study were the best measures to take. For example, a perfectly timed metronome sound, created artificially, was used as the audio stimuli, and not the recording of actual footsteps on ground, with natural variation that would most likely tally with infants motor experience from being carried. This was intentional, as we were ultimately interested in whether carrying was related to movement responses when hearing music, and was in line with the idea that recruitment of the sensorimotor system does not depend on one-to-one matching (Schubotz, 2007). However, it would be interesting to see if having been primed with walking at a fixed rate, adults show more sensorimotor alpha suppression to hearing more naturalistic sound than the perfect replica. One could also ask if experiencing exaggerated audio feedback from steps, or performing the training without background noise, thereby strengthening action-perception couplings, would produce stronger results.

Finally, our motivation for this study was to see if carrying experience facilitates rhythm *production*, through enhanced sensorimotor representations used during rhythm *perception*. If this study were to be run again, it would be interesting to see if the carrying experience has sensorimotor consequences not illuminated by the sensorimotor alpha suppression measure. For example, are infants showing increased sub-threshold EMG activation during presentation of the congruent auditory stimuli? Alternatively, could the benefit be purely perceptual, such that carried infants are infants better predictors of the auditory stimuli, as could be measured by, for example, mismatch negativity responses to deviations in the rhythm?

6.5 Summary

The aim of the current chapter was to explore if infants were recruiting a motor program gained from carrying, when they heard rhythms that matched the rate at which they were carried. Sensorimotor alpha suppression was used as an index of infant sensorimotor engagement during a passive listening task following a period of walking. We did not find evidence of sensorimotor alpha suppression at test; however, we did not see evidence for the null either. Whilst it is possible that infants do not recruit a motor programme for being walked when hearing a corresponding rhythm, further exploratory work is necessary to confirm if the paradigm used was the best test possible. In the next, final, chapter of the thesis, we summarise the findings presented across the experimental chapters, synthesizing our results and considering their strengths and limitations, and making both concrete and theoretical suggestions as to how the work presented can be extended in the future.

Chapter 7

General Discussion

The remarkable human proclivity to move to music, and the complex beat perception and production skills that this behaviour requires, is something that distinguishes us from our closest relatives (Bispham, 2006), perhaps as special to us as is our ability for spoken and written language (Merker et al., 2009), and can be the source of great beauty (Scruton, 1999). In recent years there has been a movement to understand our musicality as a set of cognitive and behavioural traits (Honing et al., 2015), and by doing so, further our understanding of where these skills come from. In particular, studying the ontogeny of such traits allows us to better understand the roots of our complex adult behaviours (Ravignani et al., 2017). According to scientific observations, infants cannot dance (Zentner & Eerola, 2009). This lack of trained expertise provides a window of opportunity, to observe, and experimentally manipulate, early rhythmic tendencies, and in doing so draw inference on the core experiences that contribute to aptitude.

Whilst many studies on the origins of human sensorimotor synchronisation (SMS) are currently focused on a social glue (Brown, 2003; Cross, 2009; Merker, 2009), or language or vocal learning hypothesis (e.g. Patel 2006), there have also been interesting explorations throughout the past decades of the idea that vestibular information may be crucial for complex beat production skill (e.g. Phillips-Silver & Trainor, 2005; 2008; Trainor et al., 2009; Todd et al., 2007; Todd & Lee, 2015), and some suggestions that bipedal locomotion (Trevarthen 2000) and infant carrying (Ayres 1973) may be the reason that this is so important for humans.

The work in this thesis aimed to see how the vestibular information we receive from locomotion; both our own, as experienced by infants as crawling, cruising, or walking, and our caregivers', as experienced when infants are carried, might impact our beat production and perception abilities. As outlined in Chapter 1, we were inspired to answer the following questions:

- Does infant SMS change with age over the first two years of life? Is infant performance related to the presence of a social partner, or, is the tempi of auditory stimulation, close or far from their natural rate of movement, important?
- Is infant SMS a function of their locomotive experience? Does novel bipedal walking experience improve SMS, and how is infant performance related to existing locomotive experience?
- What is the SMT of young infants and how does this change with age? Are the rates of these rhythms that we naturally produce the product of our own biomachinery, or alternatively, can it be linked to the rate of walking cadence that we most experience?
- Can we experimentally manipulate infant SMT with novel walking experience? In addition to the effect on spontaneous behaviour, does this experience also effect the neural processing of auditory rhythm?

This chapter summarises and amalgamates the experimental findings of this thesis, both in relation to the existing literature and by synthesising results from across the experimental chapters. Limitations of the reported studies will be acknowledged, and avenues for future work will be presented.

7.1 Summary of findings

The research program reported in this thesis began by investigating the impact of a social partner and the tempi of auditory stimuli on infant tempo-matching ability of infants. Inspired by findings of the benefit of both a human partner (Kirschner & Tomasello, 2009) and tempi close to SMT (Provasi & Bobin-Begue, 2003) on the accuracy of SMS in toddlers, in Chapter 2 we were inspired to see if the same scaffolds assist early infant markers of *synchronisation*. Ten- and 18-month-olds were engaged in a bell ringing to music task, and produced various rhythmic behaviours, including, but not limited to, bell-ringing. Ten-month-olds were unable to regulate their bell ringing, ringing at a relatively constant rate regardless of the experimental manipulations of tempi and absence/presence of a social partner. At 18-months-of-age, the infants were able to modulate their ringing somewhat, slowing down their movements to the slower ISI music. Considering that other studies had not evidenced age effects between four- and 24-months-of-age (Zentner & Eeorla, 2009), our study provided a novel indication of progression in infant SMS, and was the first to chart a developmental change in tempo-flexibility in the first two years of life. Further, though tempo-matching was not enhanced by the presence of a live partner at either age group tested, the 18-month-olds changed the types of behaviour they displayed, engaging in more non-ringing rhythmic movements in the absence, rather than presence, of the human partner. In contrast to the idea of joint action, or a common goal, motivating or informing infants to move *in time* with the experimenter, we saw the older infants seemingly suppressing their natural bouncing or head bobbing behaviours when the experimenter was present. We argue that this may reflect the 18-month-olds restricting their behaviours to match the goal of the experimenter ('she is ringing, so I should also only ring'), but the lack of an effect on tempo-matching was intriguing. That infants were improving from 10- to 18-months, but this was independent of an effect of a social partner, suggests that something other than an increased drive towards interpersonal synchrony is driving increased SMS ability. These findings spurred us to measure how locomotive abilities, which are rapidly changing between 10- and 18-months, might impact SMS.

Chapter 3 hypothesised that training (a separate group of) non-walking 10-month-olds to step on an infant treadmill would improve their tempo-matching in the bell-ringing task. We did not find evidence for our hypothesis; in fact, we saw a non-significant increase in mismatch with the auditory stimuli following training, which we think is likely the product of tiring the infant. However, we did find that infants who could crawl at the time of testing had a lower mismatch than infants who could not crawl. Further, we saw that infants who were reported to be carried by their caregiver in an infant sling had a lower mismatch than infants who were not carried, with evidence that sling use may even bring non-crawling infants on a par with crawling infants. These results confirmed our hypothesis that locomotive experience is important for infant SMS, but also highlighted that this experience does not need to be self-generated to be effective.

The fact that carried locomotive experience impacted upon SMS inspired us to question what information infants were gaining from being carried, and why this would change their rhythm capabilities. Considering past evidence that the carrying practices of a culture impact the rhythms produced by that culture (Ayres, 1973), we wondered if infant SMS ability improved because it primed the rhythms that they would spontaneously produce, giving them a different starting point (or 'base rate') for synchronisation, or SMT. Previous research linking body size to preferred tempo to perceive and move at show that larger bodies prefer slower rhythms (Mishima, 1965; Todd et al., 2007; Dahl et al., 2014). Larger bodies walk with longer strides and therefore a slower walking cadence (Beck et al., 1981; Sutherland, 1997; Dixon et al., 2014), and so this evidence could suggest that locomotion, a predominant rhythmic behaviour, contributes to our SMT. Alternatively, consistency between body size and SMT could be the result of biomechanics: larger bodies may prefer slower steps and slower taps because it is the optimal rate to move their consistently proportioned effectors. Infants, however, provide a means of dissociating body size from locomotive experience, as their predominant experience of locomotion is from their caregiver carrying them. In Chapter 4 we utilised this dissociation in a large-scale descriptive study of infant SMT. One hundred and fifteen infants aged 4- to 33-months provided SMT data in a free-drumming task. We found that infants became faster and more regular with age. We also found that caregiver body size, but not infant body size, predicted infant SMT, such that those infants with taller parents had a slower SMT than infants with shorter parents.

The use of body size as a proxy for caregiver walking cadence in Chapter 4 necessitated an experimental test of the impact of walking cadence on SMT directly, in order to confirm our interpretation of the previous data. In Chapter 5 we therefore utilised a training design to test if experience of being carried at a novel walking cadence would impact infant SMT. Ten-month-old infants' SMT were measured before and after they were carried at either a Fast or Slow walking cadence. We found that infants in the Fast condition demonstrated a faster SMT after training, and infants in the Slow condition slowed down their SMT after training. Further, we measured infant heart rate and found no overall change from pre- to post-test, and no change dependent on condition, suggesting that the results were not due to differing states of arousal caused by the walking at different rates. Infant SMT itself seemed to be primed by the rate of walking they had just experienced, lending support to our idea that our rhythmic preferences are at least in part set by our experience of locomotion.

The final question we asked was whether the experience that impacted SMT in Chapter 5 could also impact SMS, if infants exploit a motor programme for being carried when they hear music of the same tempo, enhancing their ability to *predict* the beat. We were curious if the reason that infants who were reported as carried in a sling more often were better synchronisers in the work presented in Chapter 3, was because their greater breadth of walking experience meant they were engaging their motor system more when hearing the music we played them. In Chapter 6 we therefore tested infants' neural responses to hearing rhythms after carrying them at a Fast or Slow rate. Five-month-old infants were played auditory rhythms that either matched or did not match the rate at which they were carried. Using EEG we measured sensorimotor alpha suppression, an index of infant activation of a motor programme, during the auditory presentation. We reasoned that if being carried honed the infants motor system at the tempo at which they were walked, then infants would show more sensorimotor alpha suppression to an auditory rhythm at that tempo than an alternative. We did not find evidence that infants were activating their motor system differentially for the two possible tempi dependent on the rate at which they were walked, or indeed, any evidence for sensorimotor alpha suppression during the listening task. We ran Bayesian statistics to see if our results supported the null, and found that in most cases the Bayes Factor was around one, suggesting no clear pattern of data for either the experimental or null hypotheses. Considering that we find evidence that the walking experience impacted rhythm production in Chapter 5, but no evidence for a change in rhythm perception in Chapter 6, our findings motivate future work to ascertain a more sensitive measure of how the brain uses information from carrying in musical contexts.

In sum, the work reported in this thesis documents a progression in infant SMS abilities in the first two years of life (Chapter 2), and evidence that locomotive experience, both from self-propelled locomotion and from being carried by the caregiver, impacts upon the temporal matching of infants' movement to music (Chapter 3). Whilst the work successfully describes how being carried impacts our natural rate of rhythmic movement (Chapters 4 & 5), attempts to measure a link between carrying and rhythm perception have yet to prove successful (Chapter 6).

7.2 Synthesis and limitations

The studies conducted across this thesis were formulated to meet a common aim; to elucidate the early rhythmic behaviours that build into complex beat perception and production skills. Further, the individual studies had methodological commonalities, designed to allow direct comparison across the individual studies, and offer some partial replications. Such comparisons can provide novel insight and provoke many new questions that are not possible from single studies. A synthesis of the current work will therefore be presented, and suggestions for improvements and extensions that are common to the themes introduced will be outlined.

7.2.1 Infant SMS ability in light of infant SMT

The first half of the thesis examined infants' ability to move in time with an external auditory beat. Following our finding that 18-month-olds demonstrated some SMS ability where 10-month-olds did not (Chapter 2), 10-month-olds were selected in Chapter 3 as ripe for training. Chapter 2 demonstrated that these infants were capable of a sensible, measureable response (i.e. 10-month-olds produced rhythmic movements in the presence of music), but that their performance was not going to hit the ceiling of what an infant is capable of (i.e. there was room for improvement, as evidenced by the older 18-month-olds). In Chapter 2, we saw an effect on infant accuracy of the tempo of the presented music, which is in line with investigations of SMS in young children being accurate when close to SMT (e.g. Provasi & Bobin-Begue, 2003). Using the same auditory stimuli and motoric task as Chapter 2 in Chapter 3 allowed the pre-test condition to serve as a replication, and corroborated that 10-month-olds movements were better matched to the tempo of music during faster songs. The following section expands on this finding, in light of the existing literature and the results of the chapters that followed.

In both Chapters 2 and 3, we concluded that infant performance was significantly worse in the slowest 600 ms ISI condition as the 600 ms ISI music was furthest from infants hypothesised SMT. This interpretation was in line with the extant relationship between age and SMT; younger humans prefer faster rhythms (McAuley et al., 2006). As toddlers demonstrated an SMT of around 400 ms ISI (Provasi & Bobin-Begue, 2003), it was legitimate to estimate the SMT of infants as slightly faster. Our bell-ringing data seemed to confirm this; across all auditory stimuli, in Chapter 2 10-month-olds rang at a mean of 329 ms ISI, and in Chapter 3 pre-test, 10-month-olds rang at a mean of 366 ms ISI, providing an estimate of a SMT of around 350 ms ISI for this age group. In both Chapters 2 and 3, post-hoc tests reveal infant bell-ringing was much closer to target in the 300, 350 and 450 ms ISI than to the 600 ms ISI track, but no difference between the 300, 350 and 450 ms ISI conditions, ostensibly corroborating that the SMT of our 'non-synchronising' infants lay within this faster range.

However, in Chapter 4 we carried out large-scale data collection to determine the SMT of infants across the first three years of life, which allows further interpretation of our previous results. Infant age in the large opportunity sample was dispersed, ranging from four- to 33-months. When all 115 infants were taken together, the mean ISI of infant drum hits was 542 ms, with a mean RSD of 23%, but there was a consistent relationship with age, such that older infants were faster and more regular. In Chapter 5, we were able to replicate and hone these results for the 10-month-olds tested. Pre-test SMT was measured at 508 ms, with a mean RSD of 20%. These results suggest that performance in Chapters 2 and 3 reflects not only how *close* to SMT the auditory target was that matters, but more importantly, whether infants had to accelerate or decelerate movement to match the target. This is also consistent with the early childhood literature (e.g. Provasi & Bobin-Begue, 2003; 2008; Provasi et al., 2014). If 10-month-old SMT is around 500ms, no difference in tempo mismatch between the 300, 350 and 450 ms conditions suggests that it was only when infants had to *decelerate* from their SMT that they were less accurate.

Whilst we happily accept this interpretation, it begs the question of whether a ringing rate in the 300 ms conditions of 321 ms (Chapter 2) or 335 ms (Chapter 3 pre-test), reflects a more fruitful attempt at synchronisation than infants were credited for, as they were ringing at a rate likely over 150 ms faster than their SMT. Within the chapters concerned, we reasoned that the ultimate test for synchronisation was whether infants were performing as adults, in terms of mean ISI and the variation around that mean, and found that this was not the case in our infant groups. In order to investigate progress in infant performance (even if not reaching adult level), we also applied the looser criterion of tempo-flexibility, checking the stability of their tempo-matching across different tempi - in Chapter 2 we took the result of 18-month-olds being equally good across tracks as evidence that they were adapting to the music. We maintain that the older infants' ability to slow down in the 600 ms condition, which led to equal performance across tracks, reflects more mature SMS. However, these measures, of adult-equivalent accuracy and of stability across tracks, are perhaps not as sensitive to infant skill as we had hoped. The similar performance in the 300, 350 and 450 ms conditions in both age groups may not reflect a true null, but rather the close range of target ISIs chosen, and the natural variance inherent to poor infant performance. One way of addressing this question would be to provide multiple tempi faster than 300 ms, and test to what speed we see stable performance, before an assumed drop-off in the ability to accelerate is apparent.

Another option to gain more insight into infant performance in the faster tempo tracks without changing the testing paradigm would be to use circular statistics. Our analyses took the mean ISI in milliseconds between infant rings within a bout of ringing, and calculated the distance between this mean ISI and the target ISI of the track as our measure of tempo mismatch. We did not look at the distance of each ISI from the target ISI, because the variation in infant ringing made it very difficult to align each data point to its target point on a one-to-one basis; i.e. if the target ISI was 600 ms and the beat occurred at 600, 1200 and 1800 ms, and the infants rang at 400, 800 and 1200 ms, distance from target of each data point would reveal distances of 200, 400, and 600 ms, suggesting a mean asynchrony of 400 ms in this example, and which would only get larger with time. Rather, under our measure, the infant's mismatch would be 200 ms, as they were consistently ringing with a 400ms ISI in the 600 ms condition. Adult literature is more precise, measuring *negative* mean asynchrony; as a key feature of human SMS is that movements anticipate the beat, the dependent variable is the difference from the upcoming target. The example above shows that this is near impossible with infants; with large variability we would not be able to decipher if a movement was following the previous beat or predicting the next. However, a more sensitive way to measure what is occurring without having to align data points to a linear target would be to use circular statistics, which allows measurement of the distribution of data around the natural periodicity of a circle (Fisher, 1953). Accordingly, a full circle would represent the target ISI, with the beats produced by the infant represented as vectors with a given angle around 360 degrees, dependent on their relative phase from the referent (i.e. an ISI of 300 ms in the 600 ms condition would result in a vector at 180 degrees). Following multiple instances, the length of the resultant vector can be measured and given a value between zero and one, where one is maximum consistency (all points align around zero/360 degrees) and zero is a random distribution. The Raleigh test allows for significance testing on the length and spread of the resultant vector to reject the null hypothesis, that the population is distributed uniformly around the circle (Fisher, 1995). A circular approach is considered best practice for sensitive measure of noisy rhythm data (Repp & Su, 2013).

Circular statistics have been used in studies of SMS in young children (e.g. Kirschner & Tomasello, 2009), and theoretically, were the analyses of choice for the current thesis. However, the number of rings in a bout in Chapters 2 and 3 (and similarly, hits whilst drumming in Chapters 4 and 5), never came in the quantity necessary for accurate circular statistics, where a minimum *N* of 100 is required (Wilkie, 1983). Work with animals, with whom it is also difficult to obtain large numbers of data points, has checked against low-powered circular relationships happening by chance, through Monte Carlo simulations (Patel et al., 2009). The simulations randomly pair the observed data with different target ISIs, to test if the observed degree of synchrony is likely to have arisen by chance (Patel et al., 2009). However, even in Patel's (2009) study of Snowball the cockatoo, trials had 101 head bobs on average and the minimum bout length was 12. Relying on a minimum bout length of 12 would exclude many of the infants tested across the experiments reported in this thesis. This low power is of course problematic for all analyses, and is why we stuck to the basics, and have reported the descriptives for each analysis. We believe, in charting the development of a behaviour, especially one as under studied as this, it is valuable to record and present what infants do, rather than assigning adult standard minima for what 'counts' as performance, and giving a highly selective account of the very best of what infants may achieve. This is not to say that we did not try to maximise data collection. Provasi and colleagues (2014) note that facilitation of sustained, as opposed to sporadic, rhythmic behaviour can be achieved in newborns by providing them with a dummy on which to suck. We attempted to provide a similar naturalistic and enjoyable motivation in the current studies, using bells and drums, but it is possible that there could be more successful ways of encouraging infant rhythm production. For example, providing a choice of instruments or surfaces for infants to engage with might have been more successful, allowing individual preferences to be met. In the absence of more data across the board, it may be an interesting extension of the current work to select infant 'case studies', where there are infants who contributed large quantities of data, and use more the more sensitive statistics described above to see how these infants compare to the animal case studies being reported.

Whilst it may therefore be the case that we were not able to coax enough information from our data to elucidate whether or not infants were moving away from their SMT to faster tracks, there is an alternative explanation. We may be able to reconcile the slower than hypothesised SMT found in the latter half of the thesis with the faster rate of ringing to music in the first half of the thesis, through consideration of the idea that the presence of music may have in itself changed the infants' SMT, regardless of that music's tempo. Three to five year old children have been shown to speed up their rate of tapping in the presence of auditory stimuli (Bobin-Begue et al., 2014). Adults not synchronising with the beat of music they are listening to nonetheless walk faster when listening to music than compared to hearing the same paced metronome (Styns et al., 2007). Whilst adults can purposefully entrain their motion on a rocking chair to match the beat music when instructed, *spontaneous* rocking is simply faster in the presence of music than silence, with no impact of the tempo of music presented (Demos, Chaffin & Marsh, 2010). If it is the case that we have one SMT, as measured in silence, but a different, faster SMT, as measured in the presence of music, this provokes new questions for future research. First, is an individual’s 'resting state' SMT correlated to their 'musical' SMT? What property of musical stimuli provokes the faster rate? Could the change be dependent on the perceived 'groove' of the music (Stupacher et al., 2013), or could higher arousal, such as can be easily measured through heart rate, pupil dilation or galvanic skin response, explain the difference? Is some process of phase resetting, as can cause finger tapping in traditional SMS tasks to accelerate (see Repp & Su, 2013, for a review) happening when we hear the music, which then alters our SMT? Finally, which of the two measures truly reflects our base rate of movement from which we need to adapt for synchronisation?

In sum, our finding in Chapters 4 and 5, of infant SMT being slower than hypothesised, casts a new light upon the level of tempo-matching we saw in infant attempts at SMS in Chapters 2 and 3. Closer matching in the tracks with a faster-than-SMT ISI, compared to reduced performance in the single 600 ms slower-than-SMT ISI, may reflect a more successful attempt at synchronisation during music with faster tempi than we credited the infants for. Further investigation is warranted, using more sensitive statistical measures, case studies, and by asking how infant SMT changes in the presence of music.

7.2.2 Variability

A theme that grew with the thesis was the idea of variability. In Chapter 1, we expand on the suggestion of Dusing and Harbourne (2010), that variability of motor experience is beneficial to the developing infant, mainly for the sake of trial and error, important for learning efficient patterns from noise. We further discuss Thelen's (1979; 1981) observation that volitional, coordinated movement is more variable than the preceding rhythmic stereotypies. These ideas advocate variability, suggesting it reflects more advanced performance, and yet, there are instances in the thesis where we argue the opposite. In the comparison of infant and adult SMS in Chapter 2, we highlight the significantly higher variance in the infants and conclude that this indicates they are not performing with an adult level of temporal matching. In Chapter 4, correlational analyses on infant SMT reveal a significant relationship between age and variability, such that older infants are much less variable in the rhythm they naturally produce than younger infants, and we conclude that this reflects better motor control amongst the older infants, leading to a more reliable measure of SMT.

On the other hand, in Chapter 5 we demonstrate that amongst same-aged infants, those who were more motorically advanced (i.e. cruising) showed greater variability in their SMT. We proffer an interpretation that variability in own SMT, as a product of locomotive experience, may be due to increasing control of volitional movement necessary for locomotion, which led to less 'reflexive' rhythmic movement in the SMT task in Chapter 5. Further, the same process may also contribute to a more flexible base rate of rhythmic movement from which to synchronise in Chapters 2 and 3, as reflected in the superior performance of the older infants in Chapter 2 and the locomoting infants in Chapter 3.

How then, to tally the two accounts of variability. The first, variability is bad account, seems to be prime when we are comparing across large periods development, especially to adulthood. In contrast, the variability is good account seems to well describe snapshots of development.

In a review of the development and enhancement of SMS ability, Repp and Su (2013) conclude that variability decreases as a product of development, through childhood, but a more complex relationship exists in adults; despite more experience of SMS, trained musicians do not tend to be less variable non-musicians in traditional tapping tasks, except in cases such as highly trained percussionists, who are more precise than other professional musicians. In atypical populations, including developmental coordination disorder and dyslexia, there is evidence for greater variability, which may reflect a common cerebellar dysfunction (Repp and Su, 2013). In light of these findings, the pertinent question may be, is all variability equal? The contrast between expert musicians (little effect) and young and atypical populations (strong effect), suggests healthy development matters much more than experience. Infants are not just small adults, and the huge amounts of learning they need to do in a short period of time may lead to discrepancies in what is beneficial short-term and long-term.

This idea that what is better in the short term is not better in the long term is not controversial; for example, it is well known that infants show 'perceptual narrowing' in many domains, such that 'superior' discriminative performance in early infancy decreases with experience, as infants become more specialised for relevant information contained within their normal environment (Scott, Pascalis & Nelson, 2007).

We discussed in Chapter 3 how one of the key developmental progressions during locomotion is from controlling degrees of freedom by 'freezing' muscle groups, to using them efficiently. Metcalfe and Clark (2000) measured postural sway in infants using contact with a surface to maintain balance, and found that despite better performance (less sway) when using the surface, infants showed greater 'uncoupling' of body segments (movements across the body did not correlate well), and increased temporal variability in response lag, both in response to contact, and with walking experience. These results hint that the infant learning how to best control her movement in relation to the sensory information of the environment may find more variability beneficial. However, adult performance suggests that once the necessary level of skill has been mastered, variation is no longer useful and should be minimised for efficient task performance.

In sum, the discrepancies in interpreting variability across the results of the thesis may thus reflect the wide age range that has been considered. Within a one-month age range of development, especially the 10-month-old period primarily studied in this thesis, where there is rapid progression in motor abilities, including huge transitional events such as the onset of crawling or cruising, higher variability may be an index of the maturity of the infant. This may be true even though over a longer period of months to years, higher variability may be an index of the immaturity of the infant.

7.2.3 Inhibitory control

Discussion of the SMS abilities of infants would not be complete without some consideration of infant inhibitory control. Inhibitory control is an executive function that involves overcoming a dominant response in order to perform an alternative response. In our SMS studies, infants had to overcome their own SMT to match the music. That older infants are able to slow down ringing in Chapter 2, and that crawling infants were superior in Chapter 3, may therefore reflect increased inhibitory control, which is known to improve rapidly through infant development (Diamond, 2002). Whilst it could be that infants who are more maturely developed (reflected in age or crawling status) simply have better motor skill *and* better executive function, it is interesting to consider if superior motor skill may allow for better inhibitory control, which is then reflected in superior SMS. Berger (2010) demonstrates that motoric proficiency improves performance in a locomotive version of the classic A-not-B error inhibitory control task; expert locomotors are better at inhibiting the dominant response and taking the efficient route to the B target. Berger (2010) suggests this is because they are not having to concentrate on the motoric aspect of the task, and so can allocate more attentional resources to solve the inhibitory control problem. The older and crawling infants in Chapters 2 and 3 may similarly be better synchronisers because in a motor-cognitive trade-off, higher motoric skill (implying that ringing is easier) may free up more attentional resources, required for monitoring and matching the tempi of the auditory presentations.

Intriguing evidence for both a role of executive function and motoric expertise comes from a study of children with cerebellar medulloblastoma, many of whom had damage to the medial part of the cerebellum, including the vermis (Provasi et al., 2014). Patients show a slower SMT with higher variability than control children, and a deficit in their ability to slow down to achieve SMS, which seems to reflect a lack of inhibitory control: A battery of cognitive measures were taken, and both motor control and processing speed predicted performance (Provasi et al., 2014). The benefit of higher motor control may reflect the expertise element of Berger's (2010) finding, whilst speed of processing is associated with executive function (Diamond, 2002). Further, in Provasi's analyses adding working memory as a variable, an executive function affected in the patients with cerebellar medulloblastoma, improved a model of synchronisation performance by 3%, despite not being a significant predictor. These results may therefore reflect some extra contribution of executive function to rhythm production beyond motoric competency.

These findings are also intriguing, as negative associations with cerebellar lesions may be consistent with our vestibular hypothesis. Neural studies on beat production skills in patient groups heavily implicate the cerebellum (see Nombela et al., 2013 for a review). Animal studies show that cerebellar expansion is associated with specific, specialised motor systems involved in dynamic systems, over and above an association with the main limbs for movement (e.g. systems for echolocation in bats and electrolocation in weakly electric fish; Paulin, 1993). Paulin (1993) argues that the cerebellum is likely controlling and stabilizing movements in an attempt to monitor the state of dynamical systems; estimating, filtering and predicting incoming sensory signals. In humans, a unique specialisation is bipedal locomotion. When walking, the vermis, which is implicated in Provasi's (2014) study, receives input from the vestibular system and spinocerebellar tracts, conveying information about the body's position in the gravitational field and the sensory state of the limbs (Morton & Bastian, 2004). This medial zone then projects signals out to the vestibular nuclei and the spinal cord; integrating the vestibular and spinal information necessary for smooth locomotion (Morton & Bastian, 2004).

In Chapter 3 we additionally find that sling users were superior to non-sling users, leading to an interesting possibility that being regularly carried may improve motor control in a similar way to self-produced locomotion, and thus free resources for synchronisation. Accordingly, one could hypothesise that it is the continuous modulation of complex dynamic movement by the cerebellum that is critical, and that similar information could be being projected to and from the cerebellum during both self-propelled and carried locomotion. If it is adjusting to upright postural change that is important, and considering that postural development is still undergoing dramatic development at this age (Hadders-Algra, 2005), more extended experience in this domain may free up attentional resources for the inhibitory control required for SMS. In both the current work, and the population tested by Provasi and colleagues (2014), it would be highly interesting to measure whether expertise in balance and postural control, as well as more 'active' motor measures, may predict SMS performance. A final note on this point is that the measure of inhibitory control taken should be independent of measures of balance, locomotion or rhythm, such that any additive effect of superior inhibitory control could be analysed. There are accessible paradigms, that involve visual, non-motoric tasks, such as the 'Freeze-Frame' inhibition of looking task (Holmboe, Pasco Fearon, Csibra, Tucker & Johnson, 2008), that are validated inhibitory control measures for young infants, and should not be in any way confounded with measures of rhythm or locomotion.

To summarise, though our results in Chapters 2 and 3 suggest that infants struggle to decelerate from their SMT when engaging in an SMS task, we did not measure the extent to which this may reflect a generic ability to inhibit their natural rate of movement and adapt to the tempi of the music. Future work can directly measure infant inhibitory control, using paradigms not conflated with motor control, in order to assess if individual differences in executive function contribute to infant SMS.

7.2.4 The caregiver

Finally, although this thesis presents a body of work concerned with infant development, it evolved to give much more attention to the caregiver than originally intended. Inspired by finding superior SMS in infants who were reported as carried in a sling in Chapter 3, we set out to document how carrying might impact the very rhythms that infants naturally produce. Our first attempt to do so, reported in Chapter 4, was limited by the restricted space and time we had with each infant and caregiver dyad. The study reported in Chapter 4 took place at the Polka Theatre, Wimbledon. Polka is a magical, pioneering venue for the early years arts. Polka had won a Wellcome Trust grant to fund a collaborative project between neuroscientists and theatre makers, commissioning a piece that examined infant development, suitable for an infant audience. With collaborators Dr Rosy Edey and Dr Caspar Addyman, I was lucky enough to be one of three scientific collaborators on this project, sharing general expertise, and with my own work and knowledge on infant rhythm the inspiration behind music composed for the show. I carved an opportunity for data collection, and devised a study that could address the impact of carrying on infant rhythm, but was constrained by the realities of testing 'in the wild', having to engage, recruit and test participants quickly, in a small, bespoke, low-tech laboratory within the foyer of the theatre (Figure 7.1).

Figure 7.1 Photographs of the bespoke field laboratory at the Polka Theatre, Wimbledon, where the data reported in Chapter 4 were collected.

Despite the constraints of the field work, testing infants who were coming for the show provided a unique opportunity to gather a larger than normal sample size, and to test infants over a wide range of ages. This motivated a study that could really chart development, prompting a simple primary question: How does SMT change with age? We successfully answered this question with a well-powered correlation revealing surprising results - unlike through the rest of development, in infancy, SMT becomes faster, rather than slower, with age. The second, more complex question that we wished to address was whether there was an impact of the cadence of caregiver locomotion. Whilst we could not measure walking cadence directly in this scenario, other studies had looked more generally at the impact of biomechanics on SMT, by measuring body size (Mishima, 1965; Todd et al., 2007; Dahl et al., 2014). In adults, an impact of body size could reflect the experience one has of locomotion (Trainor, 2007). We reasoned that in poor or pre-locomotive infants, an impact of *parental* body size would reflect their experience of locomotion, as this is most likely the predominant rate of regular vestibular experience they receive when being carried. In Chapter 4, we indeed found that parental body size predicts infant SMT, such that infants with taller parents, who likely have a longer gap between steps, had a slower SMT than infants with shorter parents and a likely faster walking cadence.

Using body size as a proxy for parental walking cadence is, of course, not the perfect measure of the variable of interest. However, it is important to note that our measure for the alternative hypothesis, that infant SMT is set by the comfortable rate for movement engendered by their own biomechanics, was directly measured, and we did not find evidence for this hypothesis.

Our results supporting the experience explanation are however somewhat inconsistent in that parent height was the best predictor of infant SMT, and not parent leg length, which one would hypothesise to be the most direct measure for walking cadence. We believe this might be the case for two reasons. Firstly, we took parental height as a self-report measure, but multiple assistants physically measured leg length. Although every effort was taken to train the assistants to take this measurement consistently, due to the timing demands of the testing protocol (audience members arrived shortly before, and left shortly after seeing the show, leaving a narrow window for data collection), we did not collect a measure of inter-rater reliability. Therefore, we cannot verify the accuracy of the measurements, and it may be possible that leg length data were noisier than height for this reason. Furthermore, even in the gait literature, height is often a preferred measure to leg length, as it is very easy to take head-to-floor measurements, but much harder to take accurate leg measurements, as there is no natural end to the upper extremity of the leg (Whittle, 1990). As we could not intrusively examine the participants, we took the participants' self-selected highest point of hip-bone protrusion and central point of ankle protrusion as landmarks to measure between, but again, variation in identification of these markers by participants may have added noise to the data.

To verify that the effect of parental height on infant SMT was indeed due to locomotion we therefore ran the study reported in Chapter 5. In Chapter 5, our pre-test, training, post-test design allowed us to experimentally manipulate the rate of locomotion that infants experienced and directly measure the impact of walking cadence on their SMT. We confirmed our hypothesis, showing that infant SMT was slower following experience of being walked at a slower-than-average cadence, and faster following experience of being carried at a faster-than-average cadence. However, we also took the parent and infant body measurements again, adding infant height, infant and parent weight, parent SMT (drumming and tapping) and a measure of parental cadence, as measures that were impractical in the field setting, but achievable in the laboratory. The aim of these additional measures was to add further explanatory power to the results of Chapter 4. Despite the smaller sample size, we hoped to i) replicate our previous finding of parent height predicting infant SMT and ii) clarify that parent height predicts parent SMT and parent walking cadence, in order to justify our previous interpretation. In our smaller sample in Chapter 5, we did not replicate the effect of parent height predicting infant SMT. We also did not find that parental height predicted parent's own SMT, through drumming or tapping, or parental walking cadence. This challenges our prior interpretation of results; how can the finding of parent height predicting infant SMT reflect the infant experience of their parents' walking cadence, if parent height does not predict their own walking cadence?

The first point to note is that in Chapter 5, we had the additional measure of parent weight. Weight is a known influencer of walking cadence (Pierrynowski & Galea, 2001), but was not measured in the Chapter 4 as it was deemed too sensitive a measure for the participants to provide in a public setting. In Chapter 5, weight and height were highly correlated, but weight was the only significant predictor of walking cadence. A logical explanation is that overall stature is the best measure of walking cadence, with height best reflecting stature in Chapter 4, and weight in Chapter 5. We do not find evidence for the *absence* of an effect of height in Chapter 5, and adding the corresponding data from Chapter 5 to Chapter 4 did not change the impact of parent height on SMT, suggesting our first result was not spurious. We would predict that had weight been measured in

Chapter 4, the continuity between chapters would have been stronger.

A problem that may have affected the results of both Chapters 4 and 5 is that the adult data is complicated by the possibility that body size, locomotive speed, and fitness of new mothers was changing or had recently changed. In Chapter 5, where we took weight measurements, many of the mothers tested at ten months post-partum would be categorised as overweight. We do not know how these fluctuations may affect locomotion. Mothers may have adapted locomotion to their new body size, or may resiliently stick to their preferred tempo of walking with increased energy costs. Further, those carrying infants in their arms are known to take shorter steps, but this relationship is proportional to their base tempo (Wall-Scheffler et al., 2007). It would be an interesting extension of the current work to measure body size and walking cadence in expectant mothers, new mothers and across the first year of infant development, both with and without the infant, to see how infant experience might change.

We further did not find that parent anthropometrics or parent walking cadence predicted parents' own SMT as measured through drumming or tapping in Chapter 5. This is possibly due the practical compromises in data collection from the caregiver that we had to make in order to get the infant through the testing session safely and happily. The use of a treadmill, and the dependent variable of steps per minute, is not how we would have measured parent gait if time and space had not been an issue within the laboratory. Treadmill walking is known to be different from over-ground walking (e.g. Alton, Baldey, Caplan & Morrissey, 1998). Though parents may walk differently when holding their infant

(Wall-Shceffler et al., 2007), for health and safety reasons we could not measure the cadence of the caregiver carrying her child. The stair casing procedure for parents to select their optimal walking tempo was not ideal in that the treadmill speed settings were not fully continuous so there was a forced choice in which setting felt 'best' (i.e. even if parents reported that they would prefer something in the middle of speed 11 and speed 12, there was no speed 11.5 to select). The naturalism and sensitivity of the measure were therefore significant issues. In addition, caregiver motivation to find the best tempo in our two-up-two-down stair casing procedure may not have been strong, especially if her infant was beginning to tire or fuss, as this was the end of the session, and the two were separated. Similarly, parent tapping and drumming took place after the infant testing, but whilst the infant was still in the room. It is possible that the distraction this provided may have added noise to the SMT measures. For example, the parents would sometimes speak to the infant, or hold the infant with their free hand. Some caregivers would spontaneously close their eyes to try and block the distraction from the room. The less than ideal testing scenario for adult measures (in order to ensure the comfort of the infant) may have complicated our results.

An issue that could contribute to all of the discrepancies noted between studies is sample size. In Chapter 4, we had a well-powered study for correlational/regression analyses, and found significant correlations and predictors, with small to moderate effect sizes, and supported by moderate Bayes Factors. In Chapter 5, the sample size was sufficient for the between-subjects experimental manipulation with the infants, but the correlation and regression analyses were less successful. Considering the small effect sizes for similar analyses seen in the adult literature (around 30%; Todd et al., 2007), it is a natural proposition to run a properly powered adult study to complement the infant work documented here, which could also benefit from refinements in testing the measures of walking cadence and SMT, discussed above.

In conclusion, practical considerations necessary for successful infant testing may have cost us continuity and accuracy in the adult measures taken. Our results on the contribution of caregiver cadence in Chapters 4 and 5 are highly novel, and represented a first foray into better explaining infant rhythm development by accounting for their daily locomotive experience outside of the lab. Now that there is strong preliminary evidence for an effect on infant rhythm, future work refining the capture of naturalistic infant experience will benefit from a more concentrated focus on caregiver measures.

7.3 How well can we ever ask 'why?': The importance of asking the right questions

The title of this thesis contains a bold suggestion: Do we dance *because* we walk? Nobel Prize winning Nils Tinbergen conceptualised four questions that need to be addressed in order to answer the 'why' in 'why does an animal behave in this way?' (Tinbergen, 1963). These questions have been more recently categorised as reflecting i) Phylogeny, 'what is the history of the trait?'; ii) Adaptive Significance, 'what is it for?'; iii) Ontogeny, 'how does it develop in the individual?' and iv) Mechanism, 'how does it work?', and can be subdivided as

Proximate (Ontogeny and Mechanism), and Evolutionary (Phylogeny and Adaptive Significance; Nesse, 2013). Fitch (2015) argues that to understand human musicality, as all behaviour across all species, we need to address all four questions: Moreover, we need to understand that there is no strict divide between them, and that they are highly intertwined, such as when experience through development changes neural mechanisms. The questions are not mutually exclusive, but complementary (Nesse, 2013).

The current thesis has been concerned with understanding *why* we behave in musical ways at the level of ontogeny, by contextualising rhythmic skill within the sequences of typical development. Whilst the two Proximate and two Evolutionary questions are often considered together, rarely does a research domain attempt to marry the four (Bateson & Laland, 2013). It is of course a limitation of the current work that we cannot consider all levels of 'why', and cannot falsify our vestibular hypothesis, with the ontogenetic data presented. It is important to note that the hypothesis that has been tested is the culmination of several areas of research that, when synthesised together, provoked novel questions about the nature and development of rhythmic skill. We do not claim that the evidence we have accrued to answer these questions, supporting a role of locomotion, is enough to back the larger argument that locomotion is *crucial* for rhythmic skill. Suggestions for further ways to test 'why' at the ontogenetic level have been given in the previous section. Though it fell outside of what was possible to test within one PhD, in the following section I reflect upon how we may answer the 'why' questions at the three remaining levels suggested by

Tinbergen, in order to isolate whether we really do dance, because we walk.

7.3.1 Adaptive significance

Asking 'What is it for?' could promote a heuristic that our rhythmic skill only has one value to the success of the individual, and that this value, or 'reason for', is the original value and has remained consistent throughout history, which for complex multicomponent behaviours is unlikely to be true. Such thinking led to the revision of Tinbergen's original category of 'Survival Value' to 'Adaptive Significance' (Nesse, 2013) or 'Current Utility' (Bateston & Laland, 2013). Bateson and Laland (2013) argue that the former two options create ambiguity over whether the original or current functionality is being considered, and suggest that as only the present utility of a trait can be investigated experimentally, this must be the primary scientific question we strive to answer.

In studying how the trait may influence fitness, much of the research in the field has concentrated on 'social glue' theories of musicality (Brown, 2003; Cross, 2009; Merker, 2009), and there is evidence that moving together with another person engenders moving to the beat (Kirschner & Tomasello, 2009), and promotes prosociality (Kirschner & Tomasell, 2010; Cirelli, Einarson & Trainor, 2014; Cirelli, Wan & Trainor, 2014), which lends credence to the idea that the value of rhythmic skill is in promoting cohesion. In Chapter 2, we tested whether the presence of a social partner enhanced infant SMS, and found that though the social partner impacted what the infant did, it did not impact how well the infant did it. In contrast, we found evidence of the tempi of music and age (Chapters 2

& 3) and locomotive skill and experience (Chapter 3) enhancing SMS, and influencing SMT (Chapters 4 & 5). This led us to the conclusion that 'moving together' and 'moving to the beat', often grouped together in the literature, may have separate underlying mechanisms or developmental trajectories. However, they may share a common current utility, and our results do not argue for or against any argument at this level of reasoning. Kirschner and Tomasello (2010) stress that evolutionary theories need not be mutually exclusive, with components of musicality, including beat production and perception, that may have cultural values removed from the innate products of biological evolution.

Nonetheless, our hypothesis centres on the bidirectional relationship of movement and music (e.g. Phillips-Silver & Trainor, 2005; 2008; Trainor et al., 2009), and an interesting future direction for exploring 'What is it for' is to ask if the relationship we evidence of locomotion impacting rhythmic skill is similarly bidirectional, such that rhythmic skill is also helpful for locomotion. Just as social cohesion benefits survival, so does the ability to navigate successfully around the environment. Does enhanced beat perception and production ability in anyway promote motoric or perceptual skills that aid efficient adaptation to the environment during locomotion? Experimental questions to investigate this could include: 'does sensitivity to, or enhanced prediction of a beat, allow for more efficient infant adaptation to the caregiver during carrying?', or 'does rhythmic skill protect against falls in the young and the elderly?'. Some evidence for the latter comes from studies of disorders such as Parkinson’s Disease, where rhythmic auditory stimulation training leads to improved locomotion (for a review see Nombela et al., 2013). This work could be extended to the testing of novice walkers during typical development. Such enhanced emphasis on the non-social values of rhythmic skill could provide novel insight into our understanding of what beat skills are for.

7.3.2 Phylogeny

Whilst we cannot study the history of the trait through evolutionary time, we can attempt to reconstruct some elements of history by examining precursors of the trait. The vocal learning hypothesis (Patel, 2006), described in Chapter 1, suggests that the brain circuitry involved in the necessary phenotypic precursors of interval timing and motor control are not enough to explain our beat skills, as closely related species with similar abilities and brain structures, such as chimps, do not show the same behaviours. Patel (2006) proposes that these precursive abilities around timing and motor control are amodal, and that vocal learning is what put specific demands on our nervous system that led to the tight audio-motor coupling critical to musicality. The current vestibular hypothesis puts forth that another unique set of demands, of bipedal locomotion, with an emphasis on tight vestibulomotor couplings, may be a vital clue to how the trait was constructed from its phenotypic and genotypic precursors.

Testing the phylogeny of a trait often takes the shape of constructing phylogenetic trees, that map how different species share, or do not share, certain traits. Using such trees, one can elucidate homologous traits in groups of related species, and infer the presence of the trait in a common ancestor, or, studying unrelated species can tell us about analogous traits (cf. Honing et al., 2015). Such reasoning has led to the testing of rhythm production skill in species including parrots, investigations that support the vocal learning hypothesis (e.g. Patel et al, 2009; Schachner et al., 2009). One problem with exploratory comparative work is that once some evidence is found for one species, such as YouTube sensation Snowball the cockatoo, it may bias observations that provoke the scientific study of similar species (Wilson & Cook, 2016). There is also recent evidence for non-vocal learners exhibiting SMS skill, including the cases of some primates (Hattori et al., 2013; Large & Gray, 2015) and a sea lion (Cook et al., 2013), which seem to have gained less attention.

We will therefore now consider how we might motivate and choose species for comparative work based on our vestibular hypothesis. An ostensibly logical starting point is with bipedal locomotion; however, we would not necessarily call for the study of other bipeds to evidence our hypothesis. We propose that humans, specialised for walking upright on two legs, have a unique proclivity and capacity for beat perception and production, because of the vestibular-motor relationships that feed into bipedal locomotion, and their close connection with the auditory system. Though other animals sometimes use two legs to walk or run bipedally, no other animal uses bipedal locomotion as their regular method of locomotion, with a two-peaked force on the ground and the trunk erect (Alexander, 2004). This erect body structure, which requires refined balance, is key to our vestibular hypothesis, and so animals without this combination of traits would not necessarily make good candidates. Rather, we call to test species with a need for analogously good vestibular-motor couplings, and neural structures that might support these links. As discussed previously, a specialised cerebellum may be a good place to start. One such species may be elephants, who have the complex muscular appendage of the trunk to control, and a relatively and absolutely large cerebellum, including a relatively large vermis (Maseko, Spoctor, Haagensen & Manger, 2012).

It is not only final outcome that may be of importance to compare across species. Animals with a protracted development relating to their cerebellar specialisation may also make good candidate species. The 'evo-devo' approach of looking at the highly conserved relationship across species between brain size and developmental time as one variable, suggests that the interaction between the plastic brain of the developing organism and its environment constructs the mature animal, upon which natural selection will act (e.g. Charvet & Finlay, 2012). Mature locomotion is not seen in humans until around 7 years of age (Whittle, 1990). In elephants, use of the trunk has a similarly protracted development (Lee & Moss, 1999).

Whilst elephants may therefore be a good candidate species to test, a complication is that elephants are also vocal learners. Though the proposed vestibular hypothesis and the vocal learning hypothesis are not mutually exclusive, it would be difficult to dissociate the two ideas by testing this species. An alternative species that has not been implicated as a vocal learner, and has excellent, complex motor control, is the octopus. The octopus is an interesting proposition because their cerebellum receives visual and vestibular data and is involved in whole-body and occulomotor stabilisation during locomotion (Williamson & Chrachri, 2007), much like humans. Further, as the cerebellum is a characteristic of vertebrates, but the octopus (and squid) evolved a cerebellum independently, this commonality between far removed but motorically advanced species solidifies the view of the cerebellum for dynamic motion prediction and control (Baumann et al., 2015). Evidence for rhythm skill in this species would therefore add extra credence to the mechanistic account, described below.

7.3.4 Mechanisms

Whilst the Evolutionary questions are difficult to test, the Proximate descriptions can be much more directly measured. Our understanding of the brain mechanisms involved in beat perception and production is a fast progressing area of contemporary research that has received much attention over the past years, especially since evidence came to light that motor areas of the brain are involved in beat perception, even in the absence of movement (Zatorre, Chen & Penhune, 2007).

There is extensive work showing that the primary brain areas involved in rhythmic skill are the basal ganglia (e.g. Grahn & Brett, 2009; Grahn & Rowe, 2009; Grahn, Henry & McAuley, 2011) and the cerebellum (e.g., Penhune, Zatorre & Evans, 1998; Brown, Martinez & Parsons, 2006; Provasi et al., 2014). Mechanistic accounts of the use of these structures have placed emphasis on processing in the dorsal auditory pathway (Patel & Iversen, 2014), or rewarding activation of body-maps by a vestibular sensory-motor network (Todd & Lee, 2015), dependent on the theoretical background of the researchers. The results of this thesis do not shed light on neural mechanisms involved, though Chapter 6 was an attempt to elucidate if the vestibular experience carrying impacted the motoric processing of auditory information, in line with the suggestion by Schubotz (2006), and compatible with an extension of the ASAP hypothesis (Patel & Iversen, 2014), that action simulation for auditory prediction might also make use of vestibular information. Despite the null results presented herein, future work may be able to give more insight into how the vestibular information may be critical in light of the mechanisms espoused by others, and concrete suggestions for logical extensions of this thesis work can be found in Chapter 6.

Beyond these extensions, and as a novel addition to the increasingly established neural work noted above, the prime 'How does it work' question for this hypothesis is to ask if the vestibular information from the complex task of maintaining posture during bipedal locomotion, both self-propelled or when being carried, is a critical element of the process behind beat production. One way to explore this question would be to look at the relationship between sway and rhythmic skill in typical and atypical adult populations. For example, cerebellar damage is associated with increased sway when standing (Morton & Bastian, 2004), and has been shown to be related to SMS (Provasi et al., 2014). A strong role of the vermis in balance and locomotion has been further endorsed by animal studies showing that lesions negatively impact on the timing and precision of locomotive movement (e.g. Sprague & Chambers, 1953). Morton and Bastian (2004) suggest that at a general level, the role of the medial region of the cerebellum appears to be to exert modulatory control over the rhythmic flexor and extensor muscle activations that facilitate locomotion. Our argument is that our unique need for sensory integration to control bipedal locomotion may have given rise to our need for the cerebellum to integrate auditory, visual and vestibular information in a way that is also conducive to moving to music. We have previously suggested that a correlation between beat production and balance skills would support our hypothesis; here we argue that testing for common neural activation during a postural control task, such as standing sway, and a rhythm task, such as fine motor finger tapping, would provide some evidence for a shared mechanism.

7.3.5 Summary of the Four Questions

In sum, thinking across Tinbergen's Four Questions allows us to consider our hypothesis as a whole unit: When trying to understand 'why' we have the complex rhythmic skill that is so pervasive across the human species, there are multiple questions at multiple levels that need to be addressed. We highlight that asking 'What is it for' could involve testing the bidirectional relationship between locomotion and rhythm, to ask if rhythm has adaptive value for walking. Clues to the history of the trait may be found if we ask 'Who shares our skill', and we suggest that species distantly related to us, such as the octopus, may allow insight into the complex vestibulomotor connection we believe necessary for flexible rhythm production. Finally, we ask 'How does it work', and suggest that further understanding of the processes involved in our beat skill may be elucidated through investigation of common neural substrates involved in both rhythm and balance. In the following section, we add our concluding remarks to this thesis.

7.4. Conclusions

> *'Rhythm is born in all of us'*
> \- Ginger Rogers

Our proclivity for rhythmic music is unique to our species, universal across cultures, and brings joy to our lives. Despite centuries of speculation, our understanding of where these rhythmic skills came from, what they are for, and how they develop, is still in its infancy. However, from our earliest hours we are cradled and rocked steadily in our mother's arms. This thesis has investigated our own hypothesis, that experience of rhythmic vestibular stimulation from our inherently unstable bipedal locomotion, and the consequential protracted time course of carrying of our infants, might be the basis of our audiomotor rhythmic tendencies. The resultant studies support a role of both self-propelled locomotion, and experience of being carried by the ambulating caregiver, on an infant's ability to move in time with an auditory beat. Further, we find that the rate at which we experience such stimulation biases the very rhythms that we naturally produce, which are the foundations from which all creative rhythmic tendencies come. The work in this thesis, highlighting the seemingly innocuous behaviours of walking and carrying our young, will hopefully stimulate further interest into this interesting avenue of beat perception and production, that may help us to build a more complete understanding of human musicality.

> *'Oh look out you rock 'n rollers…*
> *Pretty soon now you're gonna get older'*
> -Bowie

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