On the Meaning of Movement in Music, Development and the Brain
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This article is written from the perspective of empirical research within the broad field of the neuroscience of music (including evolutionary, behavioural, neuroimaging and neuropsychological approaches), with a central theme of the multisensory experience of rhythm and movement in music and dance. Section 1 explores some historical theories on the evolutionary origins of music that point to the important role of rhythmic synchronisation. Section 2 discusses some of the concepts of beat perception and synchronisation in the scientific literature, with examples of various methodologies that have been used to measure these abilities in the body and in the brain. Section 3 focuses on the development in infancy of the musical capacity to ‘feel the beat’, which involves the integration of auditory and movement information. Section 4 takes a neuropsychological perspective, giving examples of what can go wrong in cases of abnormal music development, and posing some provocative questions about whether or not we all ‘have rhythm’. These different perspectives, taken together, reflect a scientific interest in understanding music, movement and the brain. The goal of the article is to find points where neuroscience and music meet, while recognising certain limitations. The discussion is meant to complement important studies and observations in the fields of musicology, music pedagogy, music performance and music therapy by providing empirical support for some of the work of experts in these fields. Ultimately, musicians and scientists together can illuminate the importance of music and movement for the human mind.

Keywords: Music; Movement; Development; Dance; Brain

For meaning is not in the event, but in the motion through event.
(Robert Penn Warren)

Introduction

It has been said since antiquity that much of music’s meaning is in the motion, both metaphorical and physical, through the events (Clark, 2005). Movement is an intrinsic part of the music experience. Music and movement co-occur from the first
musical relationship—that of mother and child. Mothers of the world rock their infants while singing soothing lullabies, and bounce them joyfully to play songs (Papoušek, 2007; Trehub et al., 1993; Trehub & Trainor, 1998). Lovers press bodies together in dances of courtship. Gospel choirs sing and clap in praises of worship. Troops and tribal warriors unite in songs of attack and defence. Music and dance can brand personal and collective memories of birth, coming of age, marriage and death. There is no known culture or time in history in which this pairing of music and movement was not central to social bonding and to child rearing, in routine and in monumental life events (McNeill, 1995; Miller, 2000; Nettl, 2000; Wallin, 1991). The movement that accompanies music—whether drumming, plucking, singing, clapping, stomping or dancing—is inseparable from it, and as will be seen later, this link between music and movement may be established early in brain development.

The pairing of music and movement is reflected in our verbal description of the musical experience. When we talk about music, we describe hearing the melody, but feeling the beat. The verbal expression ‘to feel’ is used to refer to how people experience music’s rhythms, in different languages all over the world—Chinese: 感觉 (‘gan-jué’), Hindi: ‘mehsus”, Persian: ‘hess’, Polish: ‘czuc’’, Spanish: ‘sentir’, English: ‘to feel’ the beat. Why do we describe the beat in terms of feeling? More than just hearing the sounds, our description implies a role of the body. The Western rhythm pedagogy, Dalcroze Eurhythmics, teaches musicians to internalise rhythm and time via full body movement. Similar notions of the body as an instrument of rhythm can be found in many methods, including Orff's Schulwerk, the Kodály Concept, the Feldenkrais method and the Alexander technique. Ancient world traditions—the dance of African Bushmen, the religious chant of Nepali Tibetans, the commerce of indigenous Venezuelans, and the ceremonies and festivals of New Guinea peoples, to name a few—have used the body to keep time during music and maintain consistent timing between performances (Epstein, 1995). In many folk music traditions, such as Aboriginal Djanba, Andalusian Flamenco and the Viennese Waltz, the name refers at once to the music and dance forms, which traditionally occur together (seated concert halls and iPods are relatively recent phenomena). Music is often a multisensory experience, and the sensory inputs from sounds and body movement shape our conceptual definition of music.

That there is such an intimate relation between music and movement across human cultures also suggests that they form an integral part of our perceptual, cognitive and social-emotional experience. Scientific studies can test the hypothesis that when we produce or perceive music, auditory and movement systems are not only functioning simultaneously but are integrated so that what we perceive in music is a product of what we hear and feel. Why are music and movement so inextricably linked? Why is this coupling so crucial to early human development? Why is it argued that virtually all humans share certain musical capacities? And, what can music do for brain development? The following sections will review some of the scientific literature that begins to address these questions. Each section is not meant to be a comprehensive review, but rather to highlight some of the influential ideas on
the importance of movement in music, development and the brain. To provide an organisational structure, and to emphasise different scientific approaches, the review is divided into four major perspectives regarding: first, the evolutionary origins of music; second, beat perception and synchronisation; third, infant development; and fourth, a neuropsychological approach to understanding the musical brain.

**Perspective 1: Evolutionary Origins**

What are the origins of human musical activity, and why have we evolved to be the creative singing, dancing and listening beings that we are? Darwin proposed a role for music and dance in human evolution, but conclusive evidence can be difficult to find because neither music nor dance fossilise (Darwin, 1896 [1871]; Mithen, 2005). For example, the oldest man-made instrument may be a 36,000 year-old bone-carved flute from Germany (Richter et al., 2000), but if we do not require an external tool to define music, then the first musical instruments were likely the human body and voice.

Some of the theories on what functions music and dance may have served in human evolution highlight the role of synchronisation of movement with sound, and with other individuals (Huron, 2006; Merker, 2000). For example, the bond between mother and infant may rely on temporal synchrony of behaviour (Feldman, 2007; Stern, 2007; Trehub, 2003; Trevarthen, 1979). Group cohesion can also depend on synchronisation, as can be witnessed in choirs, orchestras, families and armies (Huron, 2006). These types of interpersonal synchrony and their effects on physical and emotional bonding might be related to the release of hormones, such as oxytocin, that facilitate bonding and memory in the brains of humans and other animals (Huron, 2006; Kosfeld et al., 2005).

Synchronisation has been also implicated in mate selection (Brown et al. 2005; McDermott & Hauser, 2005). During reproductive years, musical synchronisation might facilitate mating and mate choice—an idea that can be supported by the enormous importance of music during the adolescent years and the huge sex appeal of, and money spent on, famous musicians. A study performed in Jamaica demonstrated that people’s attractiveness judgments of dancers from the general community (based on stick-figure animations that were reconstructed from the dancers’ performances by motion caption technique) correlated with other features of phenotypic quality (e.g., in men, shoulder breadth or amount of body hair, which signal testosterone levels). These data were consistent with the idea that people might use music or dance ability in choosing a mate, just as they use other physical cues (perhaps unconsciously) that can indicate the quality of the mate. A question of interest in the context of the present discussion would be: to what extent would these attractiveness ratings predict the accuracy of synchronisation of the dancer with the music? In other words, would those individuals with lower ratings demonstrate poorer musical timing, or an inappropriate style of musical timing (such as straightforward downbeat accenting, as opposed to a syncopated reggae style)? Other
possibilities might be that the poorer dancers have less beautiful moves, or just a smaller repertoire of moves, or all of the above. Further research on this subject could reveal more about the musical characteristics that attract, or repel, when people evaluate other dancers for potential mate quality.

Whether musical behaviours served some adaptive functions to our ancestors, or are merely by-products of some other capacities, may be difficult to prove. Scientists have recently proposed another way to think of music that does not require it to be a direct product of natural selection. Music can be thought of as a type of invention—that is, something that humans developed because they had the brain power to do so, and once they did, they would never live without it, not because they could not survive without it, but because it is so valuable to them that they would not want to live without it (Mithen, 2005; Patel, 2008). Fire is an example of such an invention, which Patel (2008) refers to as a ‘transformative technology’ because it virtually transforms the way we live; other examples include written language, air travel and the Internet. The value of this view is that it enables us to put aside certain contentious questions that we may never be able to answer for sure (such as precisely when and how in evolution music developed), yet still offer explanations for why music is universal and explore the ways in which music has indeed changed the human brain.

What are the avenues of research that promise to reveal insight into the universality and the power of music? One is the avenue of beat perception and synchronisation, a special case of skills that may be specific to music (in contrast with the kind of rhythm processes used in language, for example) and that are universal (every human culture has some music with a regular beat that elicits synchronised movement such as dancing) (Patel, 2008). Future studies on questions such as when and how in human development beat processing abilities emerge, and whether other animals demonstrate evidence of beat processing abilities, will help us to understand the origins of music and dance (Patel, 2006, 2008; Patel et al., 2008).

Perspective 2: Beat Perception and Synchronisation

It has long been thought that only Homo sapiens spontaneously move in synchrony with the auditory rhythmic pulse of music, whether at the tactus level or at higher or lower metrical levels (Chen et al., 2002; Patel, 2006; Patel et al., 2005). A current wave of research suggests, however, that other animals show evidence of reliable synchronisation (frequently defined as a precise period- and phase-locking) to music (for an example, see Snowball, the sulphur-crested cockatoo shown on YouTube)¹ (Patel et al., 2009; Schachner et al., 2009). These studies propose that the animals that show a capacity for beat perception and synchronisation are likely to be equipped with brain mechanisms that support complex auditory-motor interactions, such as the ability to tune motor actions based on auditory feedback. The importance of auditory-motor integration will be discussed further in later sections. Whether or not musical beat perception and synchronisation is specific to humans, they are certainly
human capacities and fundamental to music. Here the focus turns to some of the known (and as yet unknown) processes that are involved in perceiving a beat in music, and synchronising movement to that beat.

Musical beat perception and synchronisation are elaborate abilities, when we consider the rhythmic complexity and ambiguity often present in music. The following is an example of such rhythmic ambiguity taken from salsa music (a genre of mixed musical forms whose name refers to the dances as much as to the music). In a score (Figure 1) for trumpets from ‘El Preso’ by the Columbian band Fruko y sus Tesos, the trumpet section comes in with a hemiola (triplets against the binary cut time), which echoes the syncopated feeling of the 3–2 (or 2–3) clave that is at the heart of salsa. This type of 2:3 hemiola is standard in the music repertoire from polyrhythmic African drumming, to Bach chorales, to New York’s Afro-Cuban mambo. However, it represents a set of complex perceptual and cognitive processes that are of interest to cognitive scientists. Feeling two versus three is a bit like looking at the famous Rubin illusion (Figure 2): we can perceive a black figure (the vase) on a white background, or a white figure (two faces) on a black background. In each case, one provides the figure and the other, the ground. Scientists refer to this as a problem of ‘figure-ground segregation’ (Pressing et al., 1996). One way in which the brain handles such ambiguity in music is via beat perception—the ability, in the context of complex rhythmic texture, to find the regular pulse of the music (the present discussion will not necessarily apply to music that does not have a periodic pulse). Often in musical experience, the pulse is inferred automatically. This involuntary process reflects one of the most basic aspects of hearing and moving to music in time: beat perception and synchronisation.

In any music with rhythmic complexity, the perception of the beat is robust and it stands up to a great deal of expressive timing and tempo variation. Highly syncopated music capitalises on this ability, putting rests on strong beats and attacks off the beat, and sometimes resulting, ironically, in an even stronger representation or feeling of the beat. In the scientific literature, syncopation is often referred to as ‘counter-evidence’ to the beat, which is what makes it unexpected and effective. The placement of a rest on a downbeat and a musical attack off the beat has been argued to cause listeners to ‘reset’ their pulse reference point (Fitch & Rosenfeld, 2007), but an

Figure 1 Excerpt of a score for trumpets of the piece ‘Preso’, by the Columbian salsa band Fruko y sus Tesos. The score demonstrates the juxtaposition of two and three beats; each triplet is played against the half note of the binary cut time meter. This is an example of figure-ground segregation in musical rhythm. (A music video of this piece performed by the band can be viewed online at: http://www.youtube.com/watch?v=6c78DyuAc4k).
alternative may be that our perceptual system ‘fills in’ the downbeat, or strong beat. For highly experienced listeners,\(^2\) multiple rhythmic streams may be processed in parallel (Keller, 1999). The end result can be quite a strong feeling of the beat, such as is felt in gospel, reggae, ragtime or soul.

Here there may be a discrepancy between the experience of syncopation in music, and the ways in which the concept of syncopation is defined and used in scientific research. In the context of experimental stimuli, simple tone sequences with tones occurring on metrical strong beats versus on metrical weak beats have often been used as examples of ‘strongly metrical’ and ‘weakly metrical’ rhythms, respectively. These stimulus sets originated with the approaches of Longuet-Higgins and Lee (1982) and continued with Povel and Essens (1985), and have been useful in experiments on meter perception in adults and infants, in healthy individuals and in patients. A finding of many of these experiments is that perception of such rhythm patterns is better in the context of higher metrical strength, and poorer in the context of lower metrical strength.

While these data are useful for understanding the perception of simple tone series, the conclusions that have been drawn from them regarding meter perception may be limited to the experimental contexts studied. Although such a perceptual disadvantage can occur in the context of a simple tone sequence, in the context of real music syncopation may serve as a tool to strengthen the perception or inference of the beat (hence the use of tools such as the hemiola). This discrepancy may bring into question the ecological validity of certain definitions of ‘strongly’ versus ‘weakly’ metrical rhythms.\(^3\) Future research on the perception of beat and meter should address the mismatch between performance in the context of impoverished experimental stimuli versus in natural music contexts in order to understand sophisticated musical skills such as syncopation that are present in average listeners to some degree and in highly experienced listeners to a much greater degree.

Despite such limitations, countless experiments using simple experimental stimuli as well as real music excerpts have yielded behavioural data that demonstrate people’s

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**Figure 2** Rubin’s illusion represents the phenomenon of figure-ground segregation, in which the visual system perceives either the black vase as a figure on a white background, or two white faces as the figure on a black background. This example in the visual world is used here as an analogy to the phenomenon of figure-ground segregation in musical rhythm—for example, in a 2:3 hemiola.
basic rhythm processing abilities. A common assessment tool of the perceived beat of rhythmic sequences, and of the accuracy with which people coordinate and maintain a physical response in tempo and phase with that beat, is sensorimotor synchronisation. For example, Western adults readily tap in synchrony with the strong beats of rhythm patterns and they tend to produce accents at potential downbeat positions, which also can reflect their perceived meter (Drake et al., 2000a; Hannon et al., 2004; Parncutt, 1994; Snyder & Krumhansl, 2001; Toiviainen & Snyder, 2003). Models of beat perception attempt to explain the mechanisms by which the brain can spontaneously perceive a beat and enable motor production in synchrony with music. An important model describes how a temporally structured sound stimulus can guide attention so that the listener becomes entrained, even in the context of timing fluctuations, and anticipates each coming beat (Jones, 1976). This process of entrainment and anticipation can enable the production of a motor response in synchrony with the stimulus. The next section summarises the available scientific evidence on children’s synchronisation abilities, and when they begin to develop.

Researchers have also begun to explore what brain regions are involved in beat perception and synchronisation, although one of the major findings is that the rhythm network in the brain is extensive (Janata & Grafton, 2003; Parsons & Thaut, 2001). For example, studies have pointed to regions in the brain, such as the basal ganglia and supplementary motor areas, which are activated during listening to music with versus music without a regular beat structure (Grahn & Brett, 2007). These regions are shown by neuroimaging experiments to be responsive to features of auditory rhythms, including the perception of timing and duration, and rhythm perception and production; damage to them can affect such responses.

In a fascinating study using positron emission tomography (PET) with experienced tango dancers as subjects, researchers were able to isolate regions of activation that seemed to support three core components of dancing to music: entrainment to music, musical meter and spatial patterning of foot movement (Brown et al., 2006). The first component, entrainment to music, was examined by comparing patterns of brain activation elicited when the dancers (while lying supine in the PET scanner and stepping on an inclined board) performed the basic tango dance step in the presence of tango music, or performed the step in a self-paced manner, in the absence of music. The principal difference observed between these two conditions, after controlling for the auditory activity elicited by the music listening, was a higher level of activation in the anterior cerebellar vermis when the dance step was entrained to music. The cerebellum is a brain region involved in timing information and motor control, and the authors propose that in this case its role might be to receive beat information from subcortical auditory areas, thereby mediating audiomotor entrainment.

The second component, musical meter, was examined by comparing patterns of brain activation elicited when the dancers performed dance steps to the natural, metric tango songs versus to edited versions of the songs in which randomly placed
accelerations and decelerations rendered the musical beat irregular and unpredictable (while holding average tempo constant). This comparison revealed a strong relative activation of the putamen in the basal ganglia (recall the basal ganglia’s involvement in listening to music with a beat-based structure) for dancing to the metric tango music. The authors interpret this finding as support for the idea that the basal ganglia, and especially the putamen, are recruited in the selection and organisation of metrically timed movement, while other pathways are recruited for non-metric movement.

The third component, spatial patterning of dance movement, was examined by comparing the brain activation elicited in the metrically timed dance movement condition (described above), versus a condition in which the dancers contracted the leg muscles to the beat of the music but without moving their feet on the inclined surface. This control condition preserved the metric movement to music, as well as muscle contraction, but removed the spatial patterning required to place the legs and feet in the appropriate spatial locations for tango dance. This comparison resulted in a higher relative activation in the medial superior parietal lobule for the spatially patterned dance movement (also observed in non-metric and self-paced spatial patterning), which means that it reflects the spatial mapping of movement, regardless of the timing of movement. This parietal region is known to be involved in processing proprioceptive information during spatial navigation; thus, the authors were able to localise the activity of this specialised region in response to the spatial patterning of dance movement.

In addition to the described comparisons, the authors found predicted activations in all movement conditions of the motor cortex, premotor cortex and supplementary motor areas, as well as predicted activations of auditory cortex, to music listening. Taken together, these results begin to map out a complex, interacting neural network that subserves dancing to music, consisting especially of the cerebellum, basal ganglia and parietal lobule. This map highlights regions of activation for the core components of music entrainment, metric movement and spatial patterning of dance steps (Brown et al., 2006). This study made an important methodological leap forward: while functional neuroimaging techniques often restrict movement (in order to be able to obtain clear images of the brain, and also due to the supine position of the subject in a scanner), clever studies such as the tango experiment have found ways to begin to explore ecologically valid forms of dance-related movement, even within the limitations of the scanning environment. Future studies will build on this neural network map, and further our understanding of the brain’s functioning in dance.

One of the most important findings related to the subject of the brain’s processing of musical beat information is that the auditory and motor systems are integrated in music perception and production (Zatorre et al., 2007). The strength of this integration can be observed, for example, when the increasing metrical salience of an auditory rhythm pattern not only facilitates more precise tapping to the rhythm, but also elicits stronger activation in secondary motor regions (including dorsal premotor cortex) in both musicians and non-musicians (Chen, et al., 2008). Such studies are...
beginning to explore whether and how this kind of auditory-motor integration can be strengthened to become more efficient, or more sophisticated (e.g., in the perception and production of highly complex rhythms) in expert musicians. The question to which we turn next is when in development such auditory-motor interactions can be observed.

**Perspective 3: Infant Development**

Coordinated interpersonal timing in auditory and movement modalities is important in infancy, as seen in the rhythmic interlocking between parents and infants (Condon & Sander, 1974; Jaffe et al., 2001). For example, the rhythmicity that characterises infant-directed speech is offered as an example of ‘intuitive parenting’ behaviour (Papousˇek & Papousˇek, 1981), which is thought to foster cognitive and social growth in infants. When speaking or singing to infants, adults modify features to which the infants are highly attentive; these features, such as pitch, contour, rhythm, tempo and prosody, are described as musical, both in the context of infant-directed speech and in the context of infant-directed song (Trainor et al., 1997; Trehub & Trainor, 1998). Furthermore, caregivers typically move while singing to their infants, which is consistent with an intrinsic connection between rhythm and movement (Cross, 2001; Merker, 2000). Thus there is support for the idea that perceptual and motor capacities that are temporally based can provide an important foundation in infancy for the development of complex temporal experiences such as music.

The available evidence of temporal processing in infants suggests that the fundamental abilities underlying perception of the beat develop early in infancy (perhaps even before the motor system is mature enough for an infant to reliably produce the beat), and can lay the groundwork for musical learning later in life. It has been proposed that the ability to extract beat structure from listening is hardwired, and should generalise across age and musical experience (Winkler et al., 2009). This is supported by recent evidence from the brain imaging technique electroencephalography (EEG), which is a preferred neuroimaging technique for studies requiring high temporal resolution (e.g., for relating events to responses over the time course of an auditory stimulus presentation). Researchers showed that the brains of newborn infants, while listening to a repeating rhythmic drum sequence, detected when a downbeat was omitted from a sequence. This electrical brain response, called the ‘mismatch negativity’ (MMN), is present when an unusual change or a structural violation occurs in a repeating stimulus. In this study, the MMN response was not elicited by similar omissions at less salient beat positions; rather, it was elicited only by the absence of a downbeat. The MMN response is observed similarly in adult listeners, and is well known to reflect a change-detection mechanism in the human brain. This study was the first to show such a response to the detection of a missing downbeat in infants, and the authors interpreted these results as evidence that newborn brains can detect a violation in the beat structure of an auditory rhythm (Winkler et al., 2009).
The neonate study is consistent with behavioural work demonstrating that infants in the first year of life are sensitive to meter, but that over time, their perception becomes fine-tuned to familiar (versus foreign) metrical structures. In an elegant study using cross-cultural musical stimuli, 6–7 month-old North American infants were sensitive to structural violations of rhythm patterns with North American (e.g., 4/4) and Balkan (e.g., 7/8) metrical structures. By comparison, while adults of a Bulgarian or Macedonian musical origin also detected violations of both types of metrical structures (both of which are familiar to them), adults of a North American musical origin were sensitive only to the familiar North American structures. These results suggested that the infants’ meter perception was more flexible than the adults’, and that metrical categories are learned. Thus, the study provides evidence that infants can perceive hierarchical beat structure in music patterns. In addition, it shows that while meter perception starts out highly responsive and flexible in infancy, that flexibility is eventually traded off for biased processing to favour native sound patterns and structures (Hannon & Trehub, 2005).

The capacity to perceive a beat might lead to the ability to synchronise with a beat, but the latter seems to undergo refinement at later stages of development. Western toddlers under the age of five years reliably produce spontaneous and periodic movements (i.e., by hopping, swaying and circling) in response to music, but of the movement data that have been recorded and analysed by motion capture techniques so far, the toddlers have not been shown to synchronise (with strict period and phase) their movements with the external pulse of the music, or to adjust their rate of movement with a change in the tempo of the music (Eerola et al., 2006).

By 6 to 8 years of age, however, there is evidence that Western children can tap in time with music (Drake, 1997). These 6–8-year-olds were asked to subdivide isochronous beats (i.e., to tap faster than the beat but still in synchrony with the beat) and were found to produce binary subdivisions of the beat more frequently than ternary subdivisions, suggesting that the former was either easier to produce or more familiar to them. However, when they listened to binary- and ternary-accented versions of the pulse and were asked to concatenate the beats into measures (i.e., to tap slower than the beat but still in synchrony), they synchronised equally well with both types of grouping structures. Moreover, they showed no preference for binary or ternary synchronisations.

These findings give an example of how children can demonstrate their ability to perceive different grouping structures, even if children and adults tend to favour binary subdivisions of the beat. Several studies have suggested that humans possess an innate perceptual bias that favours binary over ternary structures, and both of these simple duration ratios over more complex ratios (Clark, 1999; Essens & Povel, 1985; Fraisse, 1982; Lerdahl & Jackendoff, 1983). It is not yet clear from studies of Western children and adults whether their preference for simple binary structures is the result of innate biases or of culture-specific learning and experience (Clayton, 2000). An interesting addition to the literature would be further investigation into the biases in perception and production of communities with folk music traditions that contain a
higher prevalence of non-binary rhythmic structures (e.g., meters with ratios of 3:2, 5:3 or 9:7), such as those found in African, Middle Eastern, South Asian and Eastern European musical cultures (Hannon & Trehub, 2005).

The available results on sensorimotor synchronisation in childhood development may not generalise to all children, as children show a large variability in their rate of motor development, which is related in turn to changes in other abilities, including proprioception and vision (Van Braekel et al., 2007), as well as in rates of development of attunement and focal attending (Drake et al., 2000b). Nor are these results necessarily representative of children across all cultures and communities—especially those that receive a higher level of exposure and practice in music or dance. Future research must address questions about the developmental trajectory of synchronisation ability throughout childhood and across cultures. 4

Although motor planning and execution are not fully developed during infancy and childhood, making synchronisation difficult or at least variable, this does not necessarily mean that the movements that infants and children experience during music are unrelated to their perception of the beat. Specifically, we can look for indications of a relationship between audition and movement that underlies the sense of feeling the beat in music. There is evidence that young infants have the basic equipment for processing temporal structure in music, as well as sensitivity to and delight in motion, such as swinging and bouncing (Elliot, 1999).

Phillips-Silver and Trainor (2005) tested the hypothesis that movement could directly influence infants’ auditory perception of the beat in music. To test this idea, we began with a simple percussion rhythm pattern—the composite rhythm that results from playing a two against three hemiola, in a six-microbeat measure (Figure 3). This pattern, when played without any acoustic accents, is inherently ambiguous in terms of metrical structure as it could be interpreted as a compound duple or a simple triple meter (recall the 2:3 Afro-Cuban clave pattern). The

![Figure 3](https://example.com/figure3.png)

**Figure 3** Accented beats give an ambiguous rhythm feeling. The composite rhythm pattern is derived from the superposition of binary and ternary macrobeat accents of a six-beat measure. This rhythm is ambiguous until given accented (either binary or ternary) beats. The 6/8 and 3/4 time patterns correspond to the test rhythms with auditory accents. In the experimental auditory stimulus, the snare drum, and is heard as a slapstick (Phillips-Silver & Trainor, 2005).
hypothesis was that moving the body on either two or three macrobeats could bias the auditory perception of the ongoing sound pattern, so as to induce a perceived representation of that pattern with accents on either two or three beats. In other words, if the movement that we feel can shape the sound that we hear, then the experience of having moved in two or in three should produce an auditory percept and thus a feeling of the rhythm in either 6/8 or 3/4 time.

This was the basis of our perceptual test with 7-month-old infants. A sound file of the ambiguous (unaccented) pattern was played repeatedly for a period of two minutes to familiarise the infants with it. At the same time, infants were bounced in the arms of an adult in order to induce a feeling of the beat. We divided our infant pool into two groups: one group experienced the bouncing in two (on every third eighth note of the pattern), and the other group experienced the bouncing in three (on every second eighth note). After the two-minute multisensory familiarisation came the test of their auditory perception. We presented the infants with two auditory versions of the same rhythm pattern with acoustic accent on either two or three beats. On a given trial, the infant heard one version of the pattern, followed by a pause, and the other version of the pattern. Using the well-established preference test method, we measured the infants’ interest (the amount of time spent listening) in each version, over a series of twenty trials.

Our prediction was that the version that would be of most interest to an infant would be the one that was familiar to that infant; those that were moved in two would prefer to listen to the auditory version of the rhythm pattern with accents in two, and those that were moved in three would prefer the version with accents in three. The results confirmed these predictions: infants that were bounced in two preferred the auditory rhythm with two accented beats, and infants that were bounced in three preferred the one with three accented beats. Both groups had listened to the same, ambiguous auditory stimulus during training; the only difference between the groups was their movement. The babies’ preference for the auditory rhythm pattern was determined directly by their movement experience, suggesting that they transferred the beat that they felt to the beat that they heard. This suggested auditory-motor integration in the perception of musical rhythm in young infants.

To be sure that the perception of the rhythm pattern was coming from the movement, and not from other sensory information such as visual cues, we repeated the experiment with a new group of infants, who were blindfolded during training. The results were identical, which meant that visual information was not driving the effect on auditory perception. Finally, we could only be sure that the movement was responsible for the observed effect by taking it away, and seeing if the effect remained. We ran a third experiment, with new babies who sat still on their parents’ laps while watching with interest as the experimenter bounced up and down in two or in three. If the effect on the infants’ auditory encoding of the rhythm pattern depended on actual movement of his or her body, then we should see no effect in the absence of that movement. This is what we found: in this condition of passive observation, the
effect disappeared; the babies showed no preference for either test version of the rhythm pattern.

Taken together, the results of these three experiments provided the first demonstration in the scientific literature that the way we move can shape what we hear in music. This gave evidence for a two-way interaction between hearing and feeling in music—that is, music not only makes us move, but the way we move shapes what we hear. Thus ‘feeling the beat’ can apparently be taken quite literally—beat perception is a multisensory process. The brain transfers the sensory information from movement to an auditory encoding, even without our awareness. The observation of this effect in babies supported the idea that this multisensory process develops very early in life, even before the motor skills for synchronised behaviour are present. This provides one additional piece of evidence that young babies are sensitive to beat structure, and in this case, that structure arose from movement (Phillips-Silver & Trainer, 2005).

The same hypothesis was tested in adults, by having them bounce up and down while following the experimenter and then asking them to identify which auditory test stimulus corresponded to the one they had heard during familiarisation (Phillips-Silver & Trainor, 2007). These adults were never alerted to the purpose of the experiment, and so they were never asked to recall what they had felt; only what they had heard. Adults consistently identified as familiar the auditory stimulus corresponding to their movement experience, just as the infants did. Also like the infants, adults who were blindfolded during training performed in the same way, but those who sat and passively observed as the experimenter bounced in two or three failed to discriminate between the test stimuli. Of course, this experiment requires adults to choose between representations of an ambiguous stimulus. In the context of real, accented music, we can certainly perceive and interpret the beat just by listening; visual information can play an important role as well. When, after the experiment, adults were asked how they chose the pattern they recognised, they often responded simply that they had ‘listened to the rhythm’—almost never mentioning the movement at all. This seemed to illustrate just how implicit the process of beat perception is, especially if we consider that many of the participants in this study had some kind of music training or experience.

Thus, the ability for movement to influence the auditory encoding of rhythm appears to be natural, implicit and present early in life. Furthermore, in an additional experiment in which adults were moved passively by being rocked on an adult-sized seesaw, we saw similar effects on their perception of the beat when full-body or head movement occurred, though not with leg movement alone (Phillips-Silver & Trainor, 2008). To propose a neural mechanism that could account for this effect, we considered the possibility that the auditory information was being integrated with information from the vestibular system during movement. The vestibular organ, which resides in the inner ear, is responsible for our sense of movement and orientation in space. The vestibular system is phylogenetically old, and, like the auditory system, it develops in the foetus by the third trimester in the uterus.
think of the coupling of motion and auditory information that the foetus might receive as the mother breathes, walks, hums and sways. Cortical or subcortical neural networks that combine sensory information from multiple modalities might provide a mechanism for the integration of auditory and vestibular inputs (Phillips-Silver & Trainor, 2008).

In a further version of the experiment, Trainor and colleagues tested more directly the contribution of vestibular information to the effect on auditory encoding of the rhythm (Trainor et al., 2009). By stimulating the vestibular nerve via an electrode placed behind the ears on the mastoids, adult subjects were caused to experience an illusion of head movement (though no actual movement occurred), and demonstrated an effect on their perception of the ambiguous rhythm pattern. As a control, the same electrode placed on the elbows produced no effect. Thus, the proposed auditory-vestibular interaction is one candidate explanation for the behavioural effect observed in which moving shapes how rhythm is felt, and thus heard. Now, if this auditory-movement interaction develops early, and naturally, then one should predict that everyone shares musical experiences such as that of feeling the beat. In the next section, we will take the perspective of research in neuropsychology to consider what can go wrong during the development of the brain’s musical system.

Perspective 4: Neuropsychology and Amusia

The neuropsychological perspective allows us to better understand the normal brain by studying what can go wrong with it—for example, as a result of a cerebral injury or a developmental (neurogenetic) disorder. Imagine for a moment that you sing the song *You Are My Sunshine* to a loved one; the lyrics are familiar, and it evokes the appropriate feelings of love and bonding. Now imagine that you remove the words, and hum the same song; this time your loved one does not recognise the tune, and it elicits no emotional reaction or feelings of association. This can resemble the experience in a condition called ‘congenital amusia’. Approximately 4% of the population have congenital amusia (meaning ‘without music’), also known as ‘tonedeafness’, which refers to impairment in fine-grained pitch resolution (Ayotte et al., 2002; Hyde & Peretz, 2004). For congenital amusics, the semitone and tone intervals that are the basic units in Western classical music can lie below their discrimination threshold, meaning that they fail to behaviourally detect such small changes in pitch. In contrast, congenital amusia has little consequence for language perception. The pitch intervals that are meaningful in language tend to be much larger than those in music, on the order of 5 to 12 semitones (for example, ending a word or phrase with a rising versus a falling fifth can signify a question versus a statement). This more coarse level of pitch perception appears to be preserved in congenital amusics (Peretz & Coltheart, 2003).

This neurological condition is not due to a lack of exposure to music, impaired peripheral hearing or general cognitive deficits such as intelligence (Ayotte et al. 2002), but may be caused by a genetic anomaly that inhibits the normal development
of musically relevant pitch processing. Congenital amusia has been associated with a cortical malformation in a region known to be involved in musical pitch encoding (the right inferior frontal gyrus, BA 47 and 11), and this anatomical correlate could reflect genetic or experiential factors in development (Hyde et al., 2006, 2007, 2008). For the Western adults who have been studied, this condition can prevent them from recognising or remembering musical melodies without lyrics, or even short tone sequences. One of the key characteristics of congenital amusics, aside from their impoverished ability to discriminate pitches, is their lack of awareness of this problem. Thus, while most people will detect (and cringe) when an out-of-key note is hit during a musical passage, an amusic will be quite unaware and even content.

The disconnect between the acoustical information that is processed by amusics and their cognitive representation (or awareness) of it is a key subject of investigation for researchers in congenital amusia. For example, while amusics fail to behaviourally detect either mistuned or out-of-key notes in a melody, their electrical (EEG) brain responses to pitch changes on the order of a quartertone are almost normal (Peretz et al., 2009). This has been measured by components of the event-related potential—specifically, an early right-lateralised negative brain response (N200), which indicates the detection of an anomalous tone in a melody (recall the mismatch negativity (MMN) response, another example of an electrical brain potential that indicates whether a change or error has been detected subconsciously). The use of this neuroimaging technique is helpful in showing that the acoustical pitch information is being encoded at some level; however, it is insufficient to convey to the conscious representation of pitch, resulting in the amusics’ lack of awareness of the pitch changes.

Yet another technique brings to light a damaged perception-action network in amusia—that is, a structural abnormality in the pathways bridging perception and action areas of the brain. Using diffusion tensor tractography, researchers pointed to the arcuate fasciculus (AF), a fiber tract of white matter connecting temporal and frontal brain regions, and known to be involved in the perception and production of language. Not only did amusics show abnormally reduced connectivity in the AF compared to control subjects, but also the nature of the abnormality was related to amusics’ deficits in pitch discrimination and production (Loui et al., 2009). A lack of neural connectivity in the amusic brain is an account that could help explain the origin of the condition, and on which further studies will contribute to our understanding of the perception-action networks for music in the normal brain.

Music is more than pitch discrimination, intonation and melody recognition. What of the temporal music capacities in congenital amusia? Although data on rhythm, meter and beat perception in congenital amusia have been sparse, some researchers have provided evidence that basic temporal processing skills, such as the discrimination of short rhythm patterns or the detection of a compressed or extended interval in a regular rhythmic sequence, are relatively spared in this population (Foxton et al., 2006; Hyde & Peretz, 2004). This means that it is possible for an individual to possess a deficit in pitch and melody perception in the absence of any deficit in perception of the timing of the notes. Indeed, some current investigations
into the rhythmic capacities of congenital amusics are aiming to isolate the rhythmic components of music in order to determine the extent to which this population is capable of appreciating musical time, and feeling the beat, despite their pitch deficit (Champoud-Tremblay et al., 2009; Phillips-Silver et al., 2008). Such questions are critical to our understanding of amusia; if these individuals are indeed capable of precise and high-level appreciation of rhythm in music, then we might say that they are not in fact ‘without music’ as their diagnostic label suggests. To put this in other terms, one might ask whether an individual with this neurogenetic anomaly, raised in a society whose musical structure depends highly on rhythmic elements such as pulse, metrical complexity and polyrhythm, and relatively little on pitch elements such as tonality, harmony or polyphony, would be considered ‘amusic’ at all (J. Laing, personal communication). Future evidence on perception and production of rhythm, meter and beat in music will enlighten the neuropsychological perspective on congenital amusia.

If amusic individuals fail to develop a normal pitch processing system while temporal processing is relatively spared, then one might ask whether the reverse pattern can be observed. Are there cases of individuals who have normal pitch perception and melody recognition, but who fail to develop a sense of rhythm, or beat? Very few reported cases exist of selectively damaged rhythm- or beat-processing capacities as a result of brain damage (Di Pietro et al., 2003; Wilson et al., 2002), and mentions of congenital rhythm deficits are rare, anecdotal and inconclusive. Che Guevara was famously ignorant of the distinction between prominent dance forms of his South American culture, such as the tango versus the milonga (Sacks, 2008). One might wonder if Che was able to step or clap in time with the music, or even to notice when he was not in time. Just as the inability to detect when a note is out-of-key might reflect a defective pitch processing system and possibly a failure to represent the tonality of a melody, so an inability to detect when a note is out-of-time might reflect a defective rhythm processing system and possibly a failure to represent the beat of a pattern. Future investigations into the human capacity for beat perception and synchronisation will address this question.

Following the documentation of a disorder in music processing, the next aim in such a neuropsychological research programme is to discover the potential cause(s) of the disorder, and to consider the implications for intervention or rehabilitation of the same or other disorders. For example, if congenital amusia is present from birth, can it be explained by a genetic anomaly? Can amusia be diagnosed early in life, and if so, might it be possible to affect the course of development (or even the expression of the disorder) via training? Just as important as the deficit are the spared abilities: if amusics demonstrate integrity of rhythm processing despite impaired pitch perception, they may be able to develop an appreciation for music that does not rely heavily on melodic pitch—any percussion music would do. The implications of this research can extend to other populations: some congenitally deaf individuals, who might experience music via (low frequency) vibrations, or those with cochlear implants, who like amusic individuals suffer from impoverished pitch resolution, but
demonstrate normal temporal processing (Cooper et al., 2008). In such groups, we might predict a potential for early training and intervention, as well as a rich appreciation for music that does not present them with uninterpretable noise, but rather delivers a meaningful musical message. Skilled deaf musicians and dance troupes abound, and are evidence enough.

Current research in neuropsychology and neuroscience is providing evidence to support the idea that we are generally all musical, but that rare cases of real musical disorders exist. Future avenues of research will seek not only to diagnose deficits in music processing, but to assess what traces of musical abilities might yet be preserved and to build a rehabilitation programme around those abilities. Music therapeutic efforts are employed frequently in clinical settings for non-music disorders, and often with great success. Music, including song and dance, is used with clients ranging from the aphasic to the autistic, and from premature infants to elderly Alzheimer’s patients. Empirical studies can also provide support for the powerful influence of music on mental and physical functioning. In certain conditions, such as dyslexia and Parkinson’s disease, rhythm and movement seem to be at the heart of the matter, and have become the basis for some current interventions (McIntosh et al., 1997; Overy, 2003).

In healthy children and adults as well, there is a growing body of evidence to suggest that active music practice affects cognitive and neural development (Fujioka et al., 2006; Musacchia et al., 2007; Schellenberg, 2004; Schlaug et al., 2005). Such studies will have implications for childhood development and education, as well as for musical expertise. Some of the major questions for future research in this field concern the relative (and integrated) contributions of auditory, motor, vestibular, visual and other sensory processes in music and dance, and their benefits for brain functioning. As research in music neuroscience continues to take cues from the practice of music and its clinical uses, more studies will be able to address the question of ‘why’ music and movement can be such effective tools for learning and recovery.

Conclusions

The link between music and movement is pervasive in human experience, and is a topic of exploration in the broad field of neuroscience. Theories on the role of music in evolution point to the importance of rhythmic synchronisation. Studies on beat perception and sensorimotor synchronisation provide ways to measure rhythm abilities, and offer evidence that integrated auditory-motor networks in the brain support these abilities. Developmental work demonstrates that the kinds of auditory-motor interactions that are involved in rhythm and beat perception emerge early in infancy. Although some individuals show music-related impairments, the abilities that are preserved may offer a pathway to music appreciation. Within the limits of scientific research, findings such as those discussed here are contributing to the understanding of the multisensory experience of rhythm in music. The collaboration
of scientists and musicians can continue to reveal the meaning of movement in music, development and the brain.

Notes


[2] I use the expression 'highly experienced' to refer to both informally and formally trained musicians because I believe that these kinds of listening skills develop in some cultures with formal music training and in others with communal music practice.

[3] Another example of discrepancy between science and music terminology lies in these variously used terms for experimental stimuli: ‘simple meter’ and ‘complex meter’, which again do not necessarily correspond to the musical definitions of those terms (e.g., ‘complex’ meter might be used to refer to an experimental stimulus that has an irregular meter). This issue is outside the scope of this article, but for a thorough exploration of meter perception, informed both by scientific and music theory, see London (2004).

[4] For a description of how children often represent rhythms graphically, see the work of Bamberger (1991). This provides a distinction between what have been called ‘formal’ versus ‘figural’ aspects of rhythm representation.

[5] For an online version of the diagnostic test for congenital amusia, see http://www.brams.org

[6] I am grateful to John Laing for discussions on amusia from an ethnomusicological perspective.


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