

## CHAPTER 16

# The neurobiological basis of musical expectations

Laurel J. Trainor and Robert J. Zatorre

### Introduction

As recently outlined by Huron (2006), we have evolved a brain that rewards accurate prediction. The evolutionary advantages of accurately predicting future events in the world are clear. Over half a century ago, Leonard Meyer (1956) presented his theory that emotional responses to music arise through expectations set up by musical patterns. However, for the most part, music is not about events in the world. What is the link between music and brain mechanisms for prediction? Meyer noted that some chords are more likely to follow other chords in Western musical structure: a melodic fragment sets up expectations for how it will continue. He proposed that low probability realizations give rise to physiological responses, such as changes in heart rate, breathing, and skin responses at an unconscious level, and thus spark emotional responses. Interpretation of the physiological responses in the context of the music gives rise to conscious emotional experience. Meyer proposed that most musical expectations were probably the result of familiarization with a particular musical genre. Indeed, a number of psychological studies have since asked Western listeners to rate their expectations of melodic continuations, and these studies show that people base their expectations on the rules of Western musical theory, whether or not they are explicitly aware of these rules (e.g. Krumhansl 1997; Tillmann *et al.* 2006; Tillmann and

Lebrun-Guillaud 2006; Unyk and Carlson 1987). On the other hand, Eugene Narmour (1990) presented his implication–realization model of musical expectation, which included a substantial set of innate, universal, bottom-up principles that should apply to all musical genres regardless of whether or not the listener is familiar with the genre. In testing people's expectations of various continuations of melodic patterns, Schellenberg (1997) was able to simplify Narmour's principle to two main ones. All else being equal, expect the next note to be proximate in pitch to the preceding note, and expect a reversal in pitch contour after relatively large intervals, but a continuation of pitch contour after relatively small intervals.

Recent neuroscientific work on musical processing is beginning to reveal the brain mechanisms by which expectations are set up and by which musical events are evaluated. In this chapter we will explore how the auditory system processes incoming information and generates perceptual representations that allow it to make predictions about future sound events from past context, and how music appears to make use of this general processing mechanism. We will focus on expectation formation in auditory cortex because this is where the most research has been done, but there is also evidence for prediction mechanisms at subcortical levels and at levels beyond sensory areas. We do not provide a complete review of the literature, but rather present a framework for thinking

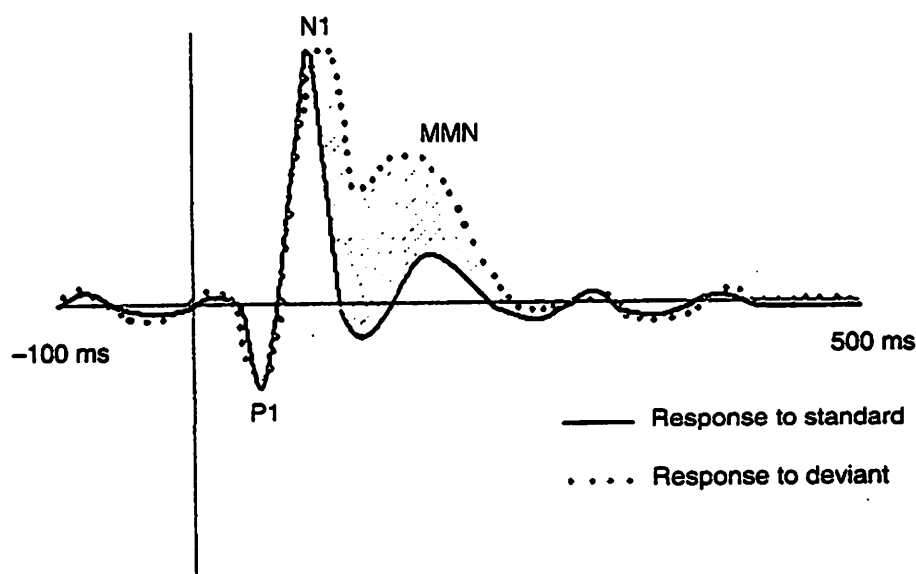
about the neurological basis of expectation and prediction in musical processing using selected examples.

## Physiological measurement of auditory expectations: predicting what will happen next

When a neuron depolarizes or fires, the flow of sodium and potassium ions in and out of the cell membrane results in the creation of electrical field potentials. When a large number of neurons whose axons point in the same direction, as between cortical layers, depolarize at the same time, a field potential is created that is large enough to be measured in a non-invasive way using an array of sensors across the scalp. When the electroencephalogram (EEG) is measured in response to an event such as a sound, it is referred to as an event-related potential (ERP). When occasional changes are made to a stream of repetitions of one sound, or when a change is made to a category of sounds, a frontally negative component is superimposed on the ERP wave form (Figure 16.1) that peaks between 150 and 250 ms, depending on the type of change. This component is called the mismatch negativity, or MMN, because it occurs

only when there is an occasional mismatch between the expected stimulus and the presented stimulus (Kujala *et al.* 2007; Näätänen *et al.* 2007; Picton *et al.* 2000). MMN is typically measured by subtracting the average response on the frequent standard trials from the average response on deviant trials (the occasional change trials). Although MMN can be influenced by attention, it occurs automatically and cannot be stopped by top-down conscious processing.

In the present context, MMN is of great interest because it reflects a process in the auditory system for predicting future sound events on the basis of the recent past, and the brain's reaction when those predictions are not fulfilled. We propose here that music fundamentally relies on expectation–realization processes, and that these processes are reflected in the MMN, whose main generators are in secondary auditory cortex (Schönwiesner *et al.* 2007). However, it should be kept in mind that there is a frontal contribution to the MMN response, that lower areas of the nervous system also employ expectation mechanisms (e.g., Csépe *et al.* 1989; Kraus *et al.* 1994; Ruusuvirta *et al.* 1995; Sonnadara *et al.* 2006b), and that some later ERP components reflecting conscious processing of music are also sensitive to expectations (e.g., Trainor *et al.* 2002; Desjardins *et al.* 1999).



**Fig. 16.1** Stylized renditions of the mismatch negativity event-related potential (MMN). Occasional deviants in a repeating stream of standard tones elicit an extra negativity (MMN) in the wave form of the deviants in comparison to standards.

## Acoustic expectations reflected in the MMN response

Mismatch responses reflect a general mechanism in auditory cortex in that MMN has been measured in response to changes in virtually every basic sound feature. Across these different types of change, the larger the change, the larger and earlier the MMN tends to be, and the more rare the deviant, the larger the MMN. Occasional changes in the frequency or pitch of a tone elicit robust MMN (see below). Changes in timbre also elicit MMN (Tervaniemi *et al.* 1997b; Toivainen *et al.* 1998), as do changes in duration, whether of a few milliseconds (e.g., Desjardins *et al.* 1999; Trainor *et al.* 2001, 2003a; Uther *et al.* 2003) or hundreds of milliseconds (e.g., Kaukoranta *et al.* 1989; Jaramillo *et al.* 2000). Changes in the spatial location of sounds produce MMN (e.g., Paavilainen *et al.* 1989; Sonnada *et al.* 2006a). Interestingly, both increases and decreases in intensity elicit MMN (Näätänen *et al.* 1989; Näätänen 1992), and even the omission of an expected sound can elicit MMN (Raij *et al.* 1997; Tervaniemi *et al.* 1994), indicating that MMN is not the result of the recruitment of additional neurons required to process a new stimulus, but rather the reflection of expectation violation processes.

What makes the MMN response so interesting is that it is elicited not only in response to the basic sound features indicated above, but also to changes in more complex stimulus features. For example, a change in speech phoneme category in the presence of multiple exemplars of each category elicits MMN (Kujala *et al.* 2001), as does a change in the order of tones in a pattern (e.g., Tervaniemi *et al.* 1997a). Furthermore, the MMN response is sensitive to complex statistical properties of the input, such as the conjunction of simple features. When a number of standard stimuli are presented that vary in simple features such as frequency, intensity and location, the presentation of a sound with a novel combination of these features elicits MMN (Näätänen and Winkler 1999). MMN is also sensitive to abstract rules governing the conjunction of features. When many standard stimuli are presented that vary in frequency and intensity, but follow the rule that stimuli with higher frequency also tend to be more intense,

MMN is elicited when this rule is violated (e.g., with a high-frequency, low-intensity sound) (Paavilainen *et al.* 2003).

Interestingly, the mismatch response to each sound feature gives rise to a slightly different pattern of electrical activation across the scalp, suggesting that the location of the neurons generating the MMN is in a slightly different place for each feature (e.g., Giard *et al.* 1995). This suggests that there is not one central MMN mechanism that processes all types of expectations but rather that there are many MMN processors, each specialized for a different sound feature. Thus, expectations for future sound events, and the evaluation of the realization of these expectations, is a widespread type of processing that is applied in many different places in auditory cortex. Furthermore, as will be discussed below, there is evidence that more than one MMN process can occur at the same time. In the next section, we focus on MMN studies probing expectancies in musical contexts.

## Expectations in musical contexts

Melody, the perceptual grouping of successive pitches into a coherent pattern, is central to musical structure. Although melodies are structured somewhat differently across different musical systems, there are universal features of melodies that probably evolved from basic constraints of the auditory system. One perceptually important feature is the contour, or up/down pattern of pitch changes without regard to the exact size of the pitch changes. Pitch contour is not specific to music as it is also important in the perception of linguistic information, playing a role in intonation, stress and, in the case of tone languages, lexical identity. However, melodies are also processed in terms of the exact size of the pitch intervals between tones, and unlike contour, interval processing does seem to be quite specific to music. In any particular musical system, pitch is not a continuous variable, but rather, only a small number of discrete intervals are used. For example, in the Western tonal musical system, the major scale defines one of the most common set of intervals used for composition. Other musical systems use different interval structures in their scales,

but virtually all scales rely on octave equivalence and a small set of tones per octave (Dowling and Harwood 1986).

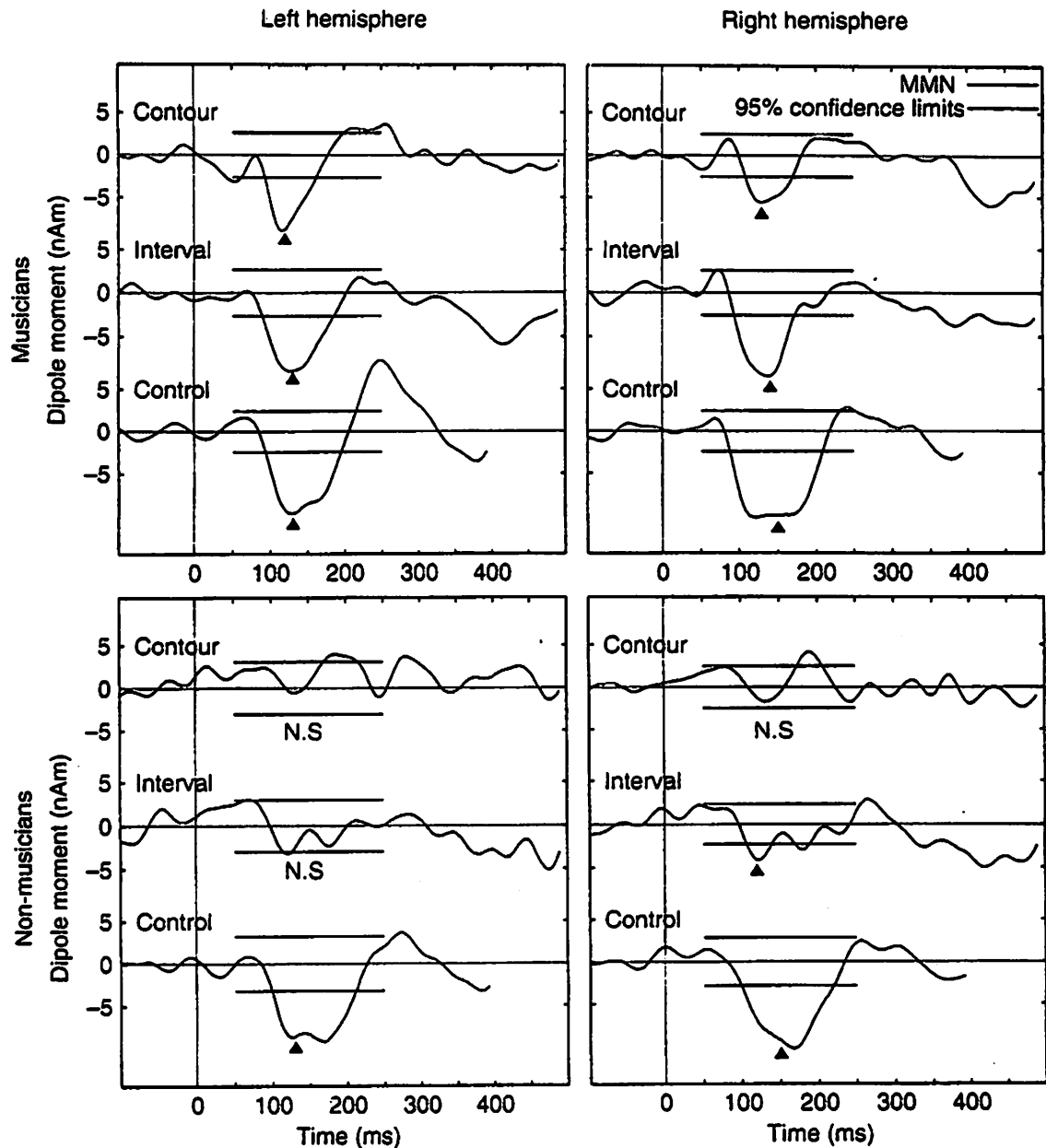
Melodic expectation arises in several ways. First, with a familiar melody, we can make predictions about the pitch of the next note that is expected based on a long-term memory representation. Second, when we hear music in a particular style, whether familiar or not, we can extract the statistical regularities and make predictions based on those. Third, whether or not a melody is familiar, we can make predictions about next notes that are based on our knowledge of universal melodic features. Fourth, we can use our culture-specific knowledge of what notes are likely to follow other notes in the music style with which we are familiar (Huron 2006; Hannon and Trainor 2007).

How might melodic expectations arise from the cortical system that handles pitch information? In order for expectations to develop, the system must first extract stable representations of the incoming input, and code relevant features in an invariant fashion (Whitfield 1985). The solution to this computational problem seems to lie in the hierarchical arrangement of sensory processing streams, which allow for different levels of abstraction to be computed at each level of processing. In the case of a melody, the interval information must be abstracted from individual tones which may vary in their fundamental frequency from one instance to another. In turn, the pitch of the individual tones must itself be computed in such a way as to achieve perceptual constancy, ignoring irrelevant variation in surface features. Substantial evidence now exists that pitch invariance is computed in an area of belt cortex lateral to primary cortex, in both monkeys (Bendor and Wang 2005), and humans (Zatorre 1988; Johnsrude *et al.* 2000; Griffiths *et al.* 1998; Penagos *et al.* 2004; Krumboltz *et al.* 2003). This region then feeds information into more distal portions of the processing stream, both anterior and posterior to the pitch-sensitive region, where melodic features are processed (Zatorre 1985; Zatorre *et al.* 1984; Patterson *et al.* 2002). The hierarchy of processing must eventually make contact with long-term memory systems where both implicit knowledge about general patterns, and specific knowledge

about a particular musical piece, are stored. Expectations could thus arise from the interplay between the feedforward sensory abstraction mechanism, and the feedback received from stored internal representations.

MMN responses reflect musical expectations at a number of levels. Violation of both contour and interval expectations set up by a melodic context give rise to MMN, even in non-musicians. Saarinen *et al.* (1992) presented standard tone pairs where the pitches of the tones varied from trial to trial, but the pitch always rose from the first to the second tone. In deviant tone pairs the pitch fell from the first to second tone. Thus, despite the fact that standards varied in absolute pitch, the auditory cortex generated an expectation for rising contour. Tervaniemi *et al.* (2001) showed that contour expectations are also generated with a more complex inverted-U-shaped contour. Given that pitch contour is important in both speech and music, it is perhaps not surprising that the brain is set up to automatically predict contour based on current context in musicians and non-musicians alike. However, Trainor *et al.* (2002) showed that non-musicians also form expectations for particular intervals in the absence of absolute pitch information. Specifically, when presented with a standard 5-note melody that was transposed to different pitch levels (keys) on successive repetitions, occasional changes to the last note that altered the interval size but not contour led to robust MMN. Such mismatch responses are typically larger and earlier in musicians than in non-musicians (Figure 16.2), (Fujioka *et al.* 2004), indicating either genetic differences between musicians and non-musicians or the plastic effects of musical training. However, at the same time, these results suggest that even in the absence of musical training, auditory cortex automatically encodes music-specific melodic information and creates expectations for future events.

In polyphonic music, two or more melody lines occur at the same time. Fujioka *et al.* (2005) demonstrated that separate memory traces are formed for each melody, and that predictive processes within each stream can be measured with MMN. On 25 per cent of trials one note was raised by a tone or a semitone in one melody, and on another 25 per cent of trials one tone



**Fig. 16.2** MMN to occasional changes in the contour or interval of a melody. Source space wave forms in auditory cortex from MEG data are shown. Musicians are shown in the upper panel and non-musicians in the lower panel. In both groups, an MMN response can be seen to changes in pitch interval and to changes in pitch contour, but MMN amplitude is much larger in musicians than in non-musicians. MMN is also seen in the control condition where the pitch of a single repeating tone is occasionally changed. However, in the control condition there are no differences between musicians and non-musicians. Reprinted with permission from Fujioka *et al.* (2004).

was lowered by a tone or a semitone in the other melody. Thus, the overall deviance rate was 50 per cent, so if separate streams were not formed, no MMN response would be expected because standard and deviant trials were equally probable. However, significant MMN was found for changes in both melodies, indicating that the

two melodies were encoded separately. In the case of two simultaneous melodies, as with single melodies (Fujioka *et al.* 2004), musicians showed more robust MMN responses than non-musicians. Interestingly, for both groups, high and low melodies were not encoded equally well, as MMN was larger for the higher voice, consist-

ent with the compositional practice of putting the melody in the highest voice, and with people's superior perception of the highest voice (Crawley *et al.* 2002). In a follow up study, Fujioka *et al.* (2008) showed that the superiority of the higher voice is a very general phenomenon, also holding in the situation where each of the two voices consists of a single pitch. Finally, across a number of studies, no difference in MMN amplitude or latency was found for changes that went outside the key of a melody compared to changes that remained within the key (Trainor *et al.* 2001; Fujioka *et al.* 2004, 2005), suggesting that some aspects of culture-specific musical structure are processed beyond the auditory areas responsible for MMN generation.

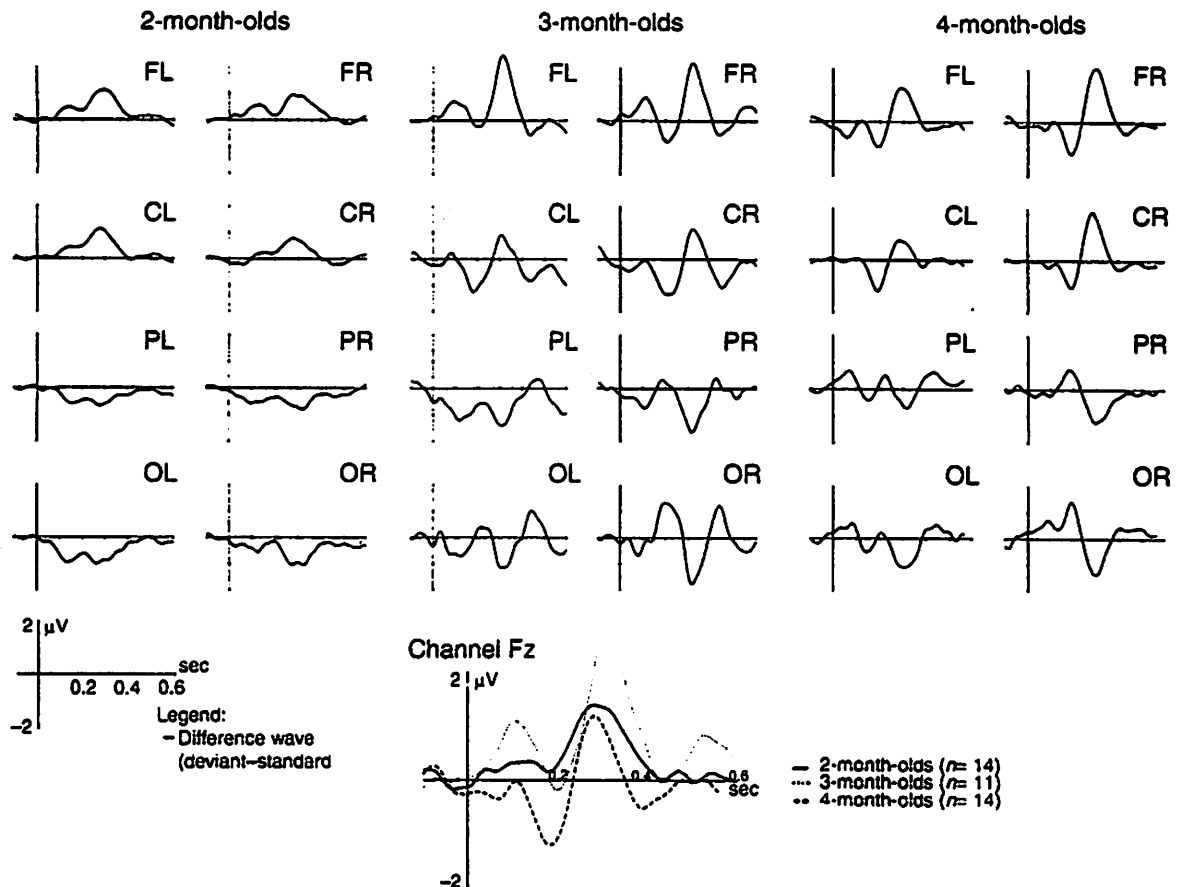
While we have focused on the MMN as a neural correlate of musical expectancy, it is important to note that there are culture-specific aspects of musical expectancy which are processed in brain areas beyond the auditory regions responsible for MMN generation. For example, in Western musical structure chords follow each other according to genre-specific syntactic rules. Koelsch and his colleagues have demonstrated that a syntactically unexpected chord, such as a Neapolitan chord at the end of a cadence where a tonic chord is expected, gives rise to an early right anterior negativity (ERAN) (Koelsch *et al.* 2000; cf. Patel *et al.* 1998). ERAN is similar to MMN, but occurs somewhat later, is sensitive to harmonic expectations (Koelsch *et al.* 2001), and appears to involve inferior frontolateral cortex (Broca's area) (Maess *et al.* 2001). ERAN is also elicited by unexpected modulations in key (Koelsch *et al.* 2003). As with MMN responses to single and polyphonic melodies (Fujioka *et al.* 2004, 2005), ERAN responses to unexpected chords are present in both musicians and nonmusicians, although larger in musicians (Koelsch *et al.* 2002a). Furthermore, ERAN for unexpected chords is present even when other factors such as simple note repetition and degree of dissonance are controlled for (Koelsch *et al.* 2007; Leino *et al.* 2007). Finally, functional magnetic resonance imaging (fMRI) studies reveal that musical syntax activates a network of brain regions that resembles that for linguistic syntax (e.g., Koelsch *et al.* 2002b; cf. Patel 2003), suggesting further that music makes use of general processing properties of the cortex.

In summary, MMN and ERAN responses demonstrate that, for musical input, the brain is continually using the recent past to predict the future, and the magnitude of these responses reflects the degree to which these expectations are not fulfilled. MMN is sensitive to changes in acoustic features and patterns of sounds, and several MMN processes can occur simultaneously. ERAN is sensitive to culture-specific knowledge that is built up through exposure to a particular music system.

## The early development of musical expectations in infants

ERP responses to sound are very immature in infancy, reflecting the protracted development of the auditory cortex that extends into the teenage years (Huttenlocher and Dabholkar 1997; Moore 2002; Moore and Guan 2001; Ponton *et al.* 2000; Shahin *et al.* 2004; Trainor *et al.* 2003). Despite this great immaturity, robust mismatch responses can be measured from infants, suggesting that infant MMN is among the first developing cortical responses to sound (Näätänen *et al.* 2007). We argued in the introduction that being able to accurately predict the future is of paramount importance to survival. From this perspective, it makes sense, then, that mismatch responses would be among the earliest cortical responses, as they may be essential for optimal wiring of the brain through experience.

In very young infants, the ERP wave form is dominated by a frontally positive, anterior-negative slow wave. Interestingly, when a repeating sound is changed in pitch (e.g., Leppänen *et al.* 1997), fine temporal structure (e.g., Trainor *et al.* 2003), or vowel category (Dehaene-Lambertz and Baillet 1998), the slow wave increases in positivity (see Figure 16.3). An adult-like MMN emerges around 4 months of age or so in response to sound feature changes (He *et al.* 2007a; Trainor *et al.* 2001, 2003a) (see Figure 16.3). The slow wave and adult-like MMN probably represent different processes as both can be seen in infants of intermediate age (He *et al.* 2007a). Furthermore, the MMN in 4-month-olds increases with larger pitch



**Fig. 16.3** Difference waves (deviant-standard) to occasional half-octave changes in the pitch of a repeating standard tone in 2-month-olds, 3-month-olds and 4-month-olds at different scalp locations: F, frontal; C, central; P, parietal; O, occipital; L, left; R, right. In 2-month-olds, a slow positive difference wave is seen. In 3- and 4-month-olds a faster negative response resembling adult MMN can be seen followed by a positivity resembling P3a in adults. Both components reverse polarity at the back of the head. MMN becomes larger with increasing age. Reprinted with permission from He *et al.* (2007).

changes and remains robust at fast presentation rates, similar to adult MMN (He *et al.* 2007b).

These mismatch responses allow investigation of the developmental origins of musical expectations. These studies are just beginning. To date, it is clear that a repeating tone of one pitch sets up expectations for future repetitions of that pitch in infants (e.g., Alho *et al.* 1990; Ceponienė *et al.* 2002; He *et al.* 2007a, b; Leppänen *et al.* 1997; Morr *et al.* 2002). Furthermore, 4-month-olds show robust MMN responses to the pitch of occasional deviants with missing fundamental components, indicating that they integrate the frequency content of complex tones into a single percept (He and

Trainor 2007). Of most interest for musical processing, 4-month-olds also exhibit an MMN response when there is a change in a sequential pitch pattern (He *et al.* 2007b). Specifically, when the order of tones in a repeating two-tone sequence is occasionally reversed, a clear MMN is seen.

In sum, mismatch responses are among the earliest cortical responses to sound. The groundwork has now been established so that future studies can investigate in much more detail how musical expectations develop in the auditory cortex of human infants, and examine questions such as the effects of particular auditory experience on the development of these expectations.

## Temporal expectations and auditory–motor interactions: predicting *when* events will occur

As music unfolds over time, the brain extracts rhythmic regularities and sets up expectancies for when events will occur as well as for what the events will be. Time structure in music involves two aspects. First, there is the sequence of sound events and silence durations, which is referred to as the *rhythmic pattern*. Second, when a pattern contains temporal regularities, listeners infer an underlying regular hierarchical beat structure (what you tap your foot to), called the *metrical structure*. Metrical structure is not given in the stimulus, and there may not actually be sound events on some beats; rather, metre is derived by the brain from temporal regularities in the rhythm pattern. Metrical structure is hierarchical, with the strong beats being spaced progressively further apart in time at higher levels of the hierarchy, such that you can clap or tap, for example, on every beat, every second beat, or every fourth beat of a rhythm pattern organized into binary groups. The strong expectancies set up by metrical structure are evident in that the sense of a beat can continue past the end of a piece of music. One plausible theory as to how this happens is that neural circuits in the brain act as oscillators that can adjust their phase and frequency to some extent in response to the input from rhythmic patterns (Large and Jones 1999). Evidence for the neurological instantiation of temporal expectancy comes from studies of the induced gamma band response. Gamma band activity is in the range of 40–60 Hz, and can be extracted from an EEG recording by doing a Fourier analysis. The evoked gamma band response occurs shortly after the onset of a sound and is tightly time-locked to the sound onset (e.g., Ross *et al.* 2005). The induced gamma-band response, on the other hand, is only loosely time-locked to the sound, and therefore has a different phase on every trial (e.g., Tallon-Baudry *et al.* 1996). The induced gamma-band response appears to reflect processes of intrinsic temporal expectation as it can be measured at points in time where a sound is expected,

even if the sound event is not realized and there is only silence (Snyder and Large 2005). Furthermore, the induced gamma-band response is larger in musicians than in non-musicians, especially for sounds of their instrument of practice, and it also develops to a greater extent over the course of a year in young children taking music lessons compared to children not studying music (Shahin *et al.* 2008).

Temporal expectancies are important both in listening to music and in performing music (Large and Palmer 2002). A number of researchers have noted the close interaction between movement and auditory rhythm (Phillips-Silver and Trainor 2007, 2008; Trainor *et al.* in press; Repp 2005; Todd *et al.* 2007), even in infants (Phillips-Silver and Trainor 2005) and in non-human species (Todd *et al.* 2007). Indeed the close connection between music and dance suggests that musical rhythm might have evolved from rhythmic movement. A number of researchers, working on both speech and music, have postulated that *perception* of timing involves interactions between auditory and motor systems (Hickok and Poeppel 2004; Phillips-Silver and Trainor 2005, 2007, 2008; Repp 2005; Warren *et al.* 2005). This idea is related to research in vision, where similar neural responses exist both to observing an action and to performing the action (Rizzolatti and Craighero 2004).

A number of recent imaging studies dealing with musical perception and production suggest that the two processes may be closely intertwined; for instance, MEG data show that activity in the vicinity of the primary motor cortex could be evoked in pianists when they listened passively to well-known melodies (Haueisen and Knosche 2001). Two other fMRI studies (Bangert *et al.* 2006; Baumann *et al.* 2005) also reported that neural regions overlapped when pianists either listened to music without playing it, or played on a keyboard without any feedback; the overlap included the premotor cortex, supplementary motor area and the posterior auditory cortex. Increased motor excitability in the primary motor cortex of pianists has also been observed as they listened to a known piano piece, compared to a piece they were not trained on (D'Ausilio *et al.* 2006).



The phenomena are not limited to trained musicians, but can also be found amongst non-musicians. For example, a common pattern of EEG activity in auditory and motor areas was found in a task in which non-musicians were trained to play a simple melody on a keyboard (Bangert and Altenmüller 2003). The effect was only apparent when sound–movement mappings were congruent, and not when the learning did not result in a consistent assignment of key-presses to sounds. Similarly Lahav *et al.* (2007) used fMRI to show that premotor cortex and Broca's area were active when non-musicians heard melodies that they had previously learned to play, but not upon hearing equally familiar but motorically untrained melodies. Other studies have also noted premotor cortex activity during music listening under less specific circumstances, such as in melodic discrimination (Brown and Martinez 2007), or while listening to consonant musical excerpts (Koelsch *et al.* 2006). These effects have been interpreted as reflecting possible subvocal rehearsal, a phenomenon also suggested to occur during musical imagery tasks (Zatorre and Halpern 2005). Thus, it is now fairly well established that auditory–motor coactivation can be observed in musicians and in non-musicians, either spontaneously, or more specifically when there is a direct learned mapping between movement and sound.

Of most interest with respect to the involvement of auditory–motor interactions in the prediction of *when* events will happen, is the idea that interactions between posterior auditory cortices and premotor cortices might mediate the cognitive representations that are responsible for integrating feedforward and feedback information during performance and perception (Zatorre *et al.* 2007). Indeed, higher-order temporal organization (metricality) might emerge from the temporal predictions that are enabled by this system. Evidence for this comes from Chen *et al.* (2006) who found that the degree to which auditory input modulates motor behaviour is enhanced by metrical saliency (the intensity of accented beats). In other words, increased predictability of auditory events in music leads to greater auditory–motor interaction. In a related study (Chen *et al.* 2008), a similar region of premotor cortex was also

found to be recruited as subjects reproduced progressively more complex rhythmic movements. These studies manipulated the abstract metrical structure of the rhythms, and therefore the organization of the movement sequences (i.e., their predictability). One hypothesis to account for these results is that what modulates premotor activity in these instances is not the direct mapping of sounds to movements, but rather, the selection of movements based on the auditory cue. The dorsal segment of premotor cortex would, according to this view, be involved in extracting higher-order features of the musical sound, including its rhythmic metrical structure, therefore allowing implementation of temporally organized actions. Listening to music may activate motor programmes directly associated with producing the music, for example when a musician knows the piece he or she is listening to; but perhaps more interesting, listening to music also appears to engage auditory–motor interactions that extract higher-order metrical information. This latter mechanism may be critical in setting up the temporal expectancies that are essential for musical understanding (Huron 2006). As such, the interplay between auditory processing streams and the premotor system could be thought of as the temporal counterpart of the pitch-based expectancies discussed above, which rely on the interplay between auditory and memory systems.

## **Future directions: understanding the neurobiology behind music expectations and emotional responses**

In 1956, Meyer argued convincingly that music induces emotional experiences through physiological responses to musical expectations and the degree to which they are realized. In the present paper, we argue that music makes use of general brain mechanisms devoted to encoding the recent past, predicting the future, and dynamically adjusting the encoding of the recent past when the prediction is not accurate. We suggest, further, that such predictive processes

are essential for adaptation, plasticity, and learning, because evaluation of the success of the prediction provides a learning signal by which neural networks can change in order to more accurately and usefully encode the sensory input. We provided extensive physiological evidence from EEG, fMRI and MEG studies that music makes use of these general-purpose mechanisms, and that musical structure constantly engages the brain in a game of prediction. Some aspects of musical prediction, such as using statistical properties of recent input, are probably relatively independent of specific experience with a musical system whereas others, such as predicting the next chord in a sequence, probably rely on experience with a specific musical system. In particular, the framework that we have presented, in which MMN responses to unexpected events occur automatically and without attention, can explain why a note or chord that is musically unexpected continues to evoke an emotional response even when we are familiar with the piece and know at a conscious level that the unexpected chord is coming.

Huron (2006) suggests that not only does the brain make predictions about the future, but that there are intrinsic reward systems for correct prediction. With less expected musical realizations, a physiological arousal occurs, but, after appraisal, it is evident that there are no 'bad' consequences from the poor prediction because music is not about events in the world. So the emotion we feel tends to be strong and positive. To date, there is little physiological data linking violation of musical expectation and emotional responses. However, one study revealed that subjective ratings of tension and emotion, electrodermal activity, and an early negativity in the ERP all increased more for very unexpected than for somewhat unexpected (Steinbeis *et al.* 2006). It remains for future research, however, to uncover the pathways in the nervous system that link the perception of unexpected events with our emotional responses to them.

## Acknowledgments

The writing of this chapter was supported by grants from the Natural Science and Engineering

Research Council of Canada and the Canadian Institutes of Health Research.

## References

- Alho K, Sainio K, Sajaniemi N, Reinikainen K and Näätänen R (1990). Event-related brain potential of human newborns to pitch change of an acoustic stimulus. *Electroencephalography and Clinical Neurophysiology*, 77, 151–155.
- Bangert M and Altenmüller EO (2003). Mapping perception to action in piano practice: a longitudinal DC-EEG study. *BMC Neurosci*, 4, 26.
- Bangert M, Peschel T, Schlaug G, Rotte M, Drescher D, Hinrichs H *et al.* (2006). Shared networks for auditory and motor processing in professional pianists: evidence from fMRI conjunction. *Neuroimage*, 30(3), 917–926.
- Baumann S, Koeneke S, Meyer M, Lutz K and Jancke L (2005). A network for sensory-motor integration: what happens in the auditory cortex during piano playing without acoustic feedback? *Annals of the New York Academy of Sciences*, 1060, 186–188.
- Bendor D and Wang X (2005). The neuronal representation of pitch in primate auditory cortex. *Nature*, 436(7054), 1161.
- Brown S and Martinez MJ (2007). Activation of premotor vocal areas during musical discrimination. *Brain and Cognition*, 63(1), 59.
- Ceponienė R, Kushnarenko E, Fellman V, Renlund M, Suominen K and Näätänen R (2002). Event-related potential features indexing central auditory discrimination by newborns. *Cognitive Brain Research*, 13, 101–113.
- Chen J, Penhune V and Zatorre R (2008). Moving in time: brain networks for auditory-motor synchronization are modulated by rhythm complexity and musical training. *Journal of Cognitive Neuroscience*, 20, 226–239.
- Chen JL, Zatorre RJ and Penhune VB (2006). Interactions between auditory and dorsal premotor cortex during synchronization to musical rhythms. *Neuroimage*, 32(4), 1771–1781.
- Crawley EJ, Acker-Mills BE, Pastore RE and Weil S (2002). Change detection in multi-voice music: the role of musical structure, musical training, and task demands. *Journal of Experimental Psychology: Human Perception and Performance*, 28, 367–378.
- Csépe V, Karmos G and Molnár M (1989). Subcortical evoked potential correlates of early information processing: mismatch negativity in cats. In E Basar, TH Bullock, eds, *Springer series in brain dynamics*, vol. 2, pp. 278–289. Springer Verlag, Berlin.
- D'Ausilio A, Altenmüller E, Olivetti Belardinelli M and Lotze M (2006). Cross-modal plasticity of the motor cortex while listening to a rehearsed musical piece. *European Journal of Neuroscience*, 24(3), 955–958.
- Dehaene-Lambertz G and Baillet SA (1998). A phonological representation in the infant brain. *NeuroReport*, 9, 1885–1888.

- Desjardins RN, Trainor LJ, Hevenor SJ and Polak CP (1999). Using mismatch negativity to measure auditory temporal resolution thresholds. *NeuroReport*, 10, 2079–2082.
- Dowling WJ, Harwood DL (1986). *Music cognition*. Academic Press, Orlando, FL.
- Fujioka T, Trainor LJ and Ross B (2008). Simultaneous pitches are encoded separately in auditory cortex: an MMNm study. *NeuroReport*, 19, 361–366.
- Fujioka T, Trainor LJ, Ross B, Kakigi R and Pantev C (2004). Musical training enhances automatic encoding of melodic contour and interval structure. *Journal of Cognitive Neuroscience*, 16, 1010–1021.
- Fujioka T, Trainor LJ, Ross B, Kakigi R and Pantev C (2005). Automatic encoding of polyphonic melodies in musicians and nonmusicians. *Journal of Cognitive Neuroscience*, 17, 1578–1592.
- Giard MH, Lavikainen J, Reinikainen K, Perrin F, Bertrand O, Thévenet M *et al.* (1995). Separate representation of stimulus frequency, intensity, and duration in auditory sensory memory. *Journal of Cognitive Neurosciences*, 7, 133–143.
- Griffiths TD, Buchel C, Frackowiak RS and Patterson RD (1998). Analysis of temporal structure in sound by the human brain. *Nature Neuroscience*, 1(5), 422–427.
- Hannon EE and Trainor LJ (2007). Music acquisition: effects of enculturation and formal training on development. *Trends in Cognitive Sciences*, 11, 466–472.
- Hauelsen J and Knosche TR (2001). Involuntary motor activity in pianists evoked by music perception. *Journal of Cognitive Neuroscience*, 13(6), 786–792.
- He C and Trainor LJ (2007). Finding the pitch of the missing fundamental in infants. Presented at the 8th Conference of the Society for Music Perception and Cognition, Montreal, QC, Canada.
- He C, Hotson L and Trainor LJ (2007a). Mismatch responses to pitch changes in early infancy. *Journal of Cognitive Neuroscience*, 19, 878–892.
- He C, Hotson L and Trainor LJ (2007b). Changes in melodic pattern perception over the first few months after birth: electrophysiological evidence. Presented at the 8th Conference of the Society for Music Perception and Cognition, Montreal, QC, Canada.
- Hickok G and Poeppel D (2004). Dorsal and ventral streams: a framework for understanding aspects of the functional anatomy of language. *Cognition*, 92(1–2), 67–99.
- Huron D (2006). *Sweet anticipation: music and the psychology of expectation*. MIT Press, Cambridge, MA.
- Huttenlocher PR and Dabholkar AS (1997). Regional differences in synaptogenesis in human cerebral cortex. *Journal of Comparative Neurology*, 387, 167–178.
- Jaramillo M, Paavilainen P and Näätänen R (2000). Mismatch negativity and behavioural discrimination in humans as a function of the magnitude of change in sound duration. *Neuroscience Letters*, 290, 101–104.
- Johnsrude IS, Penhune VB and Zatorre RJ (2000). Functional specificity in the right human auditory cortex for perceiving pitch direction. *Brain*, 123, 155–163.
- Kaukoranta E, Sams M, Hari R, Hämäläinen M and Näätänen R (1989). Reactions of human auditory cortex to changes in tone duration. *Hearing Research*, 41, 15–22.
- Koelsch S, Fritz T, von Cramon DY, Müller K and Friederici AD (2006). Investigating emotion with music: an fMRI study. *Human Brain Mapping*, 27(3), 239–250.
- Koelsch S, Gunter T, Schröger E and Friederici AD (2003). Processing tonal modulations: an ERP study. *Journal of Cognitive Neuroscience*, 15, 1149–1159.
- Koelsch S, Gunter TC and Friederici AD (2000). Brain indices of music processing: ‘nonmusicians’ are musical. *Journal of Cognitive Neuroscience*, 13, 520–541.
- Koelsch S, Gunter TC, Schröger E, Tervaniemi M, Sammler D and Friederici A (2001). Differentiating ERAN and MMN: an ERP study. *Neuroreport*, 12, 1385–1389.
- Koelsch S, Gunter TC, Yves D, von Cramon DY, Zysset S, Lohmann G and Friederici AD (2002b). Bach speaks: a cortical ‘language-network’ serves the processing of music. *Neuroimage*, 17, 956–966.
- Koelsch S, Jentschke S, Sammler D and Mietschen D (2007). Untangling syntactic and sensory processing: an ERP study of music perception. *Psychophysiology*, 44, 476–490.
- Koelsch S, Schmidt B-H and Kansok J (2002a). Effects of musical expertise on the early right anterior negativity: an event-related brain potential study. *Psychophysiology*, 39, 657–663.
- Kraus N, McGee T, Littman T and King C (1994). Nonprimary auditory thalamic representation of acoustic change. *Journal of Neurophysiology*, 72, 1270–1277.
- Krumholz K, Patterson RD, Seither-Preisler A, Lammertmann C and Lutkenhoner B (2003). Neuromagnetic evidence for a pitch processing center in Heschl’s gyrus. *Cerebral Cortex*, 13(7), 765–772.
- Krumhansl CL (1997). Effects of perceptual organization and musical form on melodic expectancies. In M Leman, ed., *Music, gestalt, and computing: studies in cognitive and systematic musicology*, pp. 294–320. Springer Verlag, Berlin.
- Kujala T, Karma K, Ceponiene R, Belitz S, Turkila P, Tervaniemi M *et al.* (2001). Plastic neural changes and reading improvement caused by audio-visual training in reading-impaired children. *Proceedings of the National Academy of Sciences*, 98, 10509–10514.
- Kujala T, Tervaniemi M and Schröger E (2007). The mismatch negativity in cognitive and clinical neuroscience: theoretical and methodological considerations. *Biological Psychology*, 74, 1–19.
- Lahav A, Saltzman E and Schlaug G (2007). Action representation of sound: audiomotor recognition network while listening to newly acquired actions. *Journal of Neuroscience*, 27(2), 308–314.
- Large EW and Jones MR (1999). The dynamics of attending: how people track time-varying events. *Psychological Review*, 106, 119–159.
- Large EW and Palmer C (2002). Perceiving temporal regularity in music. *Cognitive Science*, 26, 1–37.

- Leino S, Brattico E, Tervaniemi M and Vuust P (2007). Representation of harmony rules in the human brain: further evidence from event-related potentials. *Brain Research*, 1142, 169–177.
- Leppänen PH, Eklund KM and Lyytinen H (1997). Event-related brain potentials to change in rapidly presented acoustic stimuli in newborns. *Developmental Neuropsychology*, 13, 175–204.
- Maess B, Koelsch S, Gunter T and Friederici AD (2001). 'Musical syntax' is processed in the area of Broca: an MEG-study. *Nature Neuroscience*, 4, 540–545.
- Meyer LB (1956). *Emotion and meaning in music*. University of Chicago Press, Chicago, IL.
- Moore JK (2002). Maturation of human auditory cortex: implications for speech perception. *The Annals of Otolaryngology, Rhinology, and Laryngology*, 111, 7–10.
- Moore JK and Guan YL (2001). Cytoarchitectural and axonal maturation in human auditory cortex. *Journal of the Association for Research on Otolaryngology*, 2, 297–311.
- Morr ML, Shafer VL, Kreuzer JA and Kurtzberg D (2002). Maturation of mismatch negativity in typically developing infants and preschool children. *Ear and Hearing*, 23, 118–136.
- Näätänen R (1992). *Attention and brain function*. Lawrence Erlbaum Associates, Hillsdale, NJ.
- Näätänen R and Winkler I (1999). The concept of auditory stimulus representation in neuroscience. *Psychological Bulletin*, 125, 826–859.
- Näätänen R, Paavilainen P, Alho K, Reinikainen K and Sams M (1989). Do event-related potentials reveal the mechanism of the auditory sensory memory in the human brain? *Neuroscience Letters*, 98, 217–221.
- Näätänen R, Paavilainen P, Rinne T and Alho K (2007). The mismatch negativity (MMN) in basic research of central auditory processing: a review. *Clinical Neurophysiology*, 118, 2544–2590.
- Narmour E (1990). *The analysis and cognition of basic melodic structures: the implication-realization model*. University of Chicago Press, Chicago, IL.
- Paavilainen P, Degerman A, Takegata R and Winkler I (2003). Spectral and temporal stimulus characteristics in the processing of abstract auditory features. *NeuroReport*, 14, 715–718.
- Paavilainen P, Karlsson M-L, Reinikainen K and Näätänen R (1989). Mismatch negativity to change in the spatial location of an auditory stimulus. *Electroencephalography and Clinical Neurophysiology*, 73, 129–141.
- Patel AD (2003). Language, music, syntax, and the brain. *Nature Neuroscience*, 6, 674–681.
- Patel AD, Gibson E, Ratner J, Besson M and Holcomb P (1998). Processing syntactic relations in language and music: an event-related potential study. *Journal of Cognitive Neuroscience*, 10, 717–733.
- Patterson RD, Uppenkamp S, Johnsrude IS, Griffiths TD (2002). The processing of temporal pitch and melody information in auditory cortex. *Neuron*, 36, 767–776.
- Penagos H, Melcher JR, Oxenham AJ (2004). A neural representation of pitch salience in nonprimary human auditory cortex revealed with functional magnetic resonance imaging. *Journal of Neuroscience*, 24(30), 6810–6815.
- Phillips-Silver J and Trainor LJ (2005). Feeling the beat in music: movement influences rhythm perception in infants. *Science*, 308, 1430.
- Phillips-Silver J and Trainor LJ (2007). Hearing what the body feels: auditory encoding of rhythmic movement. *Cognition*, 105, 533–546.
- Phillips-Silver J and Trainor LJ (2008). Vestibular influence on auditory metrical interpretation. *Brain and Cognition*, 67, 94–102.
- Picton TW, Alain C, Otten L, Ritter W and Achim A (2000). Mismatch negativity: different water in the same river. *Audiology and Neuro Otolaryngology*, 5, 111–139.
- Ponton C, Eggermont JJ, Kwong B and Don M (2000). Maturation of human central auditory system activity: evidence from multi-channel evoked potentials. *Clinical Neurophysiology*, 111, 220–236.
- Raij T, McEvoy L, Mäkelä JP and Hari R (1997). Human auditory cortex is activated by omissions of auditory stimuli. *Brain Research*, 745, 134–143.
- Repp BH (2005). Sensorimotor synchronization: a review of the tapping literature. *Psychonomic Bulletin and Review*, 12, 969–992.
- Rizzolatti G and Craighero L (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27, 169–192.
- Ross B, Herdman AT and Pantev C (2005). Stimulus induced desynchronization of human auditory 40-hz steady-state response. *Journal of Neurophysiology*, 94, 4082–4093.
- Ruusuvirta T, Korhonen T, Penttonen M, Arikoski J and Kivirikko K (1995). Hippocampal event-related potentials to pitch deviances in an auditory oddball situation in the cat: experiment I. *International Journal of Psychophysiology*, 20, 33–39.
- Saarienen J, Paavilainen P, Schröger E, Tervaniemi M and Näätänen R (1992). Representation of abstract stimulus attributes in human brain. *NeuroReport*, 3, 1149–1151.
- Schellenberg EG (1997). Simplifying the implication-realization model of musical expectancy. *Music Perception*, 14, 295–318.
- Schönwiesner M, Novitski N, Pakarinen S, Carlson S and Tervaniemi M (2007). Heschl's gyrus, posterior superior temporal gyrus, and mid-ventrolateral prefrontal cortex have different roles in the activation of acoustic change. *Journal of Neurophysiology*, 97, 2075–2082.
- Shahin A, Roberts LE and Trainor LJ (2004). Enhancement of auditory cortical development by musical experience in children. *NeuroReport*, 15, 1917–1921.
- Shahin A, Roberts LE, Chau W, Trainor LJ and Miller LM (2008). Musical training leads to the development of timbre-specific gamma band activity. *NeuroImage*, 41, 113–122.
- Snyder JS and Large EW (2005). Gamma-band activity reflects the metric structure of rhythmic tone sequences. *Brain Research: Cognitive Brain Research*, 24, 117–126.
- Sonnadara RR, Alain C and Trainor LJ (2006a). Effects of spatial separation and stimulus probability on event-related potentials elicited by occasional changes in sound location. *Brain Research*, 1071, 175–185.

- Sonnadara RR, Alain C and Trainor LJ (2006b). Occasional changes in sound location enhance middle-latency-evoked responses. *Brain Research*, 1076, 187–196.
- Steinbeis N, Koelsch S and Sloboda JA (2006). The role of harmonic expectancy violations in musical emotions: evidence from subjective, physiological, and neural responses. *J Cognitive Neuroscience*, 18, 1380–1393.
- Tallon-Baudry C, Bertrand O, Delpuech C and Pernier J (1996). Stimulus specificity of phase-locked and non-phase-locked 40 Hz visual responses in human. *Journal of Neuroscience*, 16, 4240–4249.
- Tervaniemi M, Ilvonen T, Karma K, Alho K and Näätänen R (1997a). The musical brain: brain waves reveal the neurophysiological basis of musicality. *Neuroscience Letters*, 226, 1–4.
- Tervaniemi M, Rytönen M, Schröger E, Ilmoniemi RJ and Näätänen R (2001). Superior formation of cortical memory traces for melodic patterns in musicians. *Learning and Memory*, 8, 295–300.
- Tervaniemi M, Saarinen J, Paavilainen P, Danilova N and Näätänen R (1994). Temporal integration of auditory information in sensory memory as reflected by the mismatch negativity. *Biological Psychology*, 38, 157–167.
- Tervaniemi M, Winkler I and Näätänen R (1997b). Pre-attentive categorization of sounds by timbre as revealed by event-related potentials. *NeuroReport*, 8, 2571–2574.
- Tillmann B and Lebrun-Guillaud G (2006). Influence of tonal and temporal expectations on chord processing and on completion judgments of chord sequences. *Psychological Research*, 70, 345–358.
- Tillmann B, Bigand E, Escoffier N and Lalitte P (2006). The influence of musical relatedness on timbre discrimination. *European Journal of Cognitive Psychology*, 18, 343–358.
- Todd NP, Cousins R and Lee CS (2007). The contribution of anthropometric factors to individual differences in the perception of rhythm. *Empirical Music Review*, 2, 1–13.
- Toiviainen P, Tervaniemi M, Louhivuori J, Saher M, Huottilainen M and Näätänen R (1998). Timbre similarity: convergence of neural, behavioral, and computational approaches. *Music Perception*, 16, 223–241.
- Trainor L, McFadden M, Hodgson L, Darragh L, Barlow J, Matsos L *et al.* (2003a). Changes in auditory cortex and the development of mismatch negativity between 2 and 6 months of age. *International Journal of Psychophysiology*, 51, 5–15.
- Trainor LJ, Gao X, Lei J, Lehtovarara K and Harris LR (in press). The primal role of the vestibular system in determining musical rhythm. *Cortex*.
- Trainor LJ, McDonald KL and Alain C (2002). Automatic and controlled processing of melodic contour and interval information measured by electrical brain activity. *Journal of Cognitive Neuroscience*, 14, 430–442.
- Trainor LJ, Samuel SS, Galay L, Hevenor SJ, Desjardins RN and Sonnadara R (2001). Measuring temporal resolution in infants using mismatch negativity. *NeuroReport*, 12, 2443–2448.
- Trainor LJ, Shahin A and Roberts LE (2003b). Effects of musical training on auditory cortex in children. In G Avanzini, C Faienze, D Micicchi, L Lopez and M Majno, eds, *Annals of the New York Academy of Sciences*, 999, pp. 506–513.
- Unyk AJ and Carlson JC (1987). The influence of expectancy on melodic perception. *Psychomusicology*, 7, 3–23.
- Uther M, Jansen DHJ, Huottilainen M, Ilmoniemi RJ and Näätänen R (2003). Mismatch negativity indexes auditory temporal resolution: evidence from event-related potential (ERP) and event-related field (ERF) recordings. *Cognitive Brain Research*, 17, 685–691.
- Warren JE, Wise RJ and Warren JD (2005). Sounds do-able: auditory-motor transformations and the posterior temporal plane. *Trends in Neuroscience*, 28(12), 636–643.
- Whitfield I (1985). The role of auditory cortex in behavior. In A Peters and E Jones, eds, *Cerebral cortex*. Vol. 4, Association and Auditory Cortices, pp. 329–351. Plenum Press, New York.
- Zatorre RJ (1985). Discrimination and recognition of tonal melodies after unilateral cerebral excisions. *Neuropsychologia*, 23, 31–41.
- Zatorre RJ (1988). Pitch perception of complex tones and human temporal-lobe function. *Journal of the Acoustical Society of America*, 84(2), 566–572.
- Zatorre RJ and Halpern AR (2005). Mental concerts: Musical imagery and auditory cortex. *Neuron*, 47, 9–12.
- Zatorre RJ, Chen JL and Penhune VB (2007). When the brain plays music: auditory-motor interactions in music perception and production. *Nature Reviews Neuroscience*, 8(7), 547–558.
- Zatorre RJ, Evans AC and Meyer E (1994). Neural mechanisms underlying melodic perception and memory for pitch. *Journal of Neuroscience*, 14, 1908–1919.