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Predictive information processing is a fundamental learning mechanism present in early development: Evidence from infants

Laurel J. Trainor
McMaster University

Address correspondence to:
Dr. Laurel J. Trainor
Department of Psychology, Neuroscience and Behaviour
McMaster University
1280 Main Street West
Hamilton, Ontario
Canada, L8S 4L8

LJT@mcmaster.ca

The collection of articles for the special issue on *Predictive Information Coding in the Brain: Principles, Neural Mechanisms and Models* provides compelling evidence in favor of the view that the brain is fundamentally organized to make predictions about the future on the basis of incoming sensory information and long-term knowledge, to monitor the success of those predictions, and to adjust knowledge of the world accordingly in short- and long-term memory systems. Here I argue that predictive information coding is perhaps the most basic learning mechanism in the brain and that, as such, would be expected to be present very early in development. Furthermore, I argue that studying the development of different types of predictive information processing across development can inform the separability of different mechanisms for predictive coding. Yet none of the papers in this special issue address the issue of development. Specifically, I present evidence that predictive information coding is present in early infancy, and compare and contrast infant and adult responses when prediction is unsuccessful. Given limited space, I focus on the auditory system, and examples from work conducted by my research group. I comment in particular on the papers by Bendixen, SanMiguel & Schroger (this issue), Rohrmeier & Koelsch (this issue), and Schwartz, Tavano, Schroger, & Kotz (this issue).

Event-related potential (ERP) electrophysiological (EEG) responses to sound in very young infants bear little resemblance to those of adults. The ERP waveforms of young infants are dominated by frontally-positive slow waves that are not present in adult waveforms; and obligatory components in adult waveforms, such as N1 and P2, are difficult to discern in those of young infants (e.g., for reviews see Trainor, 2008, in press). As a result, there is considerable controversy concerning whether these slow positivities are early forms of P1 or P2, or whether they are unrelated to adult components. In this light it is especially interesting that the literature is consistent in reporting that when a sequence of sounds sets up a prediction for the next sound(s), young infants consistently show mismatch responses to a violation in expectation. Mismatch responses in young infants have been shown for pitch deviants (e.g., Čeponienė et al. 2002; He, Hotson, & Trainor, 2007, 2009; Leppänen, Eklund, & Lyytinen, 1997; Leppänen, Guttorm, Pihko, Takkinen, & Lyytinen, 2004), timing

deviants (Friederici, Friedrich & Weber, 2002; Trainor et al., 2001, 2003), deviants in melodies (Tew, Fujioka, He, & Trainor, 2009), and multiple deviant types present in one sequence of sounds (e.g., Sambeth et al., 2009). Furthermore, mismatch responses can change after only a few hours of exposure to a stimulus (Trainor, Lee, & Bosnyak, 2011), indicating that they reflect learning. Thus, predictive information processing is robust early in development. However, mismatch responses in very young infants tend to consist of frontally-positive slow waves, whereas those of older infants consist of faster negativities similar to the mismatch negativity (MMN) in adults (e.g., for reviews see Trainor, 2008; in press). There is evidence that the slow positivity and MMN represent different brain processes as there is a period during development when both responses are present (He et al., 2007). Thus, predictive information processing is present very early, but the particular mechanisms involved may change with development.

Predictive processing undoubtedly occurs in many parts of the brain and at different time scales. Sources of MMN activity are mainly located in secondary auditory cortex (e.g., Pincze, Lakatos, Raikoi, Ulbert, & Karmos, 2001). Bendixen et al. (this issue) present some evidence that mismatch processes also occur in primary auditory cortex at a time earlier than the MMN. Indeed, mismatch processes to violations in expected sound location in adults have also been shown to modify middle latency components known to originate in primary auditory cortex (Sonnadara, Alain, & Trainor, 2006). It might be expected that such mismatch processes are present early in development, but to our knowledge, this has not yet been tested. At the other end of the scale, predictive processing can take place over long time periods, such as across repetitions of a melody (e.g., Fujioka, Trainor, Ross, Kakigi, & Pantev, 2004; Trainor, McDonald, & Alain, 2002). Interestingly, 6-month-old infants also show evidence of long time-scale predictive processing in that they produce mismatch responses to unexpected changes in the last note of a repeating melody, even when the melody is played in transposition from repetition to repetition (Tew et al., 2009). However, the youngest age at which melodic prediction can be found remains unknown.

Rohrmeier & Koelsch (this issue) point out that it is difficult to measure the brain's predictions for complex music in which there are different melodic lines occurring at the same time. However, initial progress on the processing of simultaneous melodies has been made (Fujioka, Trainor, Ross, Kakigi, & Pantev, 2005; Fujioka, Trainor, & Ross, 2008). Fujioka et al. (2005) presented adults with two simultaneous melodies that repeated on each trial. 25% of trials had a deviant note in the higher melody and 25% had a deviant in the lower melody. Under these circumstances, adults showed MMN responses to both deviants, indicating processing of both melody lines. Furthermore, the MMN response to the higher melody was the same amplitude as when that melody was played alone, but the MMN response to the lower melody was smaller than when that melody was played alone. Thus, the adult brain is able to hold memory traces for more than one melody at a time, but the memory trace is more robust for the higher than the lower melody, consistent with music compositional practice. Of most interest here is that infants at least as young as 7 months can also form two simultaneous memory representations and, furthermore, show superior encoding of the higher melody (Marie & Trainor, under revision).

In this regard, it is also interesting that Bendixen et al. (this issue) state that the visual system needs to deal frequently with occluded objects but that the auditory system rarely does. In fact, the auditory environment typically contains many sounding objects that overlap in time and therefore mask each other. Thus, one of the main functions of the auditory system is to parse the incoming spectrotemporal stream of information into a set of auditory objects that represent the sound sources in the environment, and to perceptually fill in masked information (Bregman, 1990). One of the cues for determining whether a set of frequency components are likely from the same sound source is whether they stand in harmonic relations (integer ratios) to the fundamental frequency. When the frequency components are in harmonic relations, they fuse perceptually and only one sound is perceived. Indeed, the perceived pitch of a tone remains the same even when the fundamental frequency is removed because the fundamental is implied by the other harmonics. Infants as young as 4 months of age are able to perceive the pitch of the missing fundamental (He & Trainor, 2009). When one

harmonic in a complex tone is mistuned, that harmonic is not integrated into the pitch of that tone, but is actually perceived as a second sound or auditory object. Interestingly, infants, like adults, expect harmonics to be in integer ratios and perceive mistuned harmonics as separate sound sources (Folland, Butler, Smith, & Trainor, 2011; in press). Again, it is noteworthy that such expectations are found very early in development.

Rohrmeier & Koelsch (this issue) differentiate between expectancy violations reflected in the MMN and those reflected in the early right anterior negativity (ERAN). One difference is that MMN reflects more generic auditory processes whereas the ERAN reflects long-term learned knowledge of a particular language or musical system. For example, ERAN responses in Western listeners reflect expectations around the rules of Western tonality whereas MMN responses do not (Trainor & Zatorre, 2009).

Provocatively, Rohrmeier & Koelsch state "... little, if barely any, musical competence involved in prediction is assumed to be innate in music cognition." Whether or not this statement is true of course depends on the definition of musical competence. However, certainly, young infants can encode rhythms and melodies, and even abstract meter and pitch interval constancy across transpositions (for reviews see Hannon & Trainor, 2007; Trainor & Corrigan, 2010), so in many ways infants are very musical (e.g., see Trehub, 2006). However, during the first months after birth, infants have not yet become enculturated to a particularly musical system, just as they have not yet learned the phonemic, syntactic and semantic structure of the language in their environment (e.g., Hannon & Trainor, 2007; Trainor & Corrigan, 2010). Sensitivity to culture-specific rhythms (Hannon & Trehub, 2005a, b) and culture-specific tonality (Gerry, Unrau, & Trainor, under revision; Trainor, Marie, Gerry, Whiskin, & Unrau, in press) begins to emerge around the end of the first year after birth. In this regard, it is interesting that MMN-like mismatch processes are evident very early in development for system-independent musical processing, but we know of no evidence for ERAN-like predictive processing before 1 year of age.

Predictive timing for auditory events, as reviewed in Schwartz et al. (this issue), is particularly interesting from a developmental point of view because, in addition to

auditory areas, it clearly involves both cortical and subcortical areas of motor networks. These authors differentiate between (1) timing that involves the cerebellum (and possibly the cochlear nucleus), which is characterized as automatic and occurring over short time intervals (milliseconds), and (2) timing that involves the basal ganglia-thalamo-cortical loop (including the supplementary motor cortex), which engages attention and the analysis of longer time intervals. While there is, as yet, little data on infants, the prediction could be made that the cerebellar system develops earlier. Indeed, mismatch studies indicate that infants as young as 2 months can detect gaps of a few milliseconds in tone pips (Trainor et al., 2003). On the other hand, young infants are likely unable to engage attention, consistent with a prediction that the basal ganglia-thalamo-cortical circuits mature later. Examining this issue in infancy would be interesting with respect to the development of auditory time processing. But it would also be interesting in that if there are different trajectories for the development of cerebellar and basal ganglia-thalamo-cortical circuits, the developmental data could help to differentiate the characteristics and functions of these different circuits and examine how they interact in perception and action.

In summary, predictive information processing is present very early in development and represents a basic learning mechanism of the brain. In some respects, infants are rather sophisticated predictors, readily building up expectations for the pitch, duration, and timbre of upcoming sounds, as well as expectations for melodic and rhythmic sequences. Furthermore, infants can process more than one auditory object simultaneously. At the same time, it is not until around the end of the first year after birth that infants' musical processing becomes specialized for the rhythmic and tonal structure of the music in their environment. Thus, some types of predictive coding are present very early, whereas others are not present until later in development. Examining the developmental trajectories for different types of predictive processes not only informs us about developmental processes, but can also elucidate how these systems work in adults.

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