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A hierarchy of cortical responses to sequence violations in three-month-old infants

Anahita Basirat[a,b,c,*], Stanislas Dehaene[a,b,c,d], Ghislaine Dehaene-Lambertz[a,b,c]

[a] INSERM, U992, Cognitive Neuroimaging Unit, F-91191 Gif/Yvette, France
[b] CEA, DSV/I2BM, NeuroSpin Center, F-91191 Gif/Yvette, France
[c] University Paris-Sud, Cognitive Neuroimaging Unit, F-91191 Gif/Yvette, France
[d] Collège de France, F-75005 Paris, France

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ABSTRACT

The adult human brain quickly adapts to regular temporal sequences, and emits a sequence of novelty responses when these regularities are violated. These novelty responses have been interpreted as error signals that reflect the difference between the incoming signal and predictions generated at multiple cortical levels. Do infants already possess such a hierarchy of violation-detection mechanisms? Using high-density recordings of event-related potentials during an auditory local–global violation paradigm, we show that three-month-old infants process novelty in temporal sequences at two distinct levels. Violations of local expectancies, such as perceiving a deviant vowel "a" after repeated presentation of another vowel i-i-i, elicited an early auditory mismatch response. Conversely, violations of global expectancies, such as hearing the rare sequence a-a-a-a instead of the frequent sequence a-a-a-i, modulated this early mismatch response and led to a late frontal negative slow wave, whose cortical sources included the left inferior frontal region. These results suggest that the infant brain already possesses two dissociable systems for temporal sequence learning.

1. Introduction

The classical constructivist perspective postulates that learning starts at an early sensory level and very slowly progresses towards increasingly abstract and logical levels (Piaget, 1954; Quartz & Sejnowski, 1997). The first functional MRI and NIRS studies in infants were thus surprising, revealing the involvement of high-level brain areas such as dorsolateral prefrontal cortex and Broca's area at an early age (Dehaene-Lambertz, Dehaene, & Hertz-Pannier, 2002; Dehaene-Lambertz et al., 2010; Mahmoudzadeh et al., 2013; Perani et al., 2010), supported by an efficiency long-range connectivity (Leroy et al., 2011). Learning in infants might thus not be limited to low-level processes, but might occur at all levels along the processing hierarchy, as proposed by recent Bayesian models of child development (Tenenbaum, Kemp, Griffiths, & Goodman, 2011; Téglás et al., 2011), with high-level regions generating top-down predictions modulating the down-stream computations (Friston, 2005; Rao & Ballard, 1999). Here, we test the hypothesis that the infant brain, at three months of age, already processes information about auditory sequences at two hierarchical levels. Using an auditory violation paradigm, we demonstrate that the infant brain contains a hierarchy of error signals that respond, respectively, to violations of local and global auditory sequences. We argue that the presence of these signals suggest that the infant

* Corresponding author at: INSERM, U992, Cognitive Neuroimaging Unit, F-91191 Gif/Yvette, France.
E-mail address: anahita@basirat.fr (A. Basirat).

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brain, at three months, already generates top-down predictions about future incoming stimuli.

A simple and widely used paradigm to study infant auditory perception is the auditory oddball paradigm, in which a novel sound is introduced after a series of repeated sounds. This abrupt change generally elicits an early mismatch response (MMR), often consisting of a frontal positivity synchronous of a posterior negativity, around 200–400 ms after the deviant stimulus, generally followed, around 700 ms, by a late frontal Negative Slow Wave (NSW; Dehaene-Lambertz & Dehaene, 1994; Friederici, Friedrich, & Weber, 2002).

This two-stage response in infants is reminiscent of the MMN/P300 complex reported in adults, even if the latencies and topographies of these responses are different due to the immaturity of the infant's brain. In adults, an early and automatic mismatch response is recorded around 100 ms and consists of a frontal negativity with a polarity reversal above temporal regions (mismatch negativity or MMN, Näätänen, Gaillard, & Mäntysalo, 1978), and a late central positivity is recorded around 300 ms (P300 or P3b, Squires, Squires, & Hillyard, 1975). In adults, these two components differ in their functional properties: The MMN is present even if the subject does not pay attention to the stimuli, is asleep (Atienza, Cantero, & Gomez, 1997) or in coma (Fischer et al., 1999), but it disappears when the inter-stimulus-interval (ISI) is increased beyond a few seconds (Mäntysalo & Näätänen, 1987; Pegado et al., 2010). By contrast, the P300 is only present if the subject is conscious and attentive (Bekinschtein et al., 2009), and is not affected by long ISI (Wetter, Polich, & Murphy, 2004). The MMN has been associated with unconscious processing of auditory transition probabilities (Näätänen, Paavilainen, Rinne, & Alho, 2007; Wacongne, Changeux, & Dehaene, 2012; Winkler, 2007), and the P300 with conscious detection of novelty and "context updating" (Dehaene & Changeux, 2011; Donchin & Coles, 1988; Sergent, Baillet, & Dehaene, 2005).

Partially similar observations have been made in infants. The early MMR can be elicited in non-attentive or sleeping infants (Dehaene-Lambertz & Peña, 2001), and is reduced by long ISI (Cheour et al., 2002). Its brain sources are mainly located in the superior temporal regions (Bristow et al., 2009; Dehaene-Lambertz & Dehaene, 1994), congruent with the adults' description of the MMN sources (Celsis et al., 1999; Halgren, Sherfey, Irimia, Dale, & Marinkovic, 2011). The late response (NSW) is less often reported than the MMR, but this could simply be because it occurs too late to fit within the length of the studied ERP epoch. The NSW belongs to a set of late components observed in infants which have been linked to attention and novelty detection (Csibra, Kushnerenko, & Grossmann, 2008), and more recently to conscious perception (Kouider et al., 2013). Indeed, when comparing awake and asleep infants, Friederici et al. (2002) observed the NSW after a deviant sound only in awake infants.

The functional similarities of the MMR/NSW with the adult MMN/P300 components suggest a putative parallel with the adult functional architecture (i.e. an early automatic local response vs. a late context-dependent response). Yet at present, no study has tried to disentangle whether the MMR and NSW are sensitive to different types of violations. A recently introduced hierarchical "local–global" paradigm epitomizes the two distinct processing stages behind the generation of a MMN and a P300 in adults (Bekinschtein et al., 2009). This paradigm measures brain responses to auditory novelty at two hierarchical levels. At the first level, a novel sound is introduced after a series of repeated sounds (e.g. xxxY, where x denotes the repeated sound and Y the novel sound), generating a "local" deviancy. At the second level, a series of sounds is selected as the frequent global sequence for a block of trials (e.g. xxxY), and then this sequence is violated on a rare subset of trials (e.g. by occasionally presenting the sequence xxxx). With this paradigm, Bekinschtein et al. (2009) disentangled two properties of the adult MMN and P300 responses. First, local deviants (the last sound Y in sequence xxxY) systematically elicit a MMN, even when the sequence itself is frequent and predictable; this response is automatic and remains present in inattentive or comatose subjects. It corresponds to an automatic error-signal generated when the incoming sound differed from what was expected given the previous sounds (Garrido, Kilner, Kiebel, & Friston, 2007; Garrido et al., 2008; Näätänen et al., 1978; Wacongne et al., 2011, 2012; Winkler, 2007). Second, global deviants (rare sequences) systematically elicit a P300 response, even when the rare deviating sequence is a monotonous sequence of repeated sounds (xxxx).

The latter finding is particularly diagnostic of a second-order computation. While the first stage (MMN) simply weights the incoming sound against predictions based on past events, the second stage (P300) seems sensitive to the global rule governing the entire sequence. Especially, generating an error signal to a perfectly monotonic "xxxx" sequence (in a block where most trials are xxxY) can only be performed by a system that actively generates an expectation that the sequence should end with a different sound (xxxY). This second stage, in adults, requires attention to the sequence (Bekinschtein et al., 2009).

In the present study, we probed the existence of hierarchical novelty detection and predictive processes in three-month-old infants using high-density recordings of event-related potentials during a variant of Bekinschtein et al. (2009) auditory local–global paradigm. To maximize attention, although we were obviously unable to give instructions to our preverbal participants, we used audio-visual speech stimuli which infants spontaneously find strongly attractive (Fig. 1). Stimuli were presented in short series of four vowels, following an xxxY or xxxx pattern in distinct blocks (see Fig. 2 for experimental design). After a short training phase, which let infants learn the global sequence governing the present block, sequences violating this global pattern were randomly presented (i.e. xxxx trials in blocks with rule xxxY, and xxxY trials in blocks with rule xxxx).

Our predictions were simple. Based on the infant literature, we expected to record a mismatch response (MMR) around 200–400 ms after a deviant sound, followed by a late frontal negativity if infants direct their attention toward this novel event (Dehaene-Lambertz & Dehaene, 1994; Friederici et al., 2002). If the infant's MMR is