Perceptual biases for rhythm: The Mismatch Negativity latency indexes the privileged status of binary vs non-binary interval ratios

X. Pablos Martin [a], P. Deltenre [b,c], I. Hoonhorst [b,d], E. Markessis [e],
B. Rossion [a,d], C. Colin [b,*]

[a] *Laboratoire de Neurophysiologie & Unité Cognition et Développement, Université Catholique de Louvain (U.C.L.), Bruxelles, Belgium*
[b] *Unité de Recherches en Neurosciences Cognitives, Université Libre de Bruxelles (U.L.B.), Belgium*
[c] *Laboratoire de Neurophysiologie Clinique, Hôpital Brugmann, Bruxelles, Belgium*
[d] *F.N.R.S., Bruxelles, Belgium*
[e] *Faculté de Médecine, Université Libre de Bruxelles (U.L.B.), Belgium*

Abstract

Objective: Rhythm perception appears to be non-linear as human subjects are better at discriminating, categorizing and reproducing rhythms containing binary vs non-binary (e.a. 1:2 vs 1:3) as well as metrical vs non-metrical (e.a. 1:2 vs 1:2.5) interval ratios. This study examined the representation of binary and non-binary interval ratios within the sensory memory, thus yielding a truly sensory, pre-motor, attention-independent neural representation of rhythmical intervals.
Methods: Five interval ratios, one binary, flanked by four non-binary ones, were compared on the basis of the MMN they evoked when contrasted against a common standard interval.
Results: For all five intervals, the larger the contrast was, the larger the MMN amplitude was. The binary interval evoked a significantly much shorter (by at least 23 ms) MMN latency than the other intervals, whereas no latency difference was observed between the four non-binary intervals.
Conclusions: These results show that the privileged perceptual status of binary rhythmical intervals is already present in the sensory representations found in echoic memory at an early, automatic, pre-perceptual and pre-motor level.
Significance: MMN latency can be used to study rhythm perception at a truly sensory level, without any contribution from the motor system.
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Keywords: Mismatch Negativity; Rhythm perception; MMN latency; Sensory memory; Interval ratio

1. Introduction

Perception of rhythm is important not only for us to enjoy music and dance at the sound of it but also for speech comprehension in which appropriate temporal segmentation of the ongoing acoustic input is a prerequisite to phoneme decoding (Jusczyk and Derrah, 1987).

This study sought to investigate the early, pre-motor, attention-independent representation of rhythm in the brain by measuring the Mismatch Negativity (MMN), a component of the auditory event-related potential (ERP) reflecting sensory memory (Näätänen and Alho, 1995).

An important aspect of rhythm perception is that a context of sound sequence allows better temporal acuity than when isolated intervals are tested (Drake and Botte, 1993). Moreover, the perception of musical sequences involves non-linearities as sequences are perceived as more regular than they are (Repp, 1992). This suggests the occurrence of a supplementary process dedicated to the

* Corresponding author. Address: Clinique de Neurophysiologie; Bat. EM (rotonde –1), Hôpital Brugmann, 4, place Van Gehuchten, B-1020 Brussels, Belgium. Tel.: +32 2 650 22 86; fax: +32 2 477 24 56.
 E-mail address: cecile.colin@chu-brugmann.be (C. Colin).

extraction of a regular structure in the temporal sequence leading to the psychophysical percept of the beat. Beat perception has been shown to obey a non-linear transformation of the physical stimulus space so that inter-onset intervals are perceived in terms of discrete categories corresponding to the rhythmical musical structure (Desain and Honing, 2003). These interval categories consist in integer multiples or subdivisions of the beat, with a dominance of binary (1:2, 1:4, 2:1, etc.), rather than ternary or more complex ratios (Dowling and Harwood, 1986; Drake, 1997). As a consequence, listeners are better at discriminating, categorizing and reproducing rhythms containing 1:2 ratios than rhythms containing 1:3 ratios or even more complicated ratios (Drake and Gérard, 1989; Drake, 1993; Bergeson and Trehub, 2006). Other results suggest that, even in so-called equitone isochronous sequences, in which physically identical tones occur at a constant rate, listeners tend to perceive sounds as unequal and to spontaneously impose a default binary metrical pattern, leading to subjective accenting of the first of every two sounds, so that a ''tick-tock'' pattern emerges out of a uniform sequence (Brochard et al., 2003). However, the nature of these perceptive transforms remains unclear. On the one hand, they could be of a sensory nature, reflecting the way the perceptive system encodes auditory temporal structure. On the other hand, the bias towards binary ratios could be explained by constraints in verbal or motor production processes implicated in the majority of the tasks described in the literature as revealing the above-mentioned non-linearities (Drake, 1993; Drake and Gérard, 1989). The discovery of sensory temporal feature detectors located in the midbrain of several vertebrate species provides a plausible mechanism for the sensory hypothesis (Casseday et al., 1994; Ehrlich et al., 1997; He et al., 1997; Brand et al., 2000; Casseday et al., 2000) since these duration-tuned neurones respond selectively to specific temporal features characterizing behaviourally relevant sounds (Large and Crawford, 2002). Sakai et al. (1999) assessed the neural representation of metrical (namely: 1:2:4 and 1:2:3) vs non-metrical (1:2.5:3.5) rhythmical ratios using fMRI measurements obtained just between presentation of the rhythmical sequence and a motor reproduction task. Comparing the error rates of the motor reproduction task between the two metrical patterns on the one hand and between the 1:2:4 and the 1:2.5:3.5 ones on the other hand, they found no difference for the first comparison and significantly larger errors for the non-metrical ratios. Moreover, the increase in variance for the non-metrical ratios was due to a significant proportion of erroneous interval reproduction as the closest metrical ratio. The cerebral activation maps were quite different according to the reproduced pattern rather than according to the actually presented rhythm, showing active areas in the left pre-motor cortex and right cerebellar anterior lobe for metrical reproductions vs right pre-frontal and pre-motor cortex and bilateral cerebellar posterior lobes for non-metrical reproduction. These results, showing differential brain acti-

vation patterns in function of the reproduced rather than the presented rhythms, were interpreted as reflecting the internal representation of rhythm. Because of the task involved, it remains however uncertain whether this representation was tapped from the brain before or after transformation for motor output. The present study was designed as a pilot investigation to evaluate the involvement of attention-independent and pre-motor automatic pre-perceptual processes to the phenomenon of non-linear perception of rhythms, by recording the MMN to rhythmical contrasts with binary vs non-binary ratios.

The MMN, a component of the auditory event-related brain potential (ERP), reflects the outcome of an attention-independent and automatic change detection process that is based upon the memory of the frequently presented stimuli in an oddball sequence (for reviews, see Näätänen, 1995, 2003; Näätänen and Alho, 1995; Ritter et al., 1995). The MMN is a negative deflection expressed over the frontal and central scalp regions and of inverse polarity over the mastoids. The MMN typically peaks with a latency of 100–200 ms from the time at which violation of regularity is detected. Previous research suggests that the MMN represents an early process of deviance detection based upon a memory of the previous sound stimulation kept for a few seconds in the echoic or sensory auditory store memory (Näätänen et al., 2005; Jacobsen et al., 2003). The MMN provides objective information about the encoding and representation of sounds in sensory memory, reflecting not only the physical characteristics of stimulus contrasts but also their perceptual aspects. For example, Näätänen et al. (1997) showed that a vocalic contrast elicited a larger MMN in participants for which the vowels had a phonologic relevance than in participants for which both vowels belonged to the same phonologic category. It, therefore, appears as a unique tool for studying the central representation of auditory percepts (Näätänen and Alho, 1995). It is a classical notion that the magnitude of the deviance between deviant and standard is positively correlated with the MMN amplitude and negatively with its latency (Sams et al., 1985; Näätänen et al., 1989a,b; Tiitinen et al., 1994; Näätänen and Alho, 1995; Jaramillo et al., 2000; Kujala et al., 2001; Jääskelaäinen et al., 2004), albeit this has not been demonstrated for every dimension of the stimulus (Pakarinen et al., 2007).

The memory system reflected by the MMN encodes not only individual stimulus features like frequency, intensity, duration or spatial location, but also feature conjunctions or gestalts (Gomes et al., 1997; Deacon et al., 1998; Sussmann et al., 1998; Takegata et al., 1999). The involved memory system also temporally integrates the various durations that make up the temporal structure of sound patterns so that the MMN is also sensitive to rhythmical expectancy violations, like the periodicity of tonal sequences (Winkler and Schröger, 1995) or the metric structure of drum sounds (Vuust et al., 2005). This supports the hypothesis of early, attention-independent processes implied in the perception of rhythm. However, to

our knowledge, none of these studies have investigated the contribution of early, automatic, attention-independent processes to the perception of rhythmical categories (binary vs other ratios).

This study was therefore devoted to the measurement of MMN evoked by binary vs non-binary rhythmical contrasts in order to investigate how these two categories of violation of rhythmical expectancies are contrasted with a regular rhythm in sensory memory using an experimental paradigm which is independent of any motor response. To this aim, we created five different conditions of rhythmical expectancy violation, in which the last interval of a regular temporal sequence was manipulated in duration, leading to binary and non-binary contrasts. We hypothesized that the MMN evoked by these interval changes would be modulated by the non-linearities ruling rhythmical percepts, so that the general laws governing the relations between contrast size and MMN amplitude and latency would be overruled by the peculiar status assigned to the binary contrast. For sound duration contrasts, it has been shown that MMN amplitudes increase with contrast size similarly to what is seen for intensity, frequency or spatial location contrasts, whereas only the latter two dimensions yield MMN latencies inversely proportional to contrast sizes (Pakarinen et al., 2007). The effect of contrast size for rhythmical intervals (i.e. intervals between sound onsets within a series of sounds) is very poorly documented in the literature, the only study we are aware of (Näätänen et al., 1993) did not find any correlation either for amplitude or latency, but since it used huge contrasts (several hundreds of ms) the negative findings were attributed to a ceiling effect.

2. Method

2.1. Participants

Ten non-musician subjects (7 females, 3 males) aged 19–32 years (mean 25) participated in the experiment as paid volunteers. All were in good health and reported normal auditory function. They gave their informed consent to participate after the details of the procedure had been explained to them.

2.2. Materials

An oddball stimulation paradigm made up of standard and deviant trains was used to create the mismatch effect. Six different trains made up of five identical components were generated (see Fig. 1 for a representation of the stimuli). The components were pure tones of 392 Hz (G$_3$ or sol$_3$, tone corresponding to a medium pitch in music) and were 30 ms in duration (including 5 ms rise and fall times of a trapezoidal envelope). The onsets of the first four components of a train were separated by a fixed interval of 200 ms (Component Onset Asynchrony: COA) whereas the duration of the last interval between the fourth and
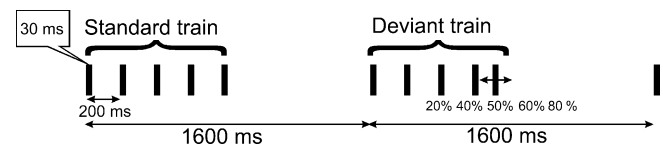

Fig. 1. Scaled representation of the standard and deviant trains. Component duration: 30 ms; Standard COA: 200 ms; TOA: 1600 ms. Deviant intervals were applied to the last COA of deviant trains by reducing the standard COA to one of the five percentages indicated.

the fifth component onsets was either 40 ms (20% COA), 80 ms (40% COA), 120 ms (60% COA), 160 ms (80% COA) for the non-binary contrasts; 100 ms (50% COA) for the binary contrast or 200 ms (100% COA) for the standard train. Contrast size therefore increased in an inversely proportional manner with respect to the COA percentage. The Train Onset Asynchrony (TOA) was always 1600 ms. The longest (standard) train therefore had an overall duration of 830 ms, which is well within the retention period of the echoic memory (Sams et al., 1993). The probability of occurrence of the deviant train within the oddball series was 16.66%.

In order to isolate a pure MMN differential waveform uncontaminated by physical differences between standard and deviant trains (Kraus et al., 1995) and by differential refractoriness effects, a control sequence made up of equiprobable trains (Jacobsen and Schröger, 2001; Jacobsen et al., 2003) was constructed. This control sequence was made up of the five possible deviant trains as well as of the standard train so that each train type had a probability of occurrence of 16.66%. For each rhythmical contrast value, the MMN was obtained by subtracting the waveform evoked by the physically corresponding train within the control, equiprobable sequence (hereafter referred to as the matched control train) from the one evoked by the deviant train within the oddball sequence.

2.3. Procedure

Stimuli were generated by Tucker-Davis Technologies (TDT) hardware (System II) and software (SigGen 3.51 and SigPlay 3.3), which controlled for their duration and intensity. The TDT system was interfaced with an InstEP stimulation system (software ver. 3.3), which controlled for the presentation order and timing of the stimuli. The stimuli were binaurally presented with Etymotic earphones (model ER-3A) connected through a 25 cm long silicon tubing ending into a hollowed foam cylinder inserted into the entrance of the ear canal. For each subject, all standard and deviant stimuli were presented 55 dB above the individual hearing threshold.

A simple ascending/descending procedure (method of limits, one trial in each direction) using 2 dB steps was used for threshold measurements.

In order to minimize the risk of MMN habituation reported to occur when sessions are too long (McGee et al., 2001), stimuli were presented in short sessions of

about 12 min. In each short session, a series of 300 standard stimuli and 60 deviant stimuli of one kind were pseudo-randomly delivered with a TOA of 1600 ms. A complete MMN data bank for each experimental condition (20%, 40%, 50%, 60% and 80% COA contrasts) was made up of five short series, in order to include 300 deviant stimuli of each kind before data analysis. Moreover, the equiprobable series was also presented five times. The order of the series was pseudo-randomized in order to avoid the occurrence of more than two consecutive identical series.

During the electrophysiological experiment, subjects were comfortably seated in an armchair fitted with a back headrest. They were instructed to ignore the auditory stimuli while watching subtitled movies or reading self-selected books. Subjects were free to take any type of break they wished between sequences.

2.4. Electrical activity recording

Brain electrical activity (EEG) was recorded with Ag–AgCl electrodes from C_z (10–20 system) as well as from left and right mastoids (M_1, M_2), all referred to the tip of the nose. Horizontal and vertical eye movements were monitored using two bipolar recordings: one between each outer eye canthus and one between a supraorbital electrode and an electrode just below the lower lid on the right side. Impedances were below 5 kΩ. After amplification (10,000 times for brain activity channels and 5000 times for eye movement channels) and analogical (0.1–70 Hz) filtering, the input signals were digitized with a sampling rate of 512 Hz and stored on the computer disk for off-line averaging.

2.5. MMN computation and measurement

Data averaging was performed separately for oddball deviant trains and matched control trains with an InstEP system (software ver 3.3). Recording epochs had a total duration of 2048 ms including a 332 ms pre-stimulus baseline. Rejection of artefacted sweeps from the final averages was performed on the basis of a ±150 μV criterion for all channels. Averaged waveforms were digitally filtered (30 Hz) and then converted into ASCII format and exported to a spreadsheet program for further analysis and plotting.

In order to maximize the intrinsically low (Lang et al., 1995; Kurtzberg et al., 1995; McGee et al., 1997) MMN Signal-to-Noise Ratio before statistical analysis, grand averages were computed by first averaging the right and left mastoid tracings followed by subtraction of this averaged mastoid signal from the C_z recorded activity (Pakarinen et al., 2007). This strategy maintains the recognition of a major identification feature of the MMN observed with a nose reference, i.e. the polarity reversal between the centro-frontal scalp and the mastoids, whereas after the subtraction procedure, it boosts the MMN amplitude by

reconstructing a scalp to mastoid derivation that records the entire equivalent dipole. Preliminary averaging of mastoid traces is meant to reduce the residual noise before the subtraction procedure.

For each subject and each rhythmical contrast, the MMN peak amplitude was computed relative to the baseline, as the most negative peak of the differential $C_z - (M_1 + M_2)/2$ waveform occurring during a period corresponding to the duration of the MMN assessed, by visual analysis, on the corresponding grand average tracing. The MMN latency was determined as the peak latency of the maximal MMN peak amplitude measured from the onset of the last component for each deviant train (i.e. when the deviance occurred).

The MMN peak latencies and amplitudes were compared between pairs of rhythmical contrasts by performing an ANOVA for repeated measurements followed, when indicated, by post hoc analyses (Tukey tests). Significance level was set at $p < 0.05$.

3. Results

Every component within standard, deviant and equiprobable trains elicited C_z waveforms morphologically similar to the classical exogenous P_{50}–N_{100}–P_{200} components albeit with much reduced N_{100}–P_{200} amplitudes due to adaptation. Furthermore, the amplitude of each of the components further decreased from the first to the fifth position within the train. Fig. 2 illustrates the grand average obtained across all subjects with the standard train.

Fig. 3 depicts, for each contrast value, the grand average of the corresponding deviant train from the oddball sequence for all subjects. The effect of shortening the last interval was quite remarkable: Instead of causing a supplementary adaptation effect bearing on the exogenous potentials evoked by the last component as expected if only exogenous components were evoked, the last component generated an enhanced negative wave. This negative wave was the first evidence of the presence of an electrophysiological mismatch effect caused by shortening the last interval of the train.

Fig. 4 shows the MMN that has been isolated by subtracting matched control trains from the corresponding deviant waveforms for both C_z and M_1/M_2 sites. An easily
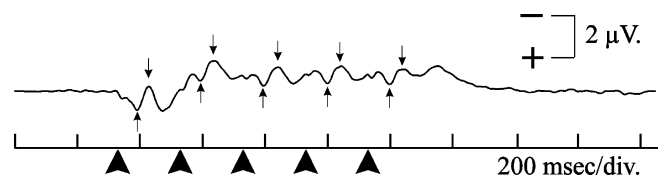

Fig. 2. Grand average obtained at C_z, across all subjects with the standard train. In this and subsequent figures, the black triangles indicate the onset of each component within the train. The classical exogenous P_{50} (up pointing arrows) and N_{100} (down pointing arrows) components can still be identified despite the major adaptation effect which increases from the first to the fifth stimulus within the train.
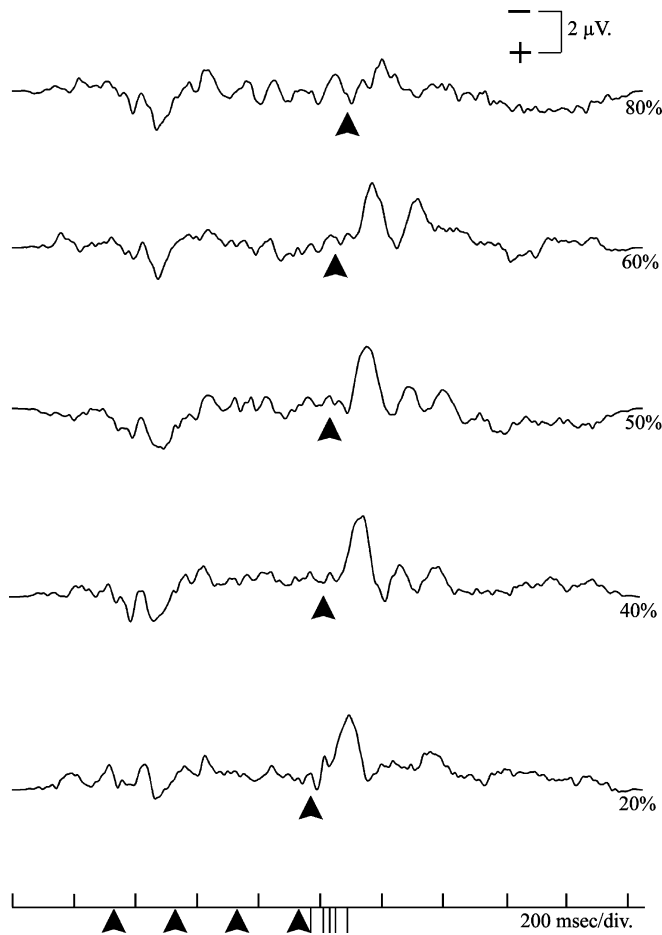
Fig. 3. Grand averages obtained at C_z, across all subjects, for each contrast value, of the corresponding deviant train from the oddball sequence. In this and subsequent figures, the triangles plotted below each waveform and the thin vertical black lines plotted below the temporal axis both indicate the onset of the fifth, deviant component within a train.
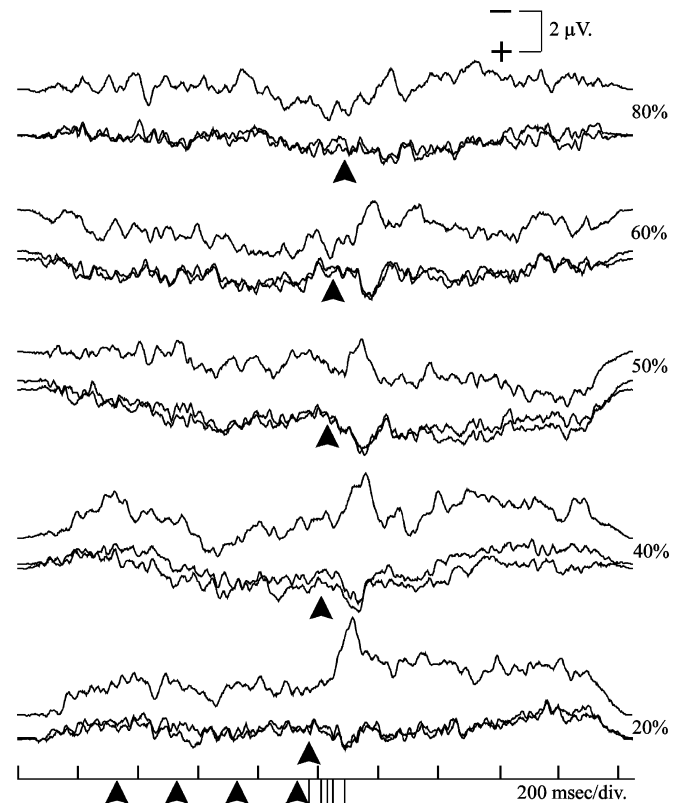

Fig. 4. Grand averages obtained at C_z and M_1/M_2, across all subjects, for each contrast value, of the differential waveform obtained by subtracting the waveform evoked by deviant trains within the oddball sequence from the waveform evoked by the matched control equiprobable train. For each contrast level, the upper trace is from C_z and the superimposed lower traces are from M_1/M_2. An easily identifiable MMN, inverted in polarity at mastoid sites, is observed for all contrasts.

identifiable MMN, inverted in polarity at mastoid sites, is observed for all contrasts. The MMN amplitude is progressively reduced from the greatest (20% COA) to the smallest (80% COA) contrast.

Fig. 5 illustrates the result of the subtraction between the C_z and the averaged mastoid waveforms. Well-defined enhanced MMNs are observed for all contrasts.

Fig. 6 illustrates the behaviour of MMN amplitude and latency values as a function of rhythmical contrast values. Amplitudes decreased monotonically as contrast values were reduced. The latency-contrast value function was marked by a non-monotonical behaviour with a marked reduction localized at the binary contrast value (50% COA).

3.1. Statistical analysis

Amplitudes: There was a significant effect of contrast values on amplitude ($F_{4,36} = 5.25$, $p < 0.01$). Post hoc analyses showed that the response to 20% contrast was significantly larger than the responses to 60% contrast ($F_{1,9} = 5.61$, $p < 0.05$) and to 80% contrast ($F_{1,9} = 21.06$,
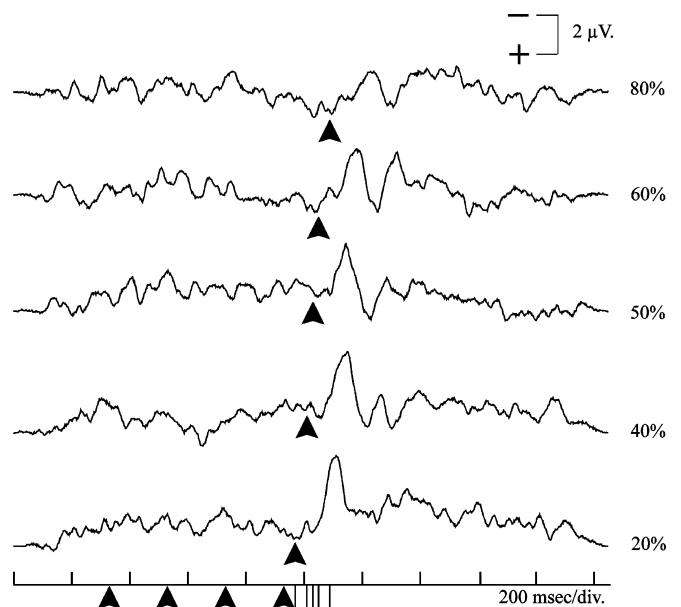

Fig. 5. Result of the subtraction between C_z and averaged mastoid waveforms for each contrast value. For all contrasts, the improvement of the signal-to-noise ratio of the grand-averaged MMN is quite significant.
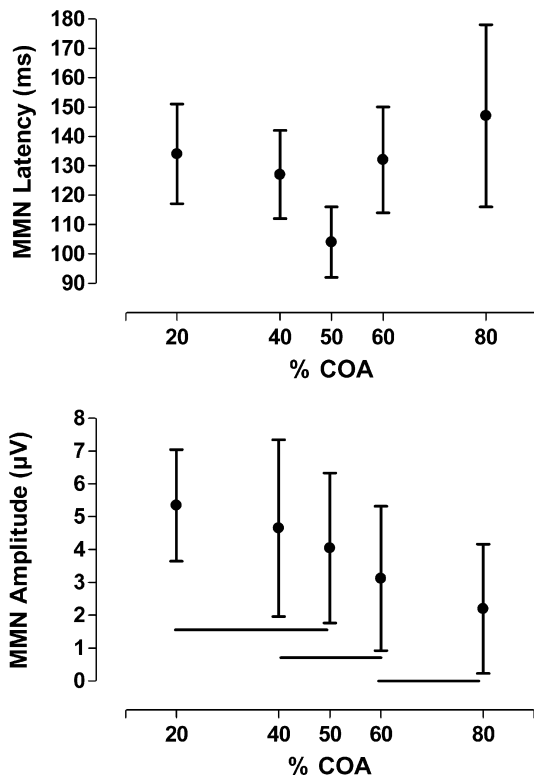
Fig. 6. MMN latency and amplitude values as a function of rhythmical contrast values (COA%). The latency-contrast value function was marked by a non-monotonical behaviour with a marked reduction localized at the binary 50% value in an otherwise flat function. Amplitudes decreased monotonically as contrast values were reduced. The three horizontal lines regroup, the amplitudes that do not differ from each other.

$p < 0.01$). Similarly, responses to 40% and 50% contrasts were significantly larger than response to 80% contrast (respectively, $F_{1,9} = 11.99$, $p < 0.01$; $F_{1,9} = 8.20$, $p < 0.05$).

Latencies: There was a significant effect of contrast values on peak latency ($F_{4,36} = 6.44$, $p < 0.01$).

Post hoc analyses showed that the only significant latency difference was due to the 50% contrast which yielded a significantly shorter latency than every other contrast (20%: $F_{1,9} = 4952$, $p < 0.01$; 40%: $F_{1,9} = 3360$, $p < 0.01$; 60%: $F_{1,9} = -3617$, $p < 0.01$ and 80%: $F_{1,9} = -4240$, $p < 0.01$). The other rhythmical contrasts did not significantly differ in terms of induced latencies, so that except for the reduction at 50% COA, the latency-contrast size function appears to be flat.

4. Discussion

As far as MMN amplitudes are concerned, the classical effect of amplitude enhancement as the magnitude of deviance eliciting the MMN increases (Näätänen and Alho, 1995) was observed without any evidence of a peculiar status being conferred to the binary rhythmical ratio. For latencies, a flat latency-contrast size function, similar to the one described for sound duration contrasts (Pakarinen et al., 2007), was found across non-binary interval ratios,

but the peak latency of the MMN elicited by 50%, binary ratio was much shorter (by at least 23 ms; $p < 0.01$) than any of the other peak latencies evoked by non-binary ratios, thus indexing the well-known perceptual privileged status conferred to binary vs non-binary ratios.

Finding a much shorter MMN latency confined to the binary ratio in a series of otherwise similar latencies for bracketing non-binary ratios indicates that the representation of the binary ratio in echoic memory was mediated through a distinct faster neural representation process. The absence of prefrontal activation for metrical vs non-metrical ratios in Sakai et al. (1999) imaging data was interpreted as suggesting that metrical brain representation does not require the additional monitoring processes needed for non-metrical representations. The latter rhythms would require explicit processing for the individual time intervals, whereas the former would operate automatically and possibly implicitly (Sakai et al., 1999). However, since like numerous other studies on timing (Mauk and Buonomano, 2004), Sakai et al.'s results included obligatory repetitive movements in the experimental paradigm, they could have been dependent on constraints specific to the motor system. By contrast, having been obtained independently of any motor response or preparation to it, the present MMN data show that the sensory representations of binary vs non-binary rhythmical ratios are already differentially processed at an early, automatic, pre-perceptual level.

The present results therefore demonstrate that the MMN can be used as an objective, attention-independent tool to study the non-linear aspects of rhythm perception at a pre-motor level. Moreover, they indicate that, within the limits of the contrast sizes used, the MMN amplitude for rhythmical intervals remains correlated with contrast size even though latencies are governed by other rules.

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