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Electrophysiological evidence for a specific neural correlate of musical violation expectation in primary-school children

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ABSTRACT

The majority of studies on music processing in children used simple musical stimuli. Here, primary 19 schoolchildren judged the appropriateness of musical closure in expressive polyphone music, while 20 high-density electroencephalography was recorded. Refined in-key harmonic transgressions at closure were 21 presented interspersed with regular endings. The children discriminated the transgressions well above chance. 22 Regular and transgressed endings evoked opposite scalp voltage configurations peaking around 400 ms after 23 stimulus onset with bilateral frontal negativity for regular and centro-posterior negativity (CPN) for transgressed 24 endings. A positive correlation could be established between strength of the CPN response and rater sensitivity 25 (d-prime). We also investigated whether the capacity to discriminate the transgressions was supported by 26 auditory domain specific or general cognitive mechanisms, and found that working memory capacity predicted 27 transgression discrimination. Latency and distribution of the CPN are reminiscent of the N400, typically observed 28 in response to semantic incongruities in language. Therefore our observation is intriguing, as the CPN occurred 29 here within an intra-musical context, without any symbols referring to the external world. Moreover, the 30 harmonic in-key transgressions that we implemented may be considered syntactical as they transgress structural 31 rules. Such structural incongruities in music are typically followed by an early right anterior negativity (ERAN) 32 and an N5, but not so here. Putative contributive sources of the CPN were localized in left pre-motor, 33 mid-posterior cingulate and superior parietal regions of the brain that can be linked to integration processing. 34 These results suggest that, at least in children, processing of syntax and meaning may coincide in complex 35 intra-musical contexts.

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42 Introduction

Western tonal music relies on a rule system of hierarchical pitch 43relationships around a key "center" or tonic. In order to study tonal 44 45expectation violation, unexpected pitches that transgress this rule system are embedded in musical contexts. This has been done either 46 in monophonic material, tone sequences or melodies (Besson and 47 03 Faïta, 1995; Nittono et al., 2000; Trainor and Trehub, 1994), or in harmonic progressions, the latter either in chord sequences (Bigand 49et al., 2003; Koelsch et al., 2001, 2007; Regnault et al., 2001) or in 5051complex polyphone music (James et al., 2008; Koelsch et al., 2008; 52Koelsch and Mulder, 2002; Oechslin et al., 2013b; Steinbeis et al., 2006). If these transgressions are in-key or in a closely related key, 53they are generally considered syntactical, because they transgress 54

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http://dx.doi.org/10.1016/j.neuroimage.2014.09.047 1053-8119/© 2014 Published by Elsevier Inc. mainly structural or grammatical rules (James et al., 2008; Koelsch, 55 2011; Koelsch et al., 2007; Patel, 2003; Tillmann et al., 2006). Such is 56 the case of the stimuli we used in the present investigation. 57

Brain substrates processing musical tonal expectation violation have 58 been shown to overlap, neighbor or mirror in the contralateral (right) 59 hemisphere those for syntax processing in language in the left 60 hemisphere (Friederici, 2002), in particular in the inferior frontal cortex 61 (Brown et al., 2006; Maess et al., 2001; Oechslin et al., 2013b; Tillmann 62 et al., 2006). A plausible observation, as both language and music 63 articulate discrete elements in embedded hierarchical structures of 64 increasing complexity (James, 2012; Schon and Francois, 2011). Like 65 in language, not only local but also long-distance structural dependencies are essential for syntactic processing in musical contexts, for 67 instance regarding musical closure at the end of a phrase (James et al., 2008; Koelsch et al., 2013; Steinbeis et al., 2006).

That music also may convey meaning is widely accepted (Koelsch, 70 2011; Koelsch et al., 2004; Meyer, 1956; Swain, 1997), however, the 71 nature of meaning in intra-musical contexts is intrinsically different 72

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from that in language, not concrete and varying between individuals even of the same culture (Lamont and Webb, 2010). Intra-musical meaning emerges as a function of interaction between musical formal structures, without any reference to the external world by means of words or other symbols (Koelsch, 2011).

78In the context of pitch processing, a melody in major versus minor 79mode, or a deceptive versus a perfect cadence, convey different 80 meanings; although hard to verbalize, then: music may express the 81 ineffable (Jankélévitch and Abbate, 2003). Some evidence exists that 82 cognitive mechanisms for higher order pitch processing, important for 83 conveying semantic meaning in language, may be shared between language and music (Perrachione et al., 2013). Despite all these 84 observations, some authors in the linguistic domain strongly deny any 85 86 existence of semantics in music (Kutas and Federmeier, 2011; Pinker, 1997). 87

The N400 response is an event-related potential (ERP) presumed to 88 process meaning. Initially observed in response to semantically 89 90 incongruent sentence endings in language (Kutas and Hillyard, 1980), the N400 was more recently linked to incongruity of meaning in a 91 wide variety of stimuli (Kutas and Federmeier, 2011). However, Kutas 92and Federmeier (2011) explicitly exclude musical stimuli from this 93 train of results, suggesting that music does not contain semantically 94 95meaningful information.

Nevertheless Koelsch et al. (2004) could demonstrate a semantic 96 priming effect on target word processing by means of musical primes 97 and therefore provided evidence in favor of semantic processing in 98 music. Primes consisted of sentences or musical passages that were 99 100 either related or unrelated to a target word for their meaning. Independently of whether a musical or a language prime was used, unexpected 101 target words provoked stronger N400 responses than target words 102preceded by related primes. The priming effect did not differ between 103 104 language and musical primes for strength, time course or neuronal 105generators. This N400 response primed by musical targets was elicited by words and not by music; such a response to unexpected 106 "extra-musical meaning" results from an association from a musical 107 sign quality to the extra-musical world (Koelsch, 2012). Daltrozzo and 108 109 Schon studied the reverse effect: the influence of visually presented 110 words on the processing of musical excerpts (Daltrozzo and Schon, 2009). They also found a larger N400 response now in response to 111 musical targets that were unrelated to the preceding extra-musical 112 word context. These studies investigated people with low level of 113 musical education or none. 04

In intra-musical contexts, transgression of intra-musical meaning by
 means of harmony transgression (thus violation of syntax) embedded
 in either chord series (Koelsch et al., 2000) or authentic musical stimuli
 (Koelsch et al., 2008), yielded an N5 response in non-musicians
 preceded by an ERAN (Koelsch et al., 2001).

Children and adults with and without formal musical education are 120able to discriminate tonal transgressions in melodies, chord progres-121 sions and complex music (Besson and Faïta, 1995; Bigand et al., 2003; 122Koelsch et al., 2000, 2005; Trainor and Trehub, 1994). Recently we 123124 could show that primary-school children with and without musical 125training perfectly rank transgressions of musical closure as a function of their salience in monophonic children's songs but also in more 126complex polyphone piano pieces (James et al., 2012). Moreover, typical 127ERP responses, similar to those of adults, occurred in 5- and 9-year old 128129non-musician children in response to unattended chord series with transgressed endings (Koelsch et al., 2003). Whether these behavioral 130and associated ERP responses persist in primary-school children when 131 irregularities are in-key and refined, moreover embedded in complex 132polyphone music, has not been investigated yet. 133

In the current experiment we presented a series of ecologically valid
 short string quartets (duration approx. 10 s) in a variety of Western
 tonal styles, to 15 randomly assigned primary-school children of around
 ten years of age. The pieces ended either regularly or contained refined
 in-key harmonic transgressions at closure. Notably, the transgressed

and thus unexpected terminal chords were perceptually just as pleasant 139 as the regular endings (see the Methods section, musical violation 140 discrimination task). Meanwhile high-density electroencephalography 141 (EEG) was recorded, that we analyzed with microstate analyses 142 comprising all electrodes, and also with classical ERP analyses, using 143 an electrode array deriving from a previous study (James et al., 2008). 144

As similar stimuli have not been presented to a child population 145 before, our study is essentially exploratory, and cannot be placed in a 146 full developmental context. However, we anticipated possible 147 occurrence of early and later ERP components known to arise in 148 response to tonal expectation violation in music in adults and children. 149 In order to investigate whether the processing of structure and meaning 150 in music is related to certain domain general cognitive functions, we 151 additionally assessed measures of working memory and fluid 152 intelligence. 153

Methods

Participants

Sixteen right-handed children (8 girls, 7 boys; mean age = 10.9 years, 156 SD = 0.8) were randomly assigned among the population of a local public 157 primary school. Their parents gave written informed consent. One child 158 was excluded from the sample because of excessive blinking during EEG 159 recordings. The protocol was approved by the school and by the local 160 ethics committee. Only right-handed participants were included for Q6 brain organizational reasons (Isaacs et al., 2006). Handedness was 162 assessed with the "Edinburgh Handedness Inventory" (Oldfield, 1971; 163 mean score 87.3 \pm 16.7). According to reporting of the parents, all 164 children possessed normal hearing and had no history of neurological 165 illnesses. Of the 15 final participants, 10 children did not receive any 166 extra-curricular musical training, 5 practiced musical instruments for 167 2.8 ± 0.5 years; one played the cello, two the flute and two the piano. 168 Intra-curricular music lessons at public schools in the French speaking 169 part of Switzerland are not strictly protocolled and differ strongly as a 170 function of the teacher. Thus, some explicit knowledge of musical scales 171 may have been provided to the non-musician children. 172

General procedure

All children were tested twice. At first the children accomplished a 174 musical violation discrimination test while continuous EEG was 175 recorded (see Experimental procedure I: EEG). On average 3 days later 176 (SD: 5 days), the children passed 2 additional behavioral tests in the 177 following order: 178

- 1) Raven's "standard progressive matrices" (SPM; Raven et al., 1998) 179
- 2) "Digit span" of the Wechsler Intelligence Scale for Children 180 (Wechsler, 2005) 181

We applied those tests aiming to evaluate possible relationships 182 between short-term memory (Digit span forward), working memory 183 (Digit span backward), fluid intelligence (Raven's) and musical 184 violation discrimination. 185

Experimental procedure I: EEG 186

Musical violation discrimination task

We presented 78 original polyphone expressive musical stimuli at 188 two levels of musical transgression at musical closure: regular and 189 harmonically¹ transgressed endings. The original stereo sound-files 190 were converted to single track/mono stimuli in order to cancel out 191 any left ear versus right ear differences and presented binaurally via 192 EEG compatible headphones. The stimuli (n = 156) were presented in 193

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¹ Musical harmony refers to the use of simultaneous pitches or chords.

2 different pseudo-randomized sequences, the second in reverse order of the first to prevent serial position effects. The series were presented in 4 blocks, separated by short breaks.

197The musical score of an example stimulus showing both transgression levels at closure is depicted in Fig. 1; the corresponding sound-198file is available in the supplementary material. Similar stimuli were 199used in a recent fMRI study (Oechslin et al., 2013b) that examined 200adults with 3 distinct levels of musical expertise (non-musicians, 201 202amateurs and experts). The latter study contained a supplementary 203transgression level: a very subtly transgressed ending, which was 204almost exclusively discriminated by professional musicians and 205therefore omitted here. These ecological stimuli were manufactured 206specifically for our experiments by a professional composer, and cover 207 a large range of musical styles from baroque to late romanticism. They were balanced for all 24 minor and major tonalities. The compositions 208 are string quartets with a mean duration of around 10 s, arranged 209 with the "Sibelius" software (Avid Technology, Inc. and "Logic Pro", 210 Apple Inc.); real instrumental timbers (violin, viola and cello) were 211implemented using the "Garritan Personal Orchestra" (http://www. 212 garritan.com). Regular endings consisted in a first degree or tonic in 213root position; transgressed endings consisted of the 4th degree or sub-214 dominant in first inversion. We used the first inversion (the so-called 215216 sixth chord) because this allows better voicing (vertical ordering and spacing of the pitches), making the transgressions as refined as possible, 217 by avoiding the fourth note of the scale in the bass. Both the tonic and 218 the subdominant chord played by a string quartet, thus widely spread 219over the octaves, in major and minor tonalities, in root position or first 220221inversion, may contain the same intervals (octaves, perfect fifths, major and minor thirds and their inversions: perfect fourths, major 222 223and minor sixths) and therefore induce approximately the same degree 224of consonance or pleasantness.

All terminal chords were cut off at 1400 ms from onset and faded 07 226linearly over the last 150 ms. The carefully voiced transgressions all remained within the tonality ("in-key") of the preceding context and 227would be suitable if the music continued. However, as endings, these 228 chords represent transgressions according to the Western tonal rule 229 system, only the tonic chord in root position is appropriate at closure. 230 231 As we systematically conserved the melody in the upper voice between regular and transgressed endings, and also because the final chord was 232always in-key and carefully voiced with respect to the preceding 233context, these stimuli can be considered refined and thus relatively 234

difficult to discriminate, even more so because of the polyphone and 235 thus complex nature of the musical material. 236

Participant's appraisals consisted of expressing whether end- 237 formulas were correct with respect to the preceding musical context, 238 yes or no, by means of right hand button presses on a computer 239 mouse, using the left button labeled "no" (middle finger) for incorrect 240 endings, and the right labeled "yes" (index) for correct endings. We 241 will refer to this task as the "musical violation discrimination task". 242 The children were instructed to withhold their response and hold still 243 and relaxed after the onset of the final target chord, until a prompt 244 ("please respond") was presented on the screen, appearing 1900 ms 245 after stimulus onset, in order to prevent contamination of the 246 stimulus-related EEG signal with motor activity. This is why no reaction 247 times are reported, and why the use of index and middle finger was not 248 counterbalanced. 249

Based on these binary responses we computed accuracy (percent250correct) of responses to regular and transgressed endings and consecu-251tively d-prime values. The d-prime index is a statistic derived from252signal detection theory (Macmillan and Creelman, 1997) and provides253an index of rater sensitivity: higher d-prime values indicate better254discrimination between regular and transgressed endings.255

EEG acquisition and raw data processing

EEG was continuously recorded at 64 electrode sites (BioSemi 257 Active-Two, V.O.F., Amsterdam, The Netherlands), equally distributed 258 across the scalp. Data were digitized at a sampling rate of 1024 Hz in a **O**8 bandwidth filter of 0-268 Hz. Prior to analysis, data were offline 260 recomputed against average reference and band-pass filtered between 261 0.25 and 30 Hz within a 2nd-order Butterworth filter (-12 dB/octave 262roll-off). As we recorded in a classroom and not in a Faraday cage, we 263 applied a 50 Hz notch filter in order to cancel out power-line interfer- 264 ence. However, the BioSemi Active-Two system already annihilates 265 the effect of interference currents in the electrode wires by using active 266 electrodes, and is therefore ideal for field research. Average evoked 267 potentials were computed from 100 ms before stimulus onset (i.e. the 268 onset of the terminal chord) to 800 ms post stimulus. We then applied 269 average referencing that consists of a spatial correction of the voltage 270 configuration on the scalp of all electrodes at each data point by the 271 mean voltage of all electrodes. We also applied a classical baseline 272 correction using the 100 ms preceding stimulus onset in order to better 273 compare the ERPs to the existing literature. We used pre-processing 274



Fig. 1. This figure displays the score of an example musical stimulus, here in D major. All musical pieces were presented in 2 versions: with a regular ending (R, piece ends on the tonic, "I"), or a harmonic transgression at closure (T, the piece ends on the first inversion of the fourth degree or subdominant "IV⁶"). Corresponding audio files are provided in the supplementary material (respectively D_Maj_R.wav, D_Maj_T.wav).

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methods as described in Brunet et al. and Michel and Brandeis (Brunet et al., 2011; Michel and Brandeis, 2009): in addition to an automated threshold rejection criterion of 100 μ V, all epochs were visually inspected for oculomotor and other artifacts (movement, muscular tension, loss of electrode contact following discrete movement or perspiration). Only artifact-free epochs were retained with an average of 63.9 \pm 6 epochs per condition per participant.

Channels exhibiting substantial noise were interpolated with a 3D spherical spline interpolation accounting for the real geometry of the head (Brunet et al., 2011; Perrin et al., 1989). These interpolation methods are recommended for high density ERP source analysis (Brunet et al., 2011; Michel and Brandeis, 2009).

287 Procedure of ERP analyses

288 The ERPs were analyzed in 4 consecutive stages.

Stage 1: ERP waveform analyses. We computed average ERPs in response
to both experimental conditions and also ERP difference waves in an
8-electrode site array divided into two zones, frontal (F1, F2, Fz and
Afz), and parietal (P1, P2, Pz and POz). To compute difference waves,
ERP responses of regular endings were subtracted from ERP responses
to transgressed endings.

The choice of these electrodes was based on an ERP response of non-musician adults revealed by a previous study (James et al., 2008), using similar harmonic transgressions in piano pieces, and also on visual inspection of the current data, because we did use a 64 electrode recording here and a 128 electrode setting in James et al. (2008).

We conducted a repeated-measures ANOVA on the mean amplitude of ERPs over the time period 350–450 ms after stimulus onset with the factors Condition (2, within) × Zone (2, within).

303 This time period corresponds with the robust peak latency of the 304 N400 component (Kutas and Federmeier, 2011) and also comprises the period of occurrence of the ERP responses of adult non-musicians 305 mentioned above (James et al., 2008). The peak latency of the Central 306 Posterior Negativity (CPN) observed here for the 8 chosen electrodes 010 was 407.9 \pm 3.6 ms. For the difference waves (subtraction of ERP 308 responses to regular endings from ERP responses to transgressed 309 endings) of these 8 electrodes, the peak latency was 408.9 ± 2.6 ms. 310

Stage 2: spatiotemporal ERP analyses I: topographic dissimilarity analysis. 311 312 In a second stage of the analysis we computed a measure of topographic dissimilarity over time that allowed determining whether the observed 313 314 differences between the ERPs of the two experimental conditions in stage 1 were due to topographical changes of the whole scalp potential 315 configuration or to local amplitude changes only. According to physical 316 laws, only if the whole scalp potential configuration changes significantly 317 318 over time, can differences in underlying active generators in the brain be 01 assumed (Vaughan, 1982).

In order to check for such topographic modulations, we performed 320 statistical comparisons between the two experimental conditions of 321 the mean normalized ERP topographies at each time point using a 322 nonparametric bootstrapping method on the global map dissimilarity 323 324 values (Kondakor et al., 1997; Michel et al., 2004b; Murray et al., 2006, 325 2008; Srebro, 1996). Global dissimilarity is a single measure expressing 326 the topographic difference between 2 scalp voltage topographies, normalized to unitary strength by dividing all amplitudes by the GFP 327 at each time point (Lehmann and Skrandies, 1980; Murray et al., 328 2008). For this analysis we only retained periods lasting for at least 30 329 consecutive ms during which this topographic test exceeded a 0.05 330 alpha criterion. 331

Stage 3: spatiotemporal ERP analyses II: microstate analysis & statistical
 fitting procedure. Classic ERP waveform analysis focuses on explicit
 components defined in time and space. This analysis allows detecting
 differences between populations or conditions over time.

In microstate analysis we study the scalp voltage topographies over 336 time of all recorded electrodes in one unified analysis. These microstates 337 reflect the sum of all neuronal populations active at a given moment in 338 time and manifest as discrete segments of electrical stability lasting tens 339 to hundreds of milliseconds separated by brief intervening intervals 340 (Brunet et al., 2011; Murray et al., 2008; Pascual-Marqui et al., 1995). 341 Lehmann et al. (1987) conceptualized these stable periods as 342 *microstates* of information processing, basic psychophysiological units 343 of cognition. 344

The principal aim of the microstate analysis is to look for changes in 345 configuration of the potential field over time that directly informs when 346 different generators are active in the brain. 347

Microstate analysis thus provides intrinsically different information 348 as compared to classic ERP analysis, and the 2 analyses can be 349 considered complementary. 350

We applied a hierarchical cluster analysis (CarTool software; http:// 351 brainmapping.unige.ch/cartool.htm) to reduce our grand-average ERP 352 topography time series of both experimental conditions into an optimal 353 number of microstates or map topographies. The optimal number is 354 determined based on cross validation criteria that minimize the residual 355 variance, and the Krzanowski-Lai criterion (Brunet et al., 2011; Michel 356 and Brandeis, 2009; Michel et al., 2004a; Murray et al., 2008; 357 Pascual-Margui et al., 1995; Tibshirani and Walther, 2005). The 358 resulting series of microstates over time can be considered an a priori 359 hypothesis that has to be statistically tested. This statistical testing is 360 done by means of a statistical fitting procedure, namely by fitting the 361 microstates to the time series of each individual participant. For that 362 purpose spatial correlation coefficients are computed for each 363 time-point between the microstates identified by the cluster analysis 364 in the grand-average ERPs and the ERPs of each participant for each 365 condition. This procedure yields measures of microstate presence or 366 "microstate duration" (expressed in ms) for each participant and 367 condition that can be submitted to statistical testing, thus "fitting" the 368 microstates to the actual data. 369

The distributions of the microstate durations showed some 370 asymmetry. But no outliers were present, so we used repeated 371 measures ANOVAs to compare microstate durations between the 372 experimental conditions. As no reliable tests exist to verify normality 373 with small sample sizes (Razali and Wah, 2011), we verified these Q12 results by means of non-parametric contrasts (Wilcoxon signed-rank 375 test). 376

Stage 4: statistical analysis of ERP sources: estimation & comparison of 377 neuronal generators. Because the inverse problem is ill-posed with 378 scalp EEG, the inverse solution to estimate neuronal generators must 379 be stabilized via a priori constraints (Grech et al., 2008; Michel et al., 380 2004a). Statistically verified microstate series provide such a priori 381 constraints and consequently reduce the dimensionality of the inverse 382 problem (see Stage 3: spatiotemporal ERP analyses II: microstate 383 analysis & statistical fitting procedure). We therefore limited source Q13 estimation to time periods during which spatiotemporal analysis of 385 scalp ERP demonstrated significantly different microstates/map 386 topographies between stimulus types. Changes of scalp voltage configu- 387 rations are indicative of changes in the underlying generator configura- 388 tion (also see Stage 3: spatiotemporal ERP analyses II: microstate 389 analysis & statistical fitting procedure; Michel et al., 2004a; James 390 et al., 2008; Murray et al., 2008; Vaughan, 1982). 391

As a first step we estimated the intracranial current distribution at 392 each moment in time for the evoked potential of each subject in each 393 condition with a depth-weighted minimum norm (WMN) distributed 394 linear inverse solution (Hamalainen and Ilmoniemi, 1994; Michel 395 et al., 2004a). The current distribution was calculated within the gray 396 matter of the average brain provided by the Montreal Neurological 397 Institute. A discrete grid of 3005 solution points was regularly distributed 398 within this volume. After applying a homogeneous transformation 399 operation to the volume that rendered it to the best fitting sphere 400

(SMAC model; Spinelli et al., 2000), a 3-shell spherical head model was 401 used to calculate the lead field for the 64 electrodes and the inverse 402 solution based on the weighted minimum norm (WMN) constraint. As 403 404 a second step, Bonferroni corrected two-tailed t-tests were applied to compare mean current density values over each selected time period 405between both experimental conditions; a procedure of statistical 406 parametric mapping (SPM). In distributed EEG/MEG inverse solutions, 407 the number of independent variables used for the Bonferroni corrections 408 409corresponds to the number of recording sensors on the scalp (Grave de Peralta Menendez et al., 2004; Michel et al., 2004a; Murray et al., 2008). 410 411 This procedure allows detecting brain areas in which enhanced activity occurs for either one of the experimental conditions (or groups) and 412413 also cancels out residual random noise present in both conditions. 414 These methods have been successfully used in many domains in recent years (Britz et al., 2009, 2014; James et al., 2008; Plomp et al., 2013; 014 Rihs et al., 2013). However, source imaging from grand-averaged EEG 416 data has limited accuracy (Plomp et al., 2010) and the areas we depicted 417as generators should therefore be interpreted as coarse estimates. 418

419 Experimental procedure II: additional behavioral measures

"Digit span" of the Wechsler Intelligence Scale for Children (Wechsler, 2005) 420 421 The Memory for Digit Span assessment, a component of the 422Wechsler Intelligence Scales for Children-Revised (WISC-R), is a measure of short-term memory for children aged seven and over 423 (Wechsler, 1974). During these tests children are orally given sequences 424 of numbers and asked to repeat them, either as heard (Digit span 425426 forward) or in reverse order (Digit span backward). Digit span forward and Digit span backward assess distinct but interdependent cognitive 427functions (Grégoire, 2009). Digits Forward primarily evaluates 428 short-term auditory memory whereas Digits backward measures the 429430child's ability to manipulate verbal information while in temporary storage thus working memory capacity. 431

432 Raven's "standard progressive matrices" (Raven et al., 1998)

We used Raven's "standard progressive matrices" (Raven et al., 433 1998) in a time-limited version (20 min) to assess a measure of fluid/ 434 435general intelligence. Fluid intelligence is the capacity to reason and solve new problems without relying on previously acquired knowledge 436 and skills. The test consists of 60 visuo-spatial problems that become 437 increasingly difficult. The items require inferring a rule relative to a 438 collection of visuo-spatial patterns presented in a matrix. The subject 439has to identify the last missing element of the pattern from a certain 440 number of choices provided (6 or 8 options), based on the previously 441 inferred rule. 442

443 Results

444 Behavioral results

445 Musical violation discrimination task

446On average, the children discriminated the regular endings ("R";447 $82.05 \pm 17.42\%$ (SD)) better than the harmonic transgressions ("T";448 $67.27 \pm 18.57\%$; $t_{14} = 2.86$, p = 0.01). They discriminated both R449 $(t_{14} = 7.12, p < 0.01)$ and T $(t_{14} = 3.60, p < 0.01)$ well above chance;450mean d-prime values were 1.74 ± 1.24 points. No significant difference451existed between the d-prime scores of musician (n = 5) and452non-musician (n = 10) children ($t_{13} = 1.26, p = 0.23$).

453 Additional behavioral tests

454Raven's "standard progressive matrices" yielded raw scores of455 44.60 ± 4.10 . As no test norms exist for the limited time version for456French 10 year-olds, we could not compare our sample to the general457population.

The Memory for Digit Span assessment yielded mean scores (rawdata) for recall of numbers in direct order (Digit span forward, DSF) of

 8.80 ± 1.78 versus 7.27 ± 2.28 for those in inversed order (Digit span 460 backward, DSB). As typically observed, scores for direct order were 461 superior compared to those in inversed order ($t_{14} = 2.20$, p = 0.04). 462 The scores were within the norms for this age group. 463

Correlation analysis of behavioral results

We computed Pearson correlations between the d-prime scores 465 resulting from the musical violation discrimination task and the three 466 other behavioral measures: Digit span forward (DSF), Digit span 467 backward (DSB) and Raven's standard progressive matrices 468 (RSPM) scores. Only the linear relationship between DSB and d-prime 469 (r = 0.53, p = 0.04) was statistically significant, no significant correlation existed between DSF and d-prime (r = 0.33, p = 0.24) or between 471 RSPM and d-prime (r = 0.37, p = 0.17).

ERP results

Stage 1: ERP waveform analyses

We computed a repeated measures ANOVA on mean amplitude of 475 ERPs in a 350–450 ms window for the 8 selected electrodes (see the 476 Methods section), with the factors Condition (R vs. T; within) and 477 Region (frontal vs. parietal; within). The analysis revealed significant 478 interaction between both factors ($F_{1,14} = 17.45$, p < 0.01); no main 479 effects of Condition and Region were observed, because in the frontal 480 and parietal regions effects were opposite for the 2 conditions, thus 481 resulting in means close to zero. Contrasts for all electrodes between 482 the 2 conditions, corrected for multiple comparisons (Bonferroni), 483 disclosed significant effects of Condition for each separate electrode of 484 the array (Fig. 2) within the 350–450 ms period.

We also computed difference waves (T-R) that showed pronounced 486 deviations from 0 μ V peaking around 400 ms after stimulus onset, with Q15 strong positive values for the 4 frontal electrodes and strong negative 488 values for the 4 parietal ones in a remarkably symmetric configuration 489 (Fig. 3). 490

Correlation between *d*-prime and CPN component. To investigate the 491 relationship between electrophysiological data and behavior, we 492 computed Pearson correlations between *d*-prime scores and the CPN 493 component. We performed correlation analyses on *d*-prime scores and 494 mean amplitude of the ERP difference waves (350–450 ms) for the 495 frontal zone (F1, Fz, F2 and Afz) and the parietal zone (P1, Pz, P2 and 496 POz) of the 8-electrode array. We chose to use ERP difference waves 497 because, like the *d*-prime score, they express a relationship between 498 responses to transgressed and regular endings. For both zones, mean 499 amplitude and *d*-prime scores were significantly correlated (frontal 500 zone: r = 0.62, p = 0.01; parietal zone; r = -0.57; p = 0.03). So 501 higher amplitudes of difference waves for this component related 502 linearly to higher *d*-prime scores that exhibit higher rater sensitivity 503 to the harmonic transgressions.

Stage 2: spatiotemporal ERP analyses I: topographic dissimilarity analysis505The topographic dissimilarity analysis (Fig. 4a) revealed a sustained506difference between the 2 experimental conditions from 321 to 639 ms, 507507and a quasi-sustained difference from 271 to 755 ms (Fig. 4a; depicted508values correspond to p < 0.05, duration > 30 ms; periods of significant509difference: 271-312 ms; 321-639 ms; 654-690 ms; 714-755 ms).510

Stage 3: spatiotemporal ERP analyses II: microstate analysis & 511 single-subject "fitting" 512

The hierarchical cluster analysis yielded 7 distinct microstates that 513 optimally represent the data for both conditions and all participants 514 (Figs. 4b & c); this microstate series explained 92.22% of the variance 515 in the ERP data during the time period 0–800 ms. Inspection of the 516 occurrence of the microstates (M) over time disclosed several 517 differences in the grand means between responses to R and T. 518

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Fig. 2. Grand-average ERP waveforms at 8 electrode sites at (a) 4 frontal and (b) 4 parietal electrode sites. ERPs elicited by regular terminal chords (R) are plotted in black, and by transgressed ones (T) in red. The time interval used for the statistical analysis of the CPN component is indicated by gray-dashed brackets (350–450 ms). (c) Scalp positions of the 8 electrodes are highlighted within the full 64-electrode setting (view from above, nasion on top). (d) Mean whole head voltage configurations are shown for both conditions R and T over the 350–450 ms period.



Fig. 3. Grand-average ERP difference waveforms (T-R) at 8 electrode sites (cf. Fig. 2c.), 4 frontal (warm colors) and 4 parietal (cold colors). Note the marked symmetric difference from zero peaking around 400 ms. On the right, the mean whole head voltage configuration of the difference waves is depicted over the 350–450 ms period, corresponding to the gray dashed box.

An early difference, exclusive occurrence of M4 for R versus M1 for T (126–255 ms), could be observed in the grand means. After ≈ 275 ms after stimulus onset M2, M6 and M7 occurred exclusively in condition T, M3 and M5 in condition R. Observing the scalp voltage configuration, M2 can clearly be associated with the CPN component observed in the ERP waveform analyses.

We then applied the statistical fitting procedure on the variable 525526"microstate duration" (in ms; see the Methods section) over 4 consecutive time periods during which 2 different microstates occurred simul-527taneously in both conditions in the grand means. This fitting is 528necessary to verify the statistical significance of the observed differ-529ences in the grand means. We will report only interaction effects 530(main effects of condition will not occur because the total amount of 531ms is always equal for both conditions over each time period). Main 532effects of microstate that do not take into account the factor Condition 533

are not relevant in the context of the present study. As the first period 534 did not yield any significant results, we labeled it Period 0. 535

Period 0 (126–255 ms) results from the following boundaries: 536 126 ms, appearance of M4; 255 ms, extinction of M4. A repeated 537 measures ANOVA (Condition (R vs T) × Microstate (M1 vs M4)) did **Q16** not show significant interaction Condition × Microstate ($F_{1,14} = 2.94$, 539 p = 0.11). This is not surprising, as M1 and M4 display a very similar 540 voltage configuration. Moreover, the topographic dissimilarity analysis 541 did not reveal significant differences either over this period (Fig. 4a). 542

Period 1 (Fig. 4d1) 301-477 ms results from the following 543 boundaries: 301 ms, appearance of M3 for R, 477 ms, extinction of M2 544 for T. A repeated measures ANOVA (Condition (R vs T) \times Microstate 545 (M2 vs M3)) showed significant interaction Condition \times Microstate 017 $(F_{1.14} = 17.39, p = 0.01)$. M2 appeared on average 37.89 ± 53.44 ms 547 in condition R and 136.98 \pm 64.53 ms in condition T. M3 appeared on 548 average 138.87 \pm 53.44 ms for R and 39.78 \pm 64.53 ms for T. The 549 observed dominance of M2 for T (z = 3.01, p < 0.01) and M3 for R 550 (z = 3.01, p < 0.01) could be confirmed by means of Wilcoxon 551 signed-rank tests. In order to ensure that this main result, consistent 552 with the ERP waveform results in the CPN component, was not yielded 553 mainly by the 5 musician children, we repeated this test including 554 exclusively non-musician children (n = 10); an identically oriented 555 statistically significant interaction was obtained between Condition 556 and Microstate ($F_{1.9} = 9.94$, p = 0.01) confirming that this effect 557 manifested in all children. 558

Period 2 (Fig. 4d2) 477–603 ms results from the following boundaries: 559 477 and 603 ms, respectively appearance and distinction of M6 for T. A re- 560 peated measures ANOVA (Condition (R vs T) × Microstate (M3 vs M6)) **Q18** showed significant interaction Condition × Microstate (F1,14 = 8.95, 562 p = 0.01). M3 appeared on average 106.84 \pm 35.51 ms for R 563 and 50.65 \pm 49.77 ms for T. M6 appeared on average 20.12 \pm 35.51 ms 564 for R and 76.30 \pm 49.77 ms for T. The observed dominance of M6 for T 565

Fig. 4. Spatiotemporal ERP analyses. (a) Topographic dissimilarity analysis, 1-p values are plotted over time. (b, c) A hierarchical cluster analysis yielded 7 distinct microstates that optimally represent the data of both conditions of all participants. (b) Microstates for regular endings, top row: the colored segments under the global field power (GFP) curves represent the time periods during which each of these microstates was most represented in the group data; bottom row: scalp voltage configurations of the microstates (view from above, nasion on top), framed in corresponding color-code. (c) Idem for transgressed endings. (d1–3) Fitting of microstates (M) for 3 consecutive time periods during which significant interaction Condition \times Microstate occurred. On the y-axis mean duration (ms) of microstates is provided. Vertical bars depict standard errors.

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477 - 603 ms

301 - 477 ms

644 - 800 ms

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(z = 2.54, p = 0.01) and M3 for R (z = 2.54, p = 0.01) could be confirmed by means of Wilcoxon signed-rank tests.

Period 3 (Fig. 4d3) 644-800 ms results from the following bound-568 569aries: 644 ms, appearance of M5 for R, 800 ms, end of analysis. A repeated measures ANOVA (Condition (R vs T) \times Microstate (M5 vs M7)) 019 showed significant interaction Condition \times Microstate (F1,14 = 8.95, 571p = 0.01). M5 appeared on average 120.44 \pm 40.64 ms for R and 572 63.48 ± 57.43 ms for T. M7 appeared on average 35.81 ± 40.64 ms 573574for R and 92.77 \pm 57.43 ms for T. The observed dominance of M7 for 575T (z = 2.29, p = 0.03) and M5 for R (z = 2.29, p = 0.03) could be confirmed by means of Wilcoxon signed-rank tests. 576

Nota bene: Effects for Wilcoxon signed-rank tests for both microstates within each time period yielded always identical z and p-values,
because the total amount of ms is the same.

In conclusion, over all 3 periods M3 and M5 are prevalent for R,
 characterized by posterior positivity, against prevalence of M2, M6
 and M7 for T, characterized by posterior negativity.

583 Stage 4: statistical analysis of ERP sources: estimation & comparison of 584 neuronal generators

We used the results from stage 3 (microstate analysis) of the ERP 585analyses to determine periods of time with potential distinct underlying 586generators in the brain for both experimental conditions (R and T). For 587each of the 3 periods for which the fitting procedure disclosed a signif-588icant interaction between microstate incidence of R and T (see Fig. 4d.), 589we computed statistical comparisons (statistical parametric mapping), 590591 through Bonferroni corrected two-tailed t-tests,² between mean current density values (expressed $\mu A/m^3$) in response to R and T over 592 these 3 time periods: 301-477 ms, 477-603 ms and 644-800 ms after 593594stimulus onset.

The t-tests on mean current density over the full 301-477 ms 595596window did not yield significant results. Lowering the threshold from Bonferroni corrected to a more clement p < 0.005 we found stronger 597activations for condition T as compared to R in bilateral pre-motor 598areas in the medial frontal gyrus and paracentral lobule and in a discrete 599600 left auditory area with solution points in the superior and middle temporal gyrus. In order to conserve a Bonferroni corrected threshold, 601 602 we narrowed the time window around the marked GFP peak of the 603 CPN response, enhancing the signal-to-noise ratio that is known to increase with GFP strength (Lehmann et al., 2005). Stable map configu-604 ration and underlying cerebral networks are presumed during micro-605 606 states (Koenig et al., 2014), and map stability is at its maximum during the GFP peak. Computing sources at the GFP peak using SPM 607 was recently successfully used to show deficits of the ventral stream 608 in visual processing in schizophrenic patients (Plomp et al., 2013). In a 609 time window from 375 to 425 ms, we found Bonferroni corrected 610 significant differences in large clusters, with higher current density in 611 response to condition T in a network of brain areas with peak values in 612 613 the left hemisphere. The network comprised voxels in the medial frontal gyrus (-3 - 2152; BA6; t = 5.03, p = 0.00019), in the paracentral 614 615 lobule (peak value Talairach -9 - 4154; BA5; t = 6.48, p = 0.00002 & -3 - 34 66; BA4; t = 4.42, p = 0.00058), in the precuneus (peak 616 value Talairach -3 - 4754; BA7; t = 4.60, p = 0.00041) and in the 617 mid-posterior cingulate gyrus (peak value Talairach -3 - 28 42; BA31; 618 t = 4.33, p = 0.00069; see Fig. 5a). 619

The t-tests on mean current density over the following 477–603 ms period, displayed significant differences in a network in the right hemisphere, again with higher values for condition T, in voxels of the postcentral gyrus (peak value Talairach 54 -11 14; white matter; t = 5.22, p = 0.00013), of the superior temporal gyrus (peak value Talairach 53 -11 9, BA22; t = 5.22, p = 0.00013; peak value Talairach 55 -27 14, BA 42; t = 4.38, p = 0.00063) and in a sub-lobar part of the mid-posterior insula (peak value Talairach 47 -124; BA22; t = 4.50, 627 p = 0.00050; see Fig. 5b). With a more clement threshold of p < 0.005 628 without Bonferroni correction, also voxels in the anterior insula (BA 629 13) reached significance. 630

In the last time period, extending to the end of our window of 631 analysis, 644-800 ms, differences arose in a single left hemisphere 632 cluster located in the middle temporal gyrus (peak value Talairach 633 -61-38-8; BA21; t = 5.24, p = 0.00013; see Fig. 5c). 634

Discussion

The key finding of this study is the occurrence of a specific neural 636 correlate, a centro-posterior negativity (CPN), in response to musical 637 violation expectation in primary-school children of approximately 638 10 years of age. The stimuli that yielded this response were refined 639 in-key transgressions of harmony embedded in expressive string- 640 quartets; such transgressions may be considered syntactical as they 641 violate structural rules within the Western tonal system. Probably due 642 to the subtle nature of the transgressions and the complex musical 643 context, typical earlier and later ERP components, often shown in 644 response to musical syntactical incongruity, did not occur here. The 645 latency of the CPN was closely centered on 400 ms, like the classic 646 N400 observed in response to semantically incongruent sentence 647 endings in language (Friederici et al., 1999; Lau et al., 2008). Rater 648 sensitivity (d-prime) for transgressed endings was positively correlated 649 with the strength of this CPN and also to a measure of working memory 650 capacity. Statistical parametric mapping (SPM) of estimated sources, 651 comparing responses to transgressed and regular endings showed 652 enhanced brain responses to transgression in left pre-motor, 653 mid-posterior cingulate and superior parietal cortex. These brain areas 654 may be linked to information integration processing. Altogether, these 655 results induce questioning on the level of differentiation of semantic 656 and syntactic processing in a complex intra-musical context in children. 657

Behavioral results

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Interestingly, the randomly assigned child population discriminated 659 the refined transgressions well above chance, but regular endings were 660 better rated, showing that this is an easier task. This observation 661 confirms earlier findings in musically naïve adults (James et al., 2008; 662 Koelsch et al., 2007). 663

Event-related potentials in response to tonal expectation violation in music 664

In an extensive review article on the N400 (Kutas and Federmeier, 665 2011) written by the same author that first described it in 1980 666 (Kutas and Hillyard, 1980) the authors state "However, N400-like 667 activity was not observed in response to unexpected events in other 668 structured domains such as music, be they the frequency of a note 669 violating a musical scale sequence or a familiar melody" (p. 624; Kutas 670 and Federmeier, 2011). 671

N400-like responses arose in response to written, spoken, signed 672 words and pseudowords, and outside of the language domain in 673 response to pictures, film, sounds and mathematical symbols (Kutas 674 and Federmeier, 2011; Niedeggen et al., 1999), even odors (Castle 675 et al., 2000). Hence Kutas and Federmeier (2011) reason that the 676 N400 rather conveys processing of meaning, independently of the 677 linguistic dimension. Defined more precisely, the N400 reflects *semantic* 678 *integration of a word or other percept within its working context*. Because 679 it is harder to integrate an element in an implausible continuation (Lau 680 et al., 2008), incongruous elements provoke the N400 response. This 681 integration process comprises a semantic memory function that 682 compares an element with its current context, and also to prior 683 knowledge. Working memory function enables such comparison to 684 the current context.

 $^{^2}$ The Bonferroni correction corresponds to alpha = 0.05/64 (number of electrodes) = 0.00078; for the sake of transparency we will report non-corrected values for which p < 0.00078.

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Fig. 5. Statistical parametric mapping (SPM) of estimated sources, comparing responses to transgressed and regular endings for 3 consecutive time-periods resulting from the microstate analyses (Stage 3 of ERP analyses). (a) 375–425 ms after stimulus onset (onset of the terminal chord). (b) 477–603 ms after stimulus onset. (c) 644–800 ms after stimulus onset. The highlighted brain areas display voxels with enhanced activation in response to the transgressed endings over the 3 periods. The estimated sources used for the SPM were computed via a distributed linear inverse solution (WMN). Talairach coordinates are provided, corresponding to the position of the superimposed white signs that represent the peak voxels. Corresponding Brodmann areas (BA) are provided when available.

Altogether there is no theoretical reason why an intra-musical 686 context would not be able to evoke an N400-like response. We consider 687 that in order to evoke such a response, specific musical material (prime 688 and target) should be presented. Our expressive stimuli, which are 689 690 complete mini-compositions of approx. 10 s, written by a professional composer, allow a comprehensive build-up of musical expectancy. 691 Musical expectancy yields a process of integration and evaluates the 692 congruence of musical elements within their current context, and also 693 as a function of prior knowledge. In the case of non-musicians this 694 695 knowledge of the tonal system may be acquired by implicit statistical 696 learning (Schon and Francois, 2011), following mere exposure. The refined harmony transgressions at closure applied in the current study 697 698 transgress structure but possibly also non-referential meaning. Such transgressions leave the listener puzzled, because these chords would 699 be appropriate if the music continued, but not as an ending. Moreover, 700 the fact that 78 different compositions were presented, in all 24 minor 701 and major tonalities, allows drawing more generalized conclusions on 702music processing in a Western tonal context; the degree of variability 703 excludes any memory or habituation interferences. 704

Q20 The intra-musical CPN component observed here manifests some difference with the standard N400 observed in adults in response to sentential semantic incongruity (Lau et al., 2008), or conveyed by incongruent linguistic and musical primes in extra-musical contexts (Koelsch et al., 2004). The component described in the current experiment displays a strong negative voltage as such, whereas the standard N400 710 reflecting semantic incongruity is in general only negative as a 711 difference wave, i.e. the result of subtracting the response to the congru-712 ent target from the response to the transgressed one. Part of this dissim-713 ilarity may be explained by our child population, in which the N400 714 showed increased amplitude compared to adults in language contexts 715 (Benau et al., 2011). 716

The robust component observed here in response to transgression in 717 complex music is clearly not an N5 response that has a more diffuse 718 peak, occurring often well after 500 ms (see for example Koelsch 719 et al., 2000). Then, although our transgressions undeniably violate 720 structure, no ERAN or other early negativity was observed (see the 721 following section) which typically precedes the N5 in response to 722 syntactic violation. Interestingly, an exception to the rule that the N5 723 is preceded by an ERAN was also observed in another study that used 724 in-key subdominant chords as intra-musical incongruent targets at 725 musical closure (Poulin-Charronnat et al., 2006). So we may wonder 726 how typical the N5 and ERAN are for syntactic and the N400 for seman-727 tic violation, and also, how distinct semantic and syntactic processing 728 are in an intra-musical context? We are not the first to consider this 729 query (Aramaki et al., 2010; Besson et al., 2011; Featherstone et al., 730 2013). 731

The fact that our subjects are children of around 10 years of age 732 should also be considered. In 5- and 9-year-olds (Koelsch et al., 2003), 733

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an ERAN as well as an N5 response to harmonic incongruity in chord se-734735 ries could be found (Jentschke and Koelsch, 2009). Other authors also showed early negative responses (around or before 300 ms after stimu-736 737 lus onset) to small pitch incongruences ("out of tune" tones) at the end of simple melodies in musician children (Magne et al., 2006; Moreno 738 et al., 2009). In an fMRI study, activation patterns following harmonic 739 incongruent chords in 10-year-old children were very similar to those 740 of adults (Koelsch et al., 2005); laterality effects (more involvement of 741 742 the left hemisphere in children) suggested that children process music 743 and language more similarly than adults. At ten or eleven years of age, ERAN responses were indistinguishable from adult responses 744 (Jentschke and Koelsch, 2009). Comparing 10-year-old children and 745 746 adults for N400 effects in a traditional language paradigm using moder-747 ately and strongly incongruent sentence endings, did not show latency differences for the N400 (Benau et al., 2011); but amplitude of the 748 N400 was enhanced in children compared to adults. Musical abilities 749 following implicit learning seem to mature early, like those for lan-750 guage, between 9 and 11 years of age (Brandt et al., 2012; Pulli et al., 751 2008). Altogether we expected similar responses in our child population 752as we would in adults, with possibly stronger amplitudes, and maybe 753 responses that are more similar to those in language than in adults, 754resulting in different topographies. 755

756 Now why did we observe a CPN response as the earliest distinct elec-757 trophysiological reaction to the transgressions and not an ERAN that did occur in children of the same age as our participants in response to 758 musically theoretically-similar violations? The ERAN manifested in 021 non-musician and musician adults in response to relatively salient 760 761 transgressions (Neapolitan chords), but also in response to a supertonic chord containing no out-of-key notes (Koelsch et al., 2001, 2007). This 762 early negative component (peak latency \approx 200 ms in adults) is a bot-763 764 tom-up, learned but automatized pre-attentive response to relatively 765 salient incongruity that violates syntax. A recent neurocognitive model 766 of music perception (Koelsch, 2011) proposed that the ERAN is involved 767 in structure building. Later responses then rather reflect top-down processing, the P3a processing of novelty or surprise, the P3b context-based 768memory updating (Polich and Criado, 2006), with both P3 components 769 770 appearing in response to rare stimuli that are task relevant and there-771 fore only present in overt tasks, when subjects deliberately judge the transgressions. The N5 that typically follows the ERAN also when the 772 task is covert (in many studies subjects discriminate timber differences 773 ignoring harmony), represents harmonic integration and meaning 774 775 according to the authors that observed it (Koelsch et al., 2008; Poulin-Charronnat et al., 2006). A non-expected chord will be harder 776 to integrate. The N5 occurred only in musical contexts, whereas the 777 N400 is not music specific (Koelsch, 2011). Another important differ-778 ence is that the N5 does not show clear peak latency like the N400, 779 780 but rather a diffuse negative deflection, and, as its name reveals, has a longer latency than the N400, that may occur well beyond 500 ms 781 after stimulus presentation. 782

We suggest that the refinedness or ambiguousness of the transgres-783 sions used here in combination with the rich expressive and polyphone 784 785 musical context prevented typical ERP responses to musical syntactical 786 incongruity and rarity to occur (ERAN, P3a and P3b). Exactly the same syntactical transgressions, musically theoretically speaking, may induce 787 very different behavioral and ERP responses as a function of the context 788 789they occur in. The stimuli used in the current experiment induced pro-790 cessing that may be considered syntactic, but also semantic in nature. In a preceding study, we observed a similar microstate in non-musician 791 adults in response to in-key incongruous chords (James et al., 2008, 792 Fig. 3, microstate 5), although it did not show a sharp peak around 793 400 ms as in the current experiment. Yet in that study the focus was 794on comparing experts to non-musicians, therefore the comparison 795 between non-musician responses to transgressed and regular endings 796 was not directly made. By all means, the high-level experts in that 797 study did not show this microstate in response to transgression. 798 799 Although 5 musically experienced children were present in our sample here, their rater sensitivity was not different from the non-musician 800 children, and in the 10 non-musician children the CPN clearly manifest- 801 ed. The expert pianists in James et al. (2008) had practiced their instru- 802 ment on average for 20 years, and peak value of training was over 6 h 803 per day. Therefore it seems legitimate to consider our participant 804 group here as rather inexperienced listeners, and the CPN as a "non-musician" response. 806

Microstates in response to transgressed endings following the CPN 807 component in time continued to display posterior negativity (micro- 808 states 6 and 7), as if the wondering about the sense of the musical 809 phrase went on. Surprisingly, we rather observed a later posterior pos-810 itivity in response to regular endings (microstates 3 and 5). Again this 811 converges with previous findings with similar stimuli (James et al., 812 2008; Fig. 4 microstate 7). Some resemblance may exist between 813 these later positivities and the so called "music closure positive shift" 814 (Knosche et al., 2005; Neuhaus et al., 2006). After all, only regular 815 endings provide a satisfactory closure.

Generators

While centering narrowly on the peak of the CPN, SPM of brain 818 sources revealed enhanced brain activation for transgressed endings 819 in the left medial frontal gyrus, paracentral and mid-posterior cingulate 820 areas and in the precuneus. This contrasts with the literature on underlying brain sources of semantic priming (Lau et al., 2008) and N400 822 (Koelsch et al., 2004) that suggests temporal and inferior frontal 823 sources, although the results are somewhat divergent. 824

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But the present study applied SPM on distributed inverse solutions 825 over a temporally concise period close to the peak latency of the 826 N400. This contrasts to previous studies reviewed by Lau et al. (2008): 827 either windows of analysis were much larger (around 200 ms), or target 828 brain regions were identified by fMRI activations, supported by low 829 temporal resolution (Steinbeis and Koelsch, 2008). 830

Although results of the computation of distributed inverse solutions 831 should be treated with caution (see Methods), the strong pre-motor 832 activations observed here that distinguish processing of transgression 833 from processing of regular endings are plausible within the context of 834 integration processing. 835

Motor activations accompanying musical perception are common in 836 musicians and non-musicians (James et al., 2008; Sammler et al., 2013; 837 Zatorre et al., 2007). Premotor areas may be involved in some form of 838 covert mimetic representation of the musical material (Cox, 2011; 839 Glenberg, 2010; Herholz et al., 2012), which supports integration 840 processing, and is thus enhanced in the presence of incongruent 841 information. Specifically the supplementary motor area (SMA) may 842 initiate this simulation process, acting as a forward model that is the 843 fruit of previous - possibly implicit - learning. Interestingly, this error 844 prediction function also occurs in the context of complex music that 845 the listener may not at all be able to produce (Schubotz, 2007). Such 846 SMA activation in response to incongruity has been observed in musical, 847 linguistic and sensorimotor contexts (Herholz et al., 2012; James et al., 848 2008; Meyer et al., 2011; Ye et al., 2014). Finally, posterior cingulate 849 activation could be associated previously to an N400 in response to 850 semantic incongruity (Frishkoff et al., 2004) – and the precuneus is a 851 known hub for pitch processing (Platel et al., 1997; Satoh et al., 2001). 852

Classically reported sources for semantic priming/the N400 (Kutas 853 and Federmeier, 2011; Lau et al., 2008): middle and superior temporal 854 lobe and inferior frontal areas were also activated more strongly in 855 response to transgressed endings in the current experiment, but later 856 in time. The right superior temporal cortex and insula responded to 857 transgression in period 2 (477–603 ms), the left middle temporal 858 gyrus in period 3 (645–800 ms). The middle and superior temporal 859 gyrus, together with the inferior frontal cortex, form a network involved 860 in lexical representations (Lau et al., 2008) that has been associated 861 with the N400. But then, as mentioned before, no concise time windows 862 were used to determine these brain areas (Lau et al., 2008).

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864 Relationships of musical to domain general cognitive mechanisms

865 Whereas our data revealed that working memory capacity predicted 866 transgression discrimination in music, fluid intelligence did not. Working memory is crucial for the accurate performance of our task. 867 In order to judge the appropriateness of the endings of the musical 868 pieces, participants should keep the preceding context activated in 869 memory and match it with the ending. Meanwhile they must compare 870 871 the appropriateness of the ending to existing knowledge, implicitly or explicitly acquired. Interestingly this exactly corresponds to the integra-872 873 tion function of the N400 described above and thus intimately links processing of incongruity of meaning in music and language. Therefore 874 875 this finding illustrates that musical cognition shares certain basic 876 features with domain general cognitive functions.

The fact that the Raven scores did not show a relationship with the 877 ability to discriminate tonal violation suggests that on a higher level of 878 cognition, musical processing and general fluid intelligence are 879 independent. Nevertheless, there is a growing literature that shows 880 that specifically language abilities (Besson et al., 2007) but also IQ 881 (Moreno et al., 2011; Oechslin et al., 2013a; Schellenberg, 2004) and 882 even mathematical skills (Schlaug et al., 2005) may be boosted by 883 musical training. As in our sample, average level of musical education 884 885 was modest; it is thus plausible that we did not find a correlation 886 between fluid intelligence and tonal violation discrimination in music.

887 Conclusion

We observed a centro-posterior negativity (CPN) reminiscent of the semantic mismatch N400 in schoolchildren in response to refined syntactical incongruities in complex musical stimuli. Pre-motor and superior parietal areas supported the CPN that may play a role in incongruity discrimination and information integration. In a rich and varying musical context, integration of subtly incongruous musical elements may imply analysis of structure but also of meaning, at least in children.

Q22 Uncited references

- 896 Koelsch et al., 2002
- 897 Michel et al., 2009
- 898 Painter and Koelsch, 2011

899 Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.
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