

1 Frontoparietal, cerebellum network codes for accurate intention
2 prediction in altered perceptual conditions

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23 **Abstract**

24 Integrating and predicting intentions and actions of others are crucial components of social
25 interactions, but the behavioral and neural underpinnings of such mechanisms in altered perceptual
26 conditions remain poorly understood. We demonstrated that expertise was necessary to
27 successfully understand and evaluate communicative intent in spatially and temporally altered
28 visual representations of music plays, recruiting frontoparietal regions and several sub-areas of the
29 cerebellum. Functional connectivity between these brain areas revealed widespread organization,
30 especially in the cerebellum. This network may be essential to assess communicative intent in
31 ambiguous or complex visual scenes.

32

33

34 **Keywords:** communication; functional connectivity; intention; neuroimaging

35 Human ability to coordinate with others is a key evolutionary skill, allowing us to achieve tasks
36 that could not be managed individually. Beyond vocal and semantic communication (Kotz and
37 Schwartze 2010), such mechanism relies on fine-tuned non-verbal expressive behaviors that must
38 be able to communicate one's intent reliably and efficiently. Intention therefore involves the whole
39 body as a mean of communication, especially focusing on the upper body actions and movement
40 dynamics (Andersen and Cui 2009). It requires both parties to share similar representations at
41 different levels (e.g., common goal or intermediate steps to achieve a final goal), to predict shared
42 outcomes and to integrate the predicted consequences of our own actions as well as others' (Sebanz
43 and Knoblich 2009). Hence, it also requires to pay attention to one's own intentions and to be able
44 to predict and anticipate movement generation (Lau, Rogers et al. 2004). However, the neural
45 processes underlying such communication flow are not yet fully understood. Currently, the
46 literature points at the use of an internal forward model that optimizes one's motor control by
47 comparing the actual and predicted sensory consequence of movements (Wolpert, Doya et al.
48 2003). By extension, such model might also be used to predict others' actions in a social interaction
49 based on one's own action representations (Wolpert, Doya et al. 2003). Such abilities would be
50 supported by several interacting brain networks that are active both during action generation and
51 during observation of others' actions (Rizzolatti, Fadiga et al. 1996). The frontoparietal network
52 including the inferior parietal lobule (IPL), have been associated with observation of individual
53 movements (in both monkeys and humans), shared visual attention, and motor intention
54 recognition (Rizzolatti and Sinigaglia 2010). Attention to one's own intentions and actions also
55 recruited the frontoparietal network, especially the prefrontal cortex exhibiting a strong functional
56 coupling with the premotor cortex (Lau, Rogers et al. 2004). The posterior parietal cortex, on the
57 other hand, was repeatedly observed in situations pertaining to motor intention and imagery

58 (Jeannerod 1994), while the lateral parietal cortex, such as the intraparietal sulcus (IPS) and IPL,
59 were linked more directly and precisely to attention and intention itself (Lau, Rogers et al. 2004,
60 Desmurget and Sirigu 2012, Eskenazi, Rueschemeyer et al. 2015). While such simulation system
61 has been previously described as a mirror neuron system in monkeys based on single cell
62 recordings, this mirror neuron system is difficult to observe properly in humans. Recognition of
63 intentions is notably impacted by contextual information and prior knowledge (Brass, Schmitt et
64 al. 2007). It is subject to information availability and processing (full body vision vs. occluded
65 vision), context richness (familiar vs. novel context) or expertise in a given task (Rizzolatti and
66 Sinigaglia 2010) and then related to general and specific predictive aspects. A few studies in
67 humans have, in the past, highlighted the impact of expertise on prediction of movements in groups
68 of experts, such as sport athletes (Aglioti, Cesari et al. 2008), showing their improved ability to
69 anticipate the outcome of a specific action in others. In comparison to sport athletes, musicians
70 possess expertise in both specific sensorimotor skills *and* social signal analyses and exhibit
71 structural brain changes, especially in the temporal and premotor cortex, as a strong biological
72 basis for their expertise and training (Münste, Altenmüller et al. 2002). Abovementioned studies
73 did not specifically test the benefits of expertise onto the recognition of expressive intent in sub-
74 optimal conditions (when information is lacking or altered), although it should be thoroughly
75 studied. In fact, such line of research should critically contribute to the understanding of the
76 behavioral and neural mechanisms underlying a better coordination between several individuals.
77 In sub-optimal conditions, the cerebellum could be highly relied upon in order to predict accurately
78 intention based on action understanding, planning, timing especially due to its fine-tuned
79 connections with the basal ganglia and the cerebral cortex (Caligiore, Pezzulo et al. 2017). In fact,
80 the cerebellum is part of the action observation (Sokolov, Gharabaghi et al. 2010) and voluntary

81 movement (Hülsmann, Erb et al. 2003) networks and it is also a strong hub for timing and rhythm
82 processing (Molinari, Leggio et al. 2007, Chen, Penhune et al. 2008). Cerebellar activity is also
83 enhanced during sensorimotor coordination in musicians (Krause, Schnitzler et al. 2010) and
84 widely recruited by abstract social cognition, with involved sub-regions overlapping with
85 sensorimotor cerebellar territories (Van Overwalle, Baetens et al. 2014, Sokolov 2018). The
86 probability of the involvement of the cerebellum in sub-optimal action and intention decoding is
87 therefore very high.

88 To shed light on the mechanisms of communicative intent, we recruited musicians and matched
89 control participants who evaluated the visual dynamics of short pieces of violin solos with the
90 violinist represented as a point-light display (PLD) following motion capture recordings on an
91 independent group of expert violinists. Communicative intent was materialized by categorizing
92 Piano vs. Forte intentional gestures in these short musical pieces while undergoing continuous
93 brain scans using functional magnetic resonance imaging (fMRI). These short PLD video were
94 manipulated to include both original (unmodified, but only with visual information) and modified
95 PLD segments: these modified segments included 1) a condition with spatially randomized initial
96 positions of points (namely, the “Spatial shuffling” condition) and 2) a condition in which pieces
97 were cropped to keep only the first instants of the segments (namely, the “Temporal cropping”
98 condition). We then compared the performance of musicians and controls over the accurate
99 recognition of the expressive play on both normal and altered versions of the segments during
100 fMRI. We hypothesized a clear and consistent performance advantage of expert musicians over
101 control participants in assessing communicative intent (Piano vs. Forte). Regarding neuroimaging
102 data, we hypothesized enhanced activity in the frontoparietal network and the cerebellum as a
103 function of expertise that could be modulated by interindividual differences. Finally, we predicted

104 a stronger coupling between the prefrontal and premotor cortex as well as between the cerebellum
105 and the frontoparietal network for experts, i.e. musicians.

106

107 **Material and Methods**

108 *Participants*

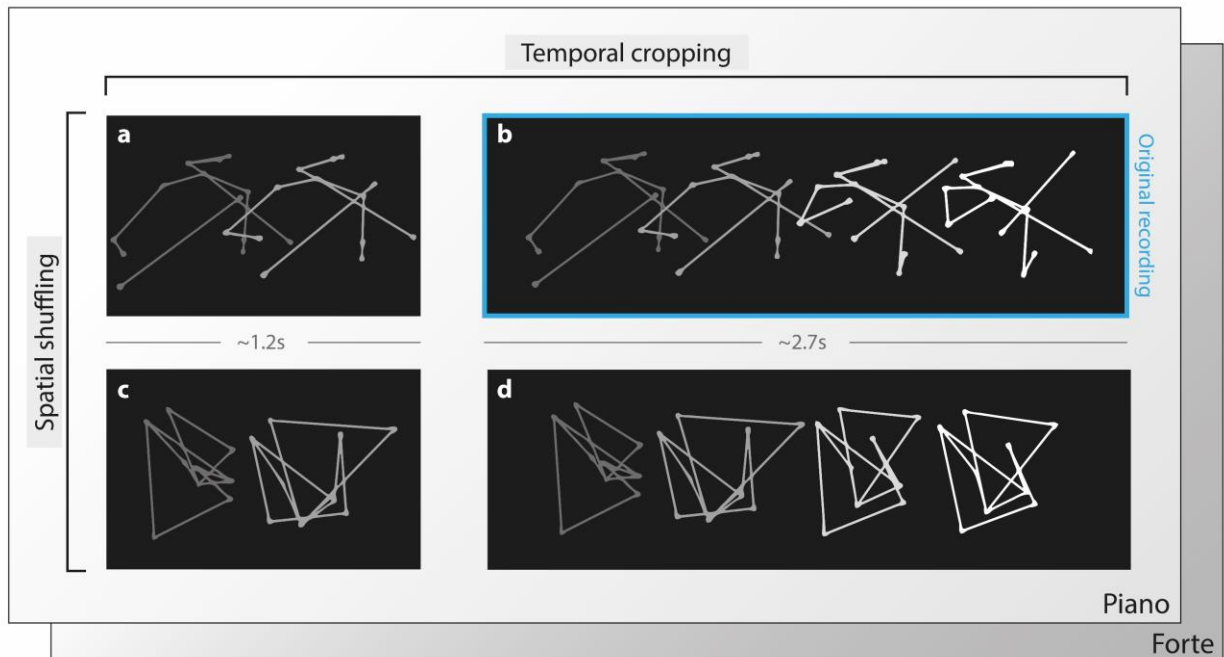
109 Thirty-seven right-handed participants took part in this study but final sample size was 35 (25
110 females, 19 experts, 17 female musicians, M age = 27 ± 7 years). In fact, two participants fell
111 asleep repeatedly during data acquisition and were therefore excluded from the final sample.
112 Participants were composed of a group of expert violinists who received at least an 8-yearlong
113 training at the high musical institution (Geneva School of Music) and a control group of non-
114 musicians. While the number of males and females differed significantly between the two groups
115 ($\chi^2(1, N=35) = 4.83, p = 0.027$) with more woman violinists than male, age did not differ between
116 the two groups ($t(30.26, N = 35) = -0.38, p = 0.7$). However, the variance induced by the sex did
117 not seem to impact our models (Supplementary Table 1 & 2). All participants were naive to the
118 experimental procedure and material and had no known history of psychiatric or neurological
119 incidents. Finally, all participants reported normal hearing abilities and normal or corrected-to-
120 normal vision (contact lenses or MRI-compatible plastic glasses). This study was conducted in
121 compliance with the protocol, the current version of the Declaration of Helsinki, the ICH-GCP or
122 ISO EN 14155 (as far as applicable) as well as all legal and regulatory requirements of the State-
123 wise Ethics Committee of the University Hospital of Geneva.

124 ***Experimental Stimuli: Communicative intent task***

125 The complete set of stimuli consisted of 64 videos. These stimuli were produced using the
126 following procedure. First, we filmed using a motion capture system (Qualisys, time sampling) the
127 first violinist of a professional string quartet during 16 rehearsals of the same musical piece, the
128 Death and the Maiden by Schubert, chosen for it offers a wide variety of writing and expressive
129 styles. For half of the rehearsals, the first violinist played alone, for the remaining half, he played
130 with the other string quartet members. During filming, the musicians were instructed to play
131 expressively as if they were giving a concert performance. The recording sessions took place over
132 two days in a concert hall for it offers naturalistic conditions, which perfectly adapt to the
133 musician's needs and expectations (e.g., quality of the acoustics). After filming, all clips were
134 edited, and the motion capture data were preprocessed to eliminate spurious data through standard
135 filtering process (despiking and smoothing using MATLAB (The Mathworks, Inc., Natick, MA,
136 USA)) in order to produce cleaned point-light displays (PLD) of the performances. The next step
137 was to select specific moments in each performance where the first violinist indicates his intent to
138 the fellow musicians with two communicative intents: piano and forte. To do so, we defined,
139 together with the musicians, these key moments in the music score and edited the corresponding
140 16 short sequences (8 Piano, 8 Forte). Two experimental visual manipulations were then applied
141 on each edited point-light sequence. The first manipulation consisted in segmenting the sequence
142 in two parts: the first part referred to the preparation of the entry, just before the production of the
143 Piano or Forte gesture; 1.2s), the second one referred to the whole sequence (i.e., movement
144 preparation plus entry; 2.7s). We refer to these sequences as Temporally cropped vs. Temporally
145 unmodified. In the temporally cropped sequences, we focused on attack sequence because
146 musicians think that it is crucial to understand the musicians' specific capacity to coordinate with

147 one another. The second manipulation consisted in destroying the anthropomorphic shape of the
148 stimuli through a single spatial scrambling process, which keeps the dynamics of each point but
149 shuffles their relative relationships with others. The final shape, which keeps the same kinetic
150 energy as the original, does not related to any anthropomorphic shape. We refer to these sequences
151 as Spatially shuffled vs. Spatially unmodified. They were designed to highlight musicians' higher
152 processing of dynamic visual information when visual bodily anthropomorphic references are
153 missing.

154 The final excerpts presented to the participants were a combination of all three conditions in a
155 pseudorandom order: the communicative intent, the temporal cropping, and the spatial shuffling.
156 For example, an excerpt could be presenting a piano gesture, temporally cropped, but spatially
157 unmodified while another one could be presenting a forte gesture, with temporal cropping and
158 spatial shuffling. In all sequences, only visual information were used and the accompanying sound
159 tracks were not presented (see an example of each condition in Fig.1).



160

161 **Fig.1:** Overview of the stimuli displayed to the participant. The sequence of expressive movement
162 is displayed through point-light display based on the collected motion capture of a string quartet
163 first violinist. The two temporal segments used in the experiment respectively refer to the
164 preparation (Temporally cropped condition, a) and the preparation plus the entry part (Temporally
165 unmodified condition, b). For each of these temporal conditions, spatial shuffling was also applied
166 as a separate condition (c, d, respectively). After watching the selected sequence, the participants
167 were asked to indicate the perceived communicative intent of the music (forte or piano) by pressing
168 a button.

169

170 ***Experimental procedure: Communicative intent task***

171 Participants, divided in two groups (musician vs control participants) were subjected to a 2
172 (communicative intents: Piano vs. Forte) x 2 (temporal cropping: Temporally cropped vs.
173 Temporally unmodified) x 2 (spatial shuffling: Spatially shuffled vs. Spatially unmodified) within-
174 subject factorial design, resulting in eight experimental conditions (Fig.1). Before scanning,
175 participants were introduced to and familiarized to the experimental task. This included performing
176 two trials from each condition (these stimuli were excluded from the MRI task) while the

177 experimenter monitored performance. During the MRI session, participants watched the point-
178 light display movies of the violinist movements. After each trial, participants had to report whether
179 they thought whether the performance is related to a communicative intents: forte or piano. During
180 debriefing, all participants reported complete comprehension of the experimental task. The
181 experimental procedure relied on a two-alternative-forced-choice task. It aimed at revealing the
182 difference in optimal decision strategies (Gold and Shadlen 2002, Ratcliff and McKoon 2008,
183 Deneve 2012) developed by groups of musicians (task experts) versus control participants (non-
184 experts).

185 ***Behavioral Data Analysis***

186 The statistical software R was used to analyze all behavioral data. We computed generalized linear
187 mixed model (GLMM) to estimate the variance explained by the fixed factors Piano/Forte and
188 Musician/Controls on the percentage of correct responses. GLMM takes advantage of the
189 modelling of random effects to improve precision of the model and allow for the computation of
190 models with non-normal distribution, here a binomial distribution. We test our predictions for the
191 effect of different fixed effect factors including the expertise of the participant, the communicative
192 intents, the spatial shuffling, and the temporal cropping. The random intercept effects encapsulated
193 the variability related to each participant. We used a step-up strategy while building the model to
194 test the different combinations of fixed effects. Based on the marginality principle, we present the
195 highest order interaction effects (Nelder 1977), namely the interaction between the expertise and
196 the other aforementioned experimental conditions. We used chi-square difference tests to
197 investigate the contribution of each variable and their interaction. We report the effect sizes in
198 accordance with the approach of Nakagawa and Schielzeth, implemented in the "MuMIn" R
199 package (Nakagawa and Schielzeth 2013). They created an approach based on two indicators, a

200 marginal and a conditional R2 (respectively, R2m and R2c). R2m is the variance explained by the
201 fixed factors, whereas R2c is the variance explained by the entire model (both fixed and random
202 effects). These two indicators allows comparability with standard methods, while taking into
203 account the variance explained by the random effects. We calculated and reported them for each
204 statistical models.

205 *Neuro-imaging Image Acquisition*

206 Imaging data were acquired using a Siemens Trio 3.0 tesla MRI scanner at the Brain and
207 Behavioral Laboratory (BBL) of the University Medical Center, University of Geneva (Geneva,
208 Switzerland). For each participant and for the run of the experimental task we acquired 290
209 functional T2* -weighted echo planar image volumes (EPIs; slice thickness=3mm, gap=1mm, 36
210 slices, TR=650ms, TE=30ms, flip angle = 90°, matrix=64·64, FOV=200mm). A T1-weighted,
211 magnetization- prepared, rapid-acquisition, gradient echo anatomical scan (slice thickness=1mm,
212 176 slices, TR=2530ms, TE=3.31ms, flip angle = 7°, matrix=256·256, FOV=256mm) was also
213 acquired. Therefore, for each participant we acquired 290 volumes of 36 slices for a total of 10'440
214 slices. The grand total for all participants was 10'150 volumes and 365'400 slices.

215 *Neuro-imaging Data Analysis*

216 Functional data were analyzed using Statistical Parametric Mapping version 12
217 (<https://www.fil.ion.ucl.ac.uk/spm>) operating in MATLAB (The Mathworks, Inc., Natick, MA,
218 USA). Preprocessing steps included realignment to the first volume of the time-series to correct
219 for head motion; slice-timing; normalization to the Montreal Neurological Institute (MNI)
220 template (resampled at 3 x 3 x 3 mm) and eventually spatial smoothing with an isotropic Gaussian
221 kernel of 8 mm full width at half-maximum. A high-pass filter of 128s was used to remove low
222 frequency components. Then, a general linear model (first-level analysis) was defined for each

223 participant separately (within-subject statistics). For the experimental task, correctly-evaluated
224 trials were modeled by specific boxcar functions defined by the duration of the video stimuli
225 spanning stimulus onset to offset and convolved with the canonical hemodynamic response
226 function. Group-level statistics were then performed using a flexible factorial design to take into
227 account the variance of all conditions and participants. Two different group-level models were
228 computed for the present data: Model 1 included eight conditions (1. Spatially unmodified,
229 Temporally unmodified, and Piano; 2. Spatially unmodified, Temporally unmodified, and Forte;
230 3. Spatially unmodified, Temporally cropped, Piano; 4. Spatially unmodified, Temporally
231 cropped, Forte; 5. Spatially shuffled, Temporally unmodified, Piano; 6. Spatially shuffled,
232 Temporally unmodified, and Forte; 7. Spatially shuffled, Temporally cropped, and Piano; 8.
233 Spatially shuffled, Temporally cropped, and Forte) and two groups (Musician; Control) with no
234 covariates [Group X Conditions] while Model 2 included task performance as a group-level
235 covariate of interest interacting with the Conditions factor [Performance X Conditions]. Both
236 models additionally included a mandatory “participant factor” that allows inter-subject variability
237 calculation. For both group-level models, specification of independence was set to true for the
238 Participant and Group factors while it was set to false for the other factor conditions. Regarding
239 variance estimation, it was set to unequal for all factors including Group, as homoscedasticity
240 criteria can usually not be met with fMRI data (default setting in SPM12). For both models, group-
241 level results were voxel-wise thresholded in SPM12 using corrected statistics with $p < .05$ False
242 Discovery Rate (FDR) and an arbitrary cluster extent threshold of $k > 10$ voxels. For all analyses,
243 regions with significant activation enhancement were labeled based on probabilistic
244 cytoarchitectonic atlases (Automated Anatomical Labelling atlas (Tzourio-Mazoyer, Landeau et
245 al. 2002), Cerebellum atlas (Diedrichsen, Balsters et al. 2009, Diedrichsen, Maderwald et al.

246 2011)) and rendered on semi-inflated brains of the CONN toolbox
247 (<http://www.nitrc.org/projects/conn>), see Fig.2.

248 *Model 1: Conditions Training group-level statistics*

249 For this first model, regressors were created for each experimental condition and for each
250 participant (N=35), leading to a first-level design matrix including 16 regressors in total among
251 which 8 regressors of interest (Conditions, see above) and 8 regressors of no interest (Incorrect
252 trials, the six motion parameters and the constant term). Each regressor of interest was used to
253 compute main effect contrast vectors that were then taken to a second-level, group analysis using
254 the flexible factorial design specification that we will detail here. Group-level analysis included
255 the following factors: Conditions (see above) and Group. The Conditions factor was used to
256 compare the musicians to the control participants regarding their ability to assess the
257 communicative intent of the stimuli, whether spatially shuffled and/or temporally cropped. The
258 following contrasts were hence computed using the above factorial architecture of the data: [piano
259 > forte * musicians > controls], [temporally cropped > temporally unmodified *Musician>Control]
260 and [spatially shuffled>spatially unmodified*Musician>Control] (see Fig.2).

261 *Model 2: Conditions Training group-level statistics with task performance as second-level*
262 *covariate*

263 The second model used the exact same settings and factorial structure as Model 1 in addition to a
264 group-level covariate taking into account task performance for each participant (percentage of hits
265 during the experimental task). This covariate was set to interact with the Conditions factor.
266 Therefore, Model 2 included the following factorial structure: Conditions*Task performance. This
267 model was used to constrain our statistical results and observe the way some brain regions may be
268 sensitive to task performance in Musicians as opposed to Non-musicians participants for the

269 following contrasts : [piano > forte * performance], [temporally cropped > temporally unmodified
270 * performance] and [spatially shuffled > spatially unmodified * performance]. Results from this
271 second model were overlaid in green-to-blue in Fig.2.

272 *Functional connectivity analyses*

273 Functional connectivity analyses were carried out using the CONN toolbox v18.a (Whitfield-
274 Gabrieli and Nieto-Castanon 2012). Spurious sources of noise were estimated and removed using
275 the automated toolbox preprocessing algorithm, and the residual BOLD time-series was band-pass
276 filtered using a low frequency window ($0.008 < f < 0.09$ Hz). Correlation maps were then created
277 for each condition of interest by taking the residual BOLD time-course for each condition from
278 atlas ROIs and computing bivariate Pearson's correlation coefficients between the time courses of
279 each voxel of each region of the atlas. These correlations were then converted to normally
280 distributed values using Fisher's transform. Finally, group-level analyses were performed on these
281 Fisher-transformed correlation maps to assess for main effects within-groups and significant
282 connectivity differences between groups for contrasts of interest. Type I error was controlled by
283 the use of seed-level false discovery rate (FDR) correction with $p < .05$ to correct for multiple
284 comparisons.

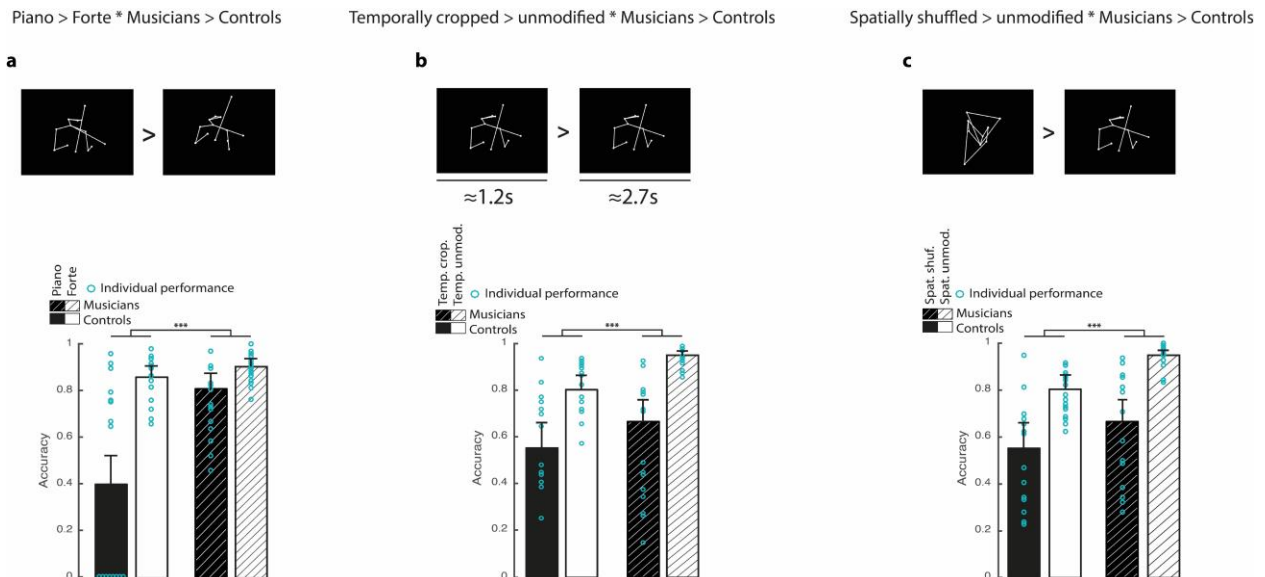
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286 **Results**

287 *Behavior*

288 Behavioral results highlighted a generalized and reliable advantage of musicians over control
289 participants for accurately evaluating piece dynamics as expressing either Piano or Forte
290 communicative intentions in a discriminative task (Fig.2). We tested how the interaction effects of

291 our factors (Group [Musicians>Controls] and Conditions [Forte>Piano, Temporally
 292 cropped>Temporally unmodified, Spatially shuffled>Spatially unmodified]) explained a larger
 293 part of variance for each statistical model compared to models with only the main effects (all
 294 $p<.001$, complete statistics in Supplementary Table 2). More specifically, for each model
 295 computed, we observed that when information is altered (Temporally cropped, Spatially shuffled;
 296 Fig.2**b,c**) or subtler (Piano, Fig.2**a**), the performance of all our participants drops significantly (all
 297 $p<.001$, complete statistics in Supplementary Table 2 & 3). At the group level, musicians
 298 outperformed control participants in assessing communicative intents regardless of the condition
 299 presented (Fig.2**a-c**, all $p<.001$). Finally, we describe a significant interaction effect between group
 300 and conditions for each model (all $p<.001$). No sex differences were observed (Supplementary
 301 Figure 1, Supplementary Table 1).



302

303 **Fig.2:** Experimental stimuli and behavioral results for the impact of expertise on intention
 304 evaluation. **(a)** Example of piano vs. forte Point Light Display (PLD) and averaged performance
 305 and individual points per group for piano vs. forte piece dynamics. **(b)** Example of temporally
 306 cropped vs. temporally unmodified PLD and averaged performance and individual points per
 307 group for piano vs. forte piece dynamics in temporally cropped vs. temporally unmodified

308 sequences. (c) Example of spatially shuffled vs. spatially unmodified PLD and averaged
309 performance and individual points per group for piano vs. forte piece dynamics in spatially
310 shuffled vs. spatially unmodified sequences. Error bars represent 95% confidence interval. [***:
311 $p < .001$, **: $p < .01$, *: $p < .05$; : $p < 0.1$; Spat.: spatial, Temp.: temporal, shuf.: shuffling, crop.:
312 cropping, unmodif.: unmodified]

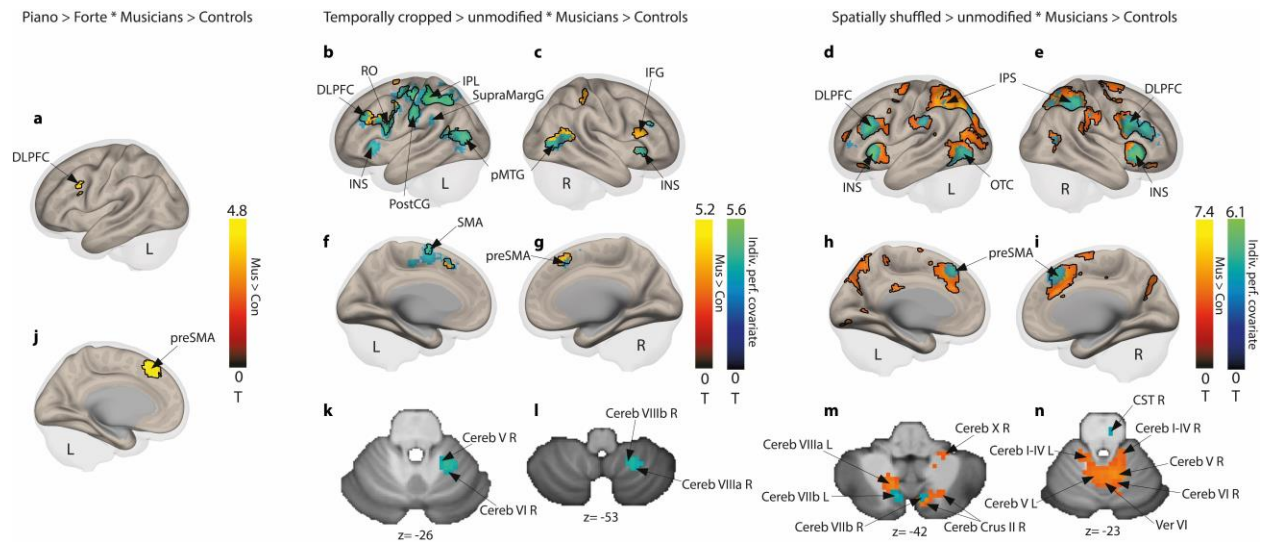
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314 *Neuroimaging*

315 *Wholebrain data*

316 Neuroimaging results focused on the regions with enhanced activations for musicians as compared
317 to control participants, for communicative intent, temporal cropping and spatial shuffling
318 conditions compared to complete excerpts. Analyses focused exclusively on trials in which
319 participants correctly identified the intention depicted in the PLD . When focusing on the excerpts
320 expressing a piano nuance (Piano>Forte*Musician>Control), we observed enhanced activations
321 in the pre supplementary area (preSMA) (MNI coordinates in Supplementary Table 4 & 5) and
322 left dorsolateral prefrontal cortex (DLPFC) (Fig.3a,j, Supplementary Table 4 & 5, Supplementary
323 Figure 2 & 3). When focusing on the temporally cropped excerpts (Temporally
324 cropped>Temporally unmodified*Musician>Control), we observed enhanced activations in the
325 left IPL, cerebellum lobules V, VI, VIIb, and VIII, the bilateral posterior middle temporal gyrus
326 (MTG), and the inferior frontal gyrus (IFG) (Fig.3b,c,f,g,k,l; Supplementary Table 4 & 5,
327 Supplementary Figure 2 & 3). Finally, when we focused on the spatially shuffled excerpts
328 (Spatially shuffled>Spatially unmodified*Musician>Control), we observed enhanced activations
329 in the bilateral intraparietal sulcus (IPS), right preSMA, and bilateral DLPFC extending to the IFG
330 pars opercularis and triangularis, cerebellum (Vermis areas IV,V, Crus II, lobules I-IV, V, VI,
331 VIIb, VIIa, VIIIb, X), and bilateral insula (Fig.3d,e,h,i,m,n; Supplementary Table 4 & 5,
332 Supplementary Figure 2 & 3). To further emphasize these enhanced activations in perspective with

333 the global individual performance of each participant, we also computed another second-level
334 analysis with individual performances of the participants as group-level covariate. Consequently,
335 we could account for brain regions with enhanced activations in relation to general performance
336 (group-level analysis) for our contrasts of interest. These results crucially include inter-individual
337 variability regarding task performance, across groups (continuous, one average value per
338 participant). Rendered in green-to-blue activations (Fig.3**b-e,f-i,k-n**; Supplementary Table 4 & 5,
339 Supplementary Figure 2), global individual performance analysis revealed a strong overlap with
340 abovementioned brain regions for the temporally cropped condition, especially in the IPL, SMA,
341 and in the cerebellum (Temporally cropped>Temporally unmodified*Musician>Control with
342 Individual Performance, Fig.3**b,c,f,g,k,l**; Supplementary Table 4 & 5, Supplementary Figure 2).
343 This result suggests that this network is highly relied on for accurately evaluating the
344 communicative intent of temporally cropped PLD as a function of both performance and expertise
345 and is sensitive to individual differences of performance as well. Such overlap between analyses
346 was smaller for the spatially shuffled excerpts (Spatially shuffled>Spatially
347 unmodified*Musician>Control with Individual Performance), especially in the cerebellum. In fact,
348 results show that portions of the bilateral insula, bilateral preSMA, bilateral DLPFC as well as the
349 right IPS did overlap, emphasizing the strong role of these regions in both performance and
350 expertise. Interestingly, the left IPS showed a much smaller overlap between analyses compared
351 to the right IPS, suggesting an interhemispheric dissociation (Fig.3**d,e,h,i,m,n**) with left IPS
352 activity enhanced massively for correctly evaluated piece dynamics as opposed to the right IPS
353 being modulated by the interindividual differences of performance. Such overlap between analyses
354 was also observed bilaterally for cerebellum area VIIb (Fig.3**m**). Additional brainstem activity was
355 observed in the right corticospinal tract (Fig.3**n**).



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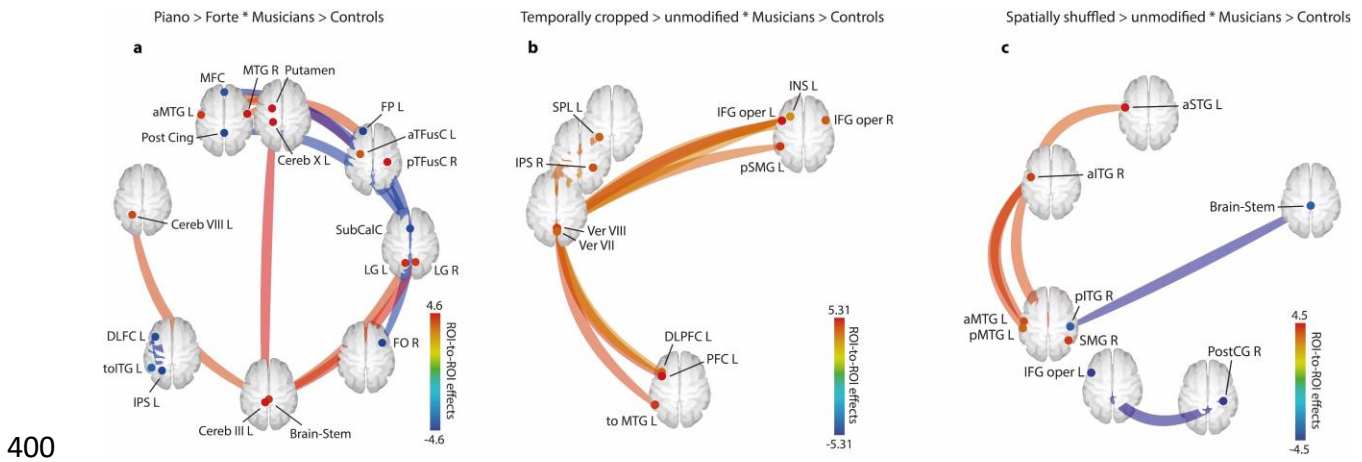
357 **Fig.3:** Neural evidence of communicative intent decoding by musicians and matched controls. (a,j)
 358 Enhanced activity in preSMA and DLPFC for piano vs. forte sequences for musicians vs. control
 359 participants. (b,c,f,g) Enhanced activity for temporally cropped vs. temporally unmodified
 360 sequences for musicians vs. control participants in red-to-yellow in IPL, and with overall task
 361 performance as group-level covariate in blue-to-green in IPL, DLPFC, pMTG, preMSA. and in
 362 subregions of the cerebellum (k,l). (d,e,h,i) Enhanced activity for spatially shuffled vs. spatially
 363 unmodified sequences for musicians vs. control participants in red-to-yellow in IPS, preSMA,
 364 DLPFC, and INS, and with overall task performance as group-level covariate in blue-to-green in
 365 IPS, preSMA, DLPFC, INS, and OTC and in the cerebellum (m,n). The color bars represent the
 366 statistical T values of the contrast. Black outlines delineate regions of the contrasts without the
 367 performance covariate. [Cereb: cerebellum lobule; Cereb Crus: cerebellum crus of ansiform
 368 lobule; CST: corticospinal tract of the brainstem; DLPFC: dorso lateral prefrontal cortex; IFG:
 369 inferior frontal gyrus; INS: insula; IPL: inferior parietal lobule; IPS: inferior parietal sulcus;
 370 lingual gyrus; OTC: occipito-temporal cortex; pMTG: medial temporal gyrus; posterior
 371 part; preSMA: pre supplementary motor area; PostCG: postcentral gyrus; RO: Rolandic
 372 operculum; SupraMargG: supra marginal gyrus; Ver: vermis; L: left; R:right]. Voxel-wise $p < .05$
 373 FDR corrected.

374

375 *Functional connectivity data*

376 Additionally, atlas-based seed-to-seed functional connectivity (FC) analyses were performed to
377 highlight the existence of widespread coupled brain activity targeting frontoparietal and cerebellar
378 regions and related to both communicative intent processing and expertise. These analyses
379 revealed the involvement of numerous regions observed in our wholebrain contrasts of interest in
380 addition to subcortical and cerebellar connectivity (Fig.4). A general effect of expertise across
381 conditions (Musician>Control, main effect of all conditions) revealed a functional coupling
382 between the left IPL and the left post central gyrus (Supplementary Figure 4). Concerning our
383 contrasts of interest, communicative intent and expertise interacted
384 (Piano>Forte*Musician>Control) and lead to both coupled and anti-coupled functional networks
385 (Fig.4a; Supplementary Table 6). Specifically, we observed coupled FC between the bilateral
386 MTG, left putamen, bilateral fusiform cortex, brainstem, and several subregions within the
387 cerebellum, such as cerebellar lobules III, VIII and X of the left hemisphere. Anti-coupled FC was
388 observed between the medial frontal cortex, posterior cingulate gyrus, frontal pole, left DLPFC,
389 and left IPS (see details in Fig.4a; Supplementary Table 6). For temporally cropped excerpts
390 (Temporally cropped>Temporally unmodified*Musician>Control), only coupled FC was
391 observed. More specifically, analyses showed widespread fronto-parieto-cerebellar FC in the
392 bilateral inferior frontal gyrus pars opercularis (IFGop), left DLPFC, left superior parietal lobule
393 (SPL), right IPS and vermis areas VII and VIII (see details in Fig.4b; Supplementary Table 6).
394 The last contrast of interest involving visually shuffled PLD (Spatially shuffled>Spatially
395 unmodified*Musician>Control) highlighted coupled FC between the anterior part of the left
396 inferior, middle and superior temporal gyri (aITG, aMTG and aSTG, respectively), left posterior
397 MTG and right supramarginal gyrus while anti-coupled FC characterized connectivity between the

398 left IFGop, right posterior ITG, posterior cingulate gyrus and brainstem (see details in Fig.4c;
 399 Supplementary Table 6).



400
 401 **Fig.4:** Functional connectivity of communicative intent decoding by musicians and matched
 402 controls. **(a)** Enhanced connectivity for piano vs. forte excerpts for musicians vs. control
 403 participants. **(b)** Enhanced connectivity for temporally cropped vs. unmodified sequences for
 404 musicians vs. control participants. **(c)** Enhanced connectivity for spatially shuffled vs. unmodified
 405 sequences for musicians vs. control participants [aITG: inferior temporal gyrus, anterior
 406 part; aMTG: medial temporal gyrus, anterior part; aSTG: superior temporal gyrus, anterior
 407 part; aTFus: temporal fusiform, anterior part; Cereb: cerebellum lobule; DLPFC: dorso lateral
 408 prefrontal cortex; FO: frontal operculum; FP: frontal pole; IFG oper: inferior frontal gyrus
 409 operculum; INS: insula; IPL: inferior parietal lobule; IPS: inferior parietal sulcus; LG: lingual
 410 gyrus; MFC: medial frontal cortex; MTG: medial temporal gyrus; PFC: prefrontal cortex; pITG:
 411 inferior temporal gyrus, posterior part; pMTG: medial temporal gyrus, posterior part; Post Cing:
 412 posterior cingulate; PostCG: posterior central gyrus; pSMG: superior medial gyrus, posterior
 413 part; pTFusC: temporal fusiform cortex, posterior part; R: right; SMG: superior medial
 414 gyrus; SPL: superior parietal lobule; SubCalC: subcallosal cortex; toITG: inferior temporal gyrus
 415 temporo-occipital part; toMTG: medial temporal gyrus, temporo-occipital part; Ver:
 416 vermis]. Seed-level $p < .05$ FDR corrected.

417

418

419 **Discussion**

420 The present study aimed at a clearer understanding of the interaction between expertise and
421 communicative intent evaluation as a potential proxy for social interactions and coordination.
422 Using point-light displays of violinists as stimuli, we asked experts and non-experts, namely
423 musicians and controls, to evaluate the expressive intent of the plays. Expressive intent could
424 materialize as *piano* or *forte* and either be visually or temporally unmodified or shuffled and
425 cropped, respectively. Our results demonstrate that musicians consistently outperformed control
426 participants, be it for unmodified or altered stimuli. Pre-motor and lateral parietal areas together
427 with dorsolateral prefrontal cortex played a major role in giving a strong hand to experts in addition
428 to numerous cerebellar regions.

429 Behavioral results confirmed and further developed the role of expertise in the perception of
430 others' intent. Musicians were more consistent and accurate in perceiving expressive gestures,
431 indicating close links between perception and action abilities (Wöllner and Cañal-Bruland 2010).
432 Importantly, such result remained true when information was lacking or altered, highlighting
433 behavioral benefits of expertise in action understanding, integration, and prediction based on the
434 short dynamics of the segments and even with altered anthropomorphic information. It stresses the
435 importance for action processing and prediction of combining perceptual information about the
436 observer's own and the others' goal-directed movements (Spunt and Lieberman 2012).

437 Our neuroimaging results revealed a widespread network of brain regions as a function of expertise
438 when decoding or inferring communicative intent, especially in strongly altered perceptual
439 conditions. The advantage of experts for understanding and assessing communicative intent
440 recruited the DLPFC, associated with observation of actions (Rizzolatti and Sinigaglia 2010) and
441 influenced by training and expertise (Moore, Cohen et al. 2006) as well as the preSMA, involved

442 most notably in internally and externally selected actions (Mueller, Brass et al. 2007). Therefore,
443 preSMA and DLPFC seem sufficient to accurately internalize action and extract communicative
444 intent, respectively, in expert participants. These regions would also explain the ability of
445 musicians to integrate the temporal structure of rhythm mediated by working memory (Chen,
446 Penhune et al. 2008). Functional connectivity analyses also revealed that expert participants relied
447 on both coupled and anti-coupled networks to successfully infer communicative intent. The
448 coupled networks include areas involved in intention probability (putamen; Zapparoli, Seghezzi et
449 al. 2018) as well as in movement prediction and motor imagery (cerebellum; Sokolov, Miall et al.
450 2017) and timing encoding (brainstem and cerebellum; Rao, Mayer et al. 2001, Molinari, Leggio
451 et al. 2007). More specifically, a large region of the cerebellum including lobule VIII (and VIIIa)
452 was shown to covary with instrumental expertise, especially for temporal complexity (Chen,
453 Penhune et al. 2008). This result raises the question of whether general or instrument-specific
454 abilities of musicians directly influence cerebellum activity, such important distinction should be
455 addressed in future studies. In a lesion study, lobule III—as well as lobules I, IV and V—was also
456 involved in action observation (Sokolov, Gharabaghi et al. 2010) while lobule IX and to a smaller
457 extent lobule X were repeatedly linked to verbal working memory (Van Overwalle, Baetens et al.
458 2014). As a functionally connected cerebellar network and through connections with the brainstem
459 and basal ganglia, these lobules therefore give strong weight to the cerebellum as a crucial
460 contributing player in action observation, processing, and prediction. On the other hand, anti-
461 coupled activity recruited brain regions known for mental states attributed to moving shapes and
462 memory for intentions (Medial prefrontal cortex and frontal pole, respectively; Blakemore and
463 Decety 2001), action observation (DLPFC: Rizzolatti and Sinigaglia 2010), and biological motion

464 perception (ITG; Blakemore and Decety 2001), as well as attention to intention and its
465 understanding (IPS; Blakemore and Decety 2001).

466 Behavioral advantage of communicative intent assessment in altered perceptual conditions by
467 expert participants relied essentially on several of the abovementioned brain areas with some
468 additions. In temporally cropped sequences, expertise further recruited positively connected
469 regions involved in interoception and motor intention awareness (insula; Craig and Craig 2009),
470 intentional action production (IFGop; Zapparoli, Seghezzi et al. 2018), intention understanding
471 (IPS and IPL; Blakemore and Decety 2001) and temporal processing linked to actions (vermis,
472 especially areas VIII and VIIIa; Rao, Mayer et al. 2001). Communicative intent understanding as
473 a function of expertise in spatially shuffled PLD recruited very similar brain areas when compared
474 to temporal cropping at the wholebrain level, but with larger clusters. This result could be
475 explained by an advantage in assessing complex visual inputs in musicians as compared to non-
476 musicians to evaluate instrumental performance (Griffiths and Reay 2018). Moreover, general task
477 performance as group-level covariate constrained our wholebrain results and showed a difference
478 between left and right IPS, with the latter showing a larger cluster of enhanced activity as a function
479 of task performance in experts vs. controls. This suggests a specific role of the right IPS region
480 related to inter-individual differences in performances and this region was indeed reported to
481 contribute to interpersonal synchronization related to action (Bhat, Hoffman et al. 2017).

482 Additionally, functional connectivity analyses revealed coupled temporal cortices (anterior STG,
483 MTG, ITG; posterior MTG, ITG) and anti-coupled connectivity in the IFGop, brainstem and
484 posterior cingulate cortex. The coupled networks revealed processing of biological motion
485 independent of motor information (superior and middle temporal cortices; Rizzolatti and
486 Sinigaglia 2010) and attribution of intentions to spatially shuffled stimuli (posterior STG; Lee,

487 Gao et al. 2012), regions interestingly known for their feedforward connections to the IPS and IPL
488 (Rizzolatti and Sinigaglia 2010). Anti-coupled functional connectivity stressed again intentional
489 action production and respectively unusual action intention processing (IFGop; Zapparoli,
490 Seghezzi et al. 2018) and movement initiation and control (brainstem (Nandi, Aziz et al. 2002)
491 and cerebellum (Rao, Mayer et al. 2001)).

492 While our data shed new light on intention encoding and decoding and further highlight behavioral
493 contexts favorable to expert participants over non-experts, some limitations should be taken into
494 account. First, sample size could have been larger, although it was difficult to recruit several
495 additional musicians who would fit our inclusion criteria. Second, past studies emphasized
496 structural brain differences between musicians and non-musicians (Gaser and Schlaug 2003) and
497 therefore we could constrain our results even more had we acquired diffusion tensor images, for
498 instance. Third, our stimuli included point-light displays of violinists only, therefore restricting
499 our conclusions regarding other types of expert musicians. Finally, other ways of altering the
500 stimuli, such as modifying rhythmicity or adding sublevels of visual shuffling, could have been
501 employed to further specify the impact of expertise on more fine-grained perceptual alterations
502 and their impact on communicative intent decoding.

503 Taking our behavioral and neuroimaging data as well as study limitations into consideration, our
504 results reveal the strong role of expertise in understanding and predicting action and
505 communicative intentions. Such assertion is especially true in altered perceptual conditions,
506 namely with visually or temporally altering of stimuli, and this advantage of musicians over non-
507 musicians would rely on regions of the frontoparietal network in addition to several areas of the
508 cerebellum, basal ganglia and brainstem. Such neural systems might be at play in numerous other

509 conditions in everyday social interactions as humans are experts in predicting others when they
510 interact with them daily.

511

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521

522 **Data availability statement**

523 The datasets generated during and/or analyzed during the current study are available from the
524 corresponding author on request.

525

526 **Code availability statement**

527 The codes used to analyze the data of the current study are available from the corresponding author
528 on request.

529

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