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1 Emergence of β and γ networks following multisensory
2 training

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9 **Abstract**

Our perceptual reality relies on inferences about the causal structure of the world given by multiple sensory inputs. In ecological settings, multisensory events that cohere in time and space benefit inferential processes: hearing and seeing a speaker enhances speech comprehension, and the acoustic changes of flapping wings naturally pace the motion of a flock of birds. Here, we asked how a few minutes of (multi)sensory training could shape cortical interactions in a subsequent unisensory perceptual task. For this, we investigated oscillatory activity and functional connectivity as a function of individuals' sensory history during training. Human participants performed a visual motion coherence discrimination task while being recorded with magnetoencephalography. Three groups of participants performed the same task with visual stimuli only, while listening to acoustic textures temporally comodulated with the strength of visual motion coherence, or with auditory noise uncorrelated with visual motion. The functional connectivity patterns before and after training were contrasted to resting-state networks to assess the variability of common task-relevant networks, and the emergence of new functional interactions as a function of sensory history. One major finding is the emergence of a large-scale synchronization in the high γ (gamma: 60 – 120Hz) and β (beta: 15 – 30Hz) bands for individuals who underwent comodulated multisensory training. The post-training network involved prefrontal, parietal, and visual cortices. Our results suggest that the integration of evidence and decision-making strategies become more efficient following congruent multisensory training through plasticity in network routing and oscillatory regimes.

10 **Keywords:** multisensory, motion coherence, acoustic texture, oscillations,

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13 1. Introduction

14 The brain can infer the causal structure of its surroundings by integrat-
15 ing multisensory signals originating from the same physical sources, while
16 segregating those originating from different causes [1, 2, 3, 4, 5, 6]. The reso-
17 lution of this causal inference problem weighs in the reliability and the degree
18 of correspondence between multisensory inputs [7, 8, 9]. In ecological set-
19 tings, the temporal comodulation of sensory signals helps perceptual scene
20 analysis: for instance, an interlocutor’s mouth movements are temporally
21 coherent with the envelope of the acoustic speech signals providing the lis-
22 tener with strong binding cues for predictive inferences [10, 11, 12, 13, 14, 9].
23 Temporally congruent signals enhance the detectability [15, 9] and the iden-
24 tification [16, 17] of events, whereas temporally incongruent signals hinder
25 their identification [16, 9]. Herein, we explored the cortical mechanisms by
26 which the internalized temporal structure of coherent multisensory events
27 may subsequently regulate visual (unisensory) processing.

28 Using magnetoencephalography (MEG), we first characterized the im-
29 pact of uni- and multi-sensory training history on human brain activity
30 when participants ($N = 36$) performed a visual motion coherence task (Fig-
31 ure 1.A). The task consisted in reporting the color of the most coherent cloud
32 of dots amongst two intermixed red and green clouds of moving dots. After
33 initially performing the task with visual stimuli only (PRE), participants
34 were split into three experimental groups for short individualized training
35 during which participants were tested on four strengths of visual coherence
36 centered on each individual’s initial discrimination threshold measured in
37 PRE: one group performed the task with visual stimuli only (V), another one
38 with acoustic textures spectro-temporally congruent with the most coherent
39 visual cloud of the two (AV) and a third one, with distracting auditory noise
40 uncorrelated with any of the two visual clouds (CTRL). After performing
41 the training for 20 minutes, all participants were again tested with visual
42 stimuli only (POST). Behaviorally, all participants improved their percep-
43 tual discrimination with the AV group showing the largest benefits and with
44 an initial analysis of the MEG evoked activity suggesting the implication of
45 a large-scale brain network following training [17].

46 With this in mind, we assessed the changes of brain activity between
47 PRE and POST blocks, when all participants performed the unisensory

48 task with visual stimuli only (Figure 1.B). We thus did not directly focus
49 on the feedforward integration of multisensory features or on selective at-
50 tention, both of which could only occur during the AV and CTRL training.
51 Here, we thus do not contrast unisensory vs. multisensory processing *per*
52 *se* but rather focus on the subsequent effects of multisensory integration on
53 a visual only task. Nevertheless, our analytical approach builds on semi-
54 nial work suggesting the implication of distinct neural oscillatory coupling
55 within large-scale networks [18, 19], [20]). The dynamic regimes mediating
56 the binding of multisensory information across brain regions have started
57 being characterized [21, 18, 19, 22], yet little is known regarding the oscilla-
58 tory networks which may actively contribute to supramodal or multisensory
59 object representations [14, 17, 23].

60 Hence, in the present work, we re-analyzed previously collected data and
61 asked how different perceptual histories changed the functional networks hy-
62 pothesized in [17]. First, initial results suggested that selective attention in
63 this task could not be the primary cause of multisensory benefits considering
64 that the contrasts were ran only when visual stimuli were present. Hence,
65 we did not expect changes in the alpha (α) band network to be the major
66 factor in possible effects of perceptual history in this experimental paradigm.
67 Second, all groups showed behavioral improvement in the task irrespective
68 of their perceptual training; we thus expected changes in the bottom-up
69 (perceptual) analysis of sensory inputs, as captured by high frequency anal-
70 ysis (likely gamma activity, γ). Third, as the AV group improved most,
71 we also expected a strong top-down drive in the POST compared to the
72 PRE for this group. As current research assigns an important role to beta
73 (β) activity in the shaping of top-down predictions and decisional values
74 [24, 25, 26, 27, 28], beta networks were expected to be a major differential
75 driver between the three groups.

76 To characterize the different oscillatory networks, we estimated oscilla-
77 tory activity within, and across, experimental groups using univariate time-
78 frequency analyses (Figure 1.C) and large-scale functional connectivity (FC)
79 measures based on the weighted phase lag index (wPLI) [29] (Figure 1.D).
80 We investigated a large network including prefrontal, parietal, occipital and
81 temporal cortices with regions orthogonally selected for their functional rel-
82 evance in the task (cf [17], see Methods). Among regions of interest were
83 the ventro-lateral prefrontal cortex (vlPFC), a massive site of convergence
84 for visual, auditory and multisensory information processing [30, 31], whose
85 neurons selectively respond to the color of visual objects [32] and low-level
86 abstraction [33]; the intra-parietal sulcus (IPS), which plays a central role in
87 multisensory processing [34, 35, 36] and visual motion area (MT), sensitive

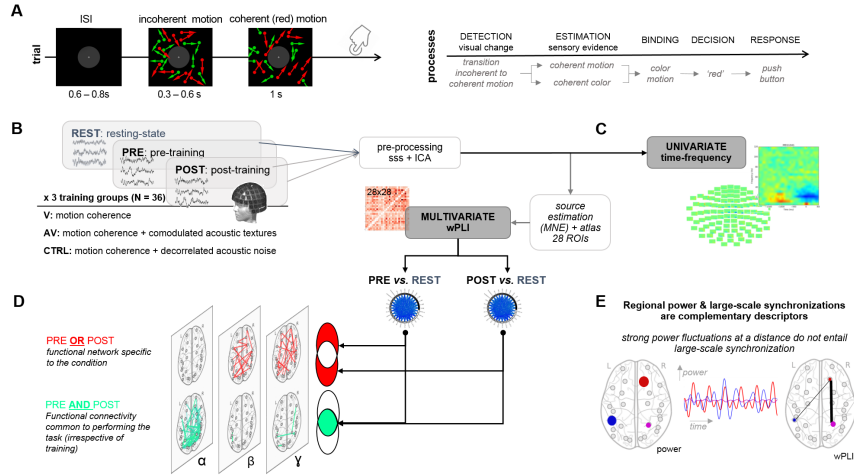


Figure 1: **Experimental procedure and Methods.** (A) Left panel: each trial started with the presentation of a fixation cross lasting 0.6 to 0.8 s followed by the presentation of two intermixed clouds of dots moving incoherently. One cloud was red, the other, green. After a variable delay (0.3–0.6 s) of incoherent motion, one of the clouds (here, red) moved coherently for 1 s while the other remained fully incoherent (here, green). Seven possible strength of motion coherence were tested; the direction and color were randomized across trials. Participants selected which of the red or green cloud was most coherent (videos S1 and S2 in [17]). Right panel: schematic operationalization of the motion coherence discrimination task entailing the integration of motion and color for decision-making. (B) MEG recordings were collected from 36 participants, who performed the task described in (A) in the PRE and POST blocks. Between the PRE and POST, participants were split in three experimental training groups who performed the task visually (V), with acoustic textures congruent with the most coherent cloud of dot (AV), or with auditory noise uncorrelated with the visual stimuli (CTRL). All new analyses were carried out on the PRE and POST blocks, when all participants were performing the visual task described in (A). All participants improved their behavioral scores in POST as compared to PRE blocks: the AV group showed the largest perceptual benefit followed by the V and the CTRL group [17]. Following preprocessing and source estimations, (C) univariate time-frequency analysis and (D) multivariate functional connectivity analyses were performed to provide (E) complementary insights on the oscillatory mechanisms implicated in the effect of (multi)sensory training history in unisensory processing.

88 to perceptual changes in this task [17]. Both IPS and MT are known to inter-
89 act in the β range during perceptual decision-making [37]. We first started
90 by exploring the modulation of local oscillatory activity during visual mo-
91 tion discrimination [38, 25], and followed up with the exploration of changes
92 in functional connectivity as a function of sensory history in training.

93 **2. Materials and methods**

94 *2.1. Participants*

95 36 healthy human participants were recruited for the study (age range:
96 18 to 28 y.o.; mean age: 22.1 ± 2.2 s.d.; 3 groups of 12 participants each: V: 4
97 females; AV: 6 females; AVr: 6 females). All participants were right-handed,
98 had normal hearing and normal or corrected-to-normal vision. Before the ex-
99 periment, all participants provided a written informed consent in accordance
100 with the Declaration of Helsinki (2008) and the local Ethics Committee on
101 Human Research at NeuroSpin (Gif-sur-Yvette, France). Prior to the MEG
102 acquisition, participants were randomly split into 3 experimental groups (V,
103 AV, and CTRL) as detailed below.

104 *2.2. Task*

105 The MEG experiment consisted of interleaved MEG blocks alternating
106 between rest and task. The first resting block occurred prior to any task
107 or training and will be thereafter referred to as REST. REST was used as
108 baseline for functional connectivity analysis. The six task blocks included:
109 a 12 minutes pre-training block (PRE) consisting of the visual coherence
110 discrimination task; a 20 minutes training (4 successive blocks of 5 minutes
111 each) on the same task using purely visual stimuli (V group), congruent
112 audiovisual stimuli (AV group) or incongruent audiovisual stimuli (CTRL
113 group); a 12 minutes post-training block (POST) consisting of the same
114 visual coherence discrimination task as in PRE. Thus, the PRE and POST
115 blocks consisted of the same visual *only* coherence discrimination task for
116 all three experimental groups and using the exact set of visual stimuli. Only
117 the training was either visual or audiovisual. The task requirements in PRE,
118 training, and in POST were otherwise identical in all runs: two clouds of
119 colored dots were intermixed on the screen and participants had to tell
120 which of the red or green cloud of dots was the most coherent. In PRE and
121 POST, participants also rated their confidence on a scale of 1 to 5 after they
122 provided their main response regarding the color of the most coherent cloud
123 of dots.

124 In PRE and POST, the initial and final motion coherence discrimination
125 threshold of each participant was assessed by testing seven strength of visual
126 motion coherence (15%, 25%, 35%, 45%, 55%, 75% and 95%). 28 trials for
127 each strength of visual motion coherence were collected in PRE and in POST
128 for a total of 196 trials in each block. In the training (4 blocks, 5 min each),
129 four visual coherence levels were tested corresponding to $\pm 10\%$ and $\pm 20\%$
130 of an individuals discrimination threshold computed in PRE (see [17] for
131 more details). 28 trials for each strength of visual motion coherence were
132 presented for a total of 112 trials in a given training block. These data were
133 not considered as our main question focused on contrasting brain activity to
134 identical experimental conditions given a different training history. Further
135 experimental details can be found in [17].

136 To localize the visual motion area, we used a passive MEG localizer (120 tri-
137 als) after POST. Participants were presented with a fully incoherent visual
138 cloud lasting 0.5 s and followed by either a highly coherent (95% of coher-
139 ence) or an incoherent (0% of coherence) interval of 1 s (60 trials each).
140 During the localizer, participants were asked to passively view the visual
141 motion stimuli.

142 2.3. Stimuli

143 Visual stimuli consisted of intermixed red and green clouds of dots (Fig-
144 ure 1.A) calibrated to isoluminance using heterochromatic flicker photom-
145 etry on a per individual basis prior to MEG data acquisition. A white
146 fixation cross was at the center of a 4° gray mask disk and dots were pre-
147 sented within an annulus of 4° to 15° of visual angle. Dots had a radius
148 of 0.2° . The motion flow was $16.7 \text{ dots per deg}^2 \times \text{s}$ with a speed of $10^\circ/\text{s}$
149 and its direction confined within an angle of $45^\circ - 90^\circ$ around the azimuth.
150 50% of the trials were upward coherent motion and the remaining 50% of
151 the trials were downward coherent motion. The color and the direction of
152 the most coherent cloud o dots were thus pseudo-randomized across trials
153 and both color and direction were orthogonal to the task goal.

154 The V group underwent training using visual only stimuli. The AV group un-
155 derwent training using temporal comodulated audiovisual associations com-
156 parable to those used in sensory substitution devices such as the vOICe [39]
157 and the EyeMusic [40], with intuitive perceptual associations between sen-
158 sory modalities [41, 42]. Here, we used parametric sounds or acoustic tex-
159 tures (cf [43] with sampling frequency = 44.1 kHz, frequency range: 0.2
160 to 5 kHz) which enabled to pair each visual dot with a linear frequency-
161 modulated acoustic sweep whose slope depended on the direction taken by

162 the visual dot (see [17] for more details). The maximal slope was 16 oc-
163 taves/s corresponding to motion directions of $82.9^\circ - 90^\circ$. A visual dot
164 moving upwards was associated with an upward acoustic ramp, whereas a
165 downward moving dot was associated with a descending acoustic ramp. The
166 duration of a ramp was also identical to the life-time of a visual dot. The
167 CTRL group underwent training with acoustic noise of the same duration
168 and amplitude as the acoustic textures used for the AV group. Unlike acous-
169 tic textures in which the dynamical properties of the fine spectral acoustics
170 were matched with the dynamical properties of the visual dot motion, the
171 acoustic noise used for the CTRL group was fully uncorrelated with the vi-
172 sual coherent motion. This served as a control so that participants trained
173 with audiovisual signals could either hear a sound designed to be temporally
174 predictive of visual coherence (under the temporal comodulation hypothesis,
175 automatic mapping between the spectral coherence in acoustics and visual
176 motion coherence; AV group) or a random acoustic noise (the lack of spec-
177 tral coherence in the acoustics could not map on visual motion coherence
178 and may act as a distractor). In sum, the CTRL group was included to
179 test the specificity of audiovisual associations in this task and the benefit of
180 temporal comodulation in audiovisual training.

181 In the task and for all experimental groups, a given trial started with a
182 variable duration (0.3 to 0.6s) mixing both red and green clouds of dots
183 being fully incoherent (0% of coherent motion). Then, one cloud of dots
184 became more coherent than the other for a duration of one second. In PRE
185 and POST, the coherence level taken by the most coherent cloud was one
186 of seven possible values described in the Task section. During training, the
187 coherence level taken by the most coherent cloud took one of four values
188 described in the Task section. Inter-trials intervals (ITI) varied from 0.6 to
189 0.8s. Samples of the video trials can be experienced (Movies S1 and S2 in
190 [17]).

191 *2.4. MEG and MRI data acquisition*

192 Electromagnetic brain activity was recorded in a magnetically shielded
193 room using a 306 MEG system (Neuromag Elekta LTD, Helsinki). MEG
194 signals were sampled at 2 kHz and band-pass filtered between 0.03-600 Hz.
195 Four head position coils (HPI) were used to measure the head position of par-
196 ticipants before each block; three fiducial markers (nasion and pre-auricular
197 points) were used during digitization as a reference for coregistration of
198 anatomical MRI (aMRI) immediately following MEG acquisition. Elec-
199 trooculograms (EOG) and electrocardiogram (ECG) were recorded simulta-
200 neously with MEG. Five minutes of empty room recordings were acquired

201 before each block for the computation of the noise covariance matrix.
202 The T1 weighted aMRI was recorded using a 3-T Siemens Trio MRI scanner.
203 Parameters of the sequence were: field-of-view: $256 \times 256 \times 176$ mm³ (transver-
204 sal orientation), voxel size: $1.0 \times 1.0 \times 1.1$ mm; acquisition time: 466 s;
205 echo time TE = 2.98 ms, inversion time TI = 900 ms, repetition time
206 TR = 2300 ms and flip angle (FA): 9°. For each participant, cortical recon-
207 struction and volumetric segmentation of T1 weighted aMRI was performed
208 using FreeSurfer¹. Once cortical models were complete, deformable proce-
209 dures were executed using the MNE software [44] to register source estimates
210 of each individual onto the FreeSurfer average brain for group analysis.

211 *2.5. MEG preprocessing*

212 The analysis of the MEG data was carried out using the MNE-python
213 toolbox [45]. After applying an anti-aliasing FIR filter (low-pass cutoff fre-
214 quency at 130 Hz), MEG data were down-sampled to 400 Hz, and prepro-
215 cessed (Figure 1.B) to remove external and internal interferences, in ac-
216 cordance with accepted guidelines for MEG research [46]. Signal Space
217 Separation (SSS) was applied with MaxFilter to remove exogenous artifacts
218 and noisy sensors [47]. Ocular and cardiac artifacts (eye blinks and heart
219 beats) were removed using Independent Component Analysis (ICA) on raw
220 signals. ICA were fitted to raw MEG signals, and sources matching the
221 ECG and EOG were automatically found and removed before signals re-
222 construction following the procedure described in [44]². On average, and
223 over the 36 participants: 39.149.91 components were extracted and 3.250.86
224 components were zeroed out for the REST conditions; 418.79 components
225 were extracted and 4.301.39 components were zeroed out for TASK.

226 *2.6. Univariate time-frequency analysis in sensor space*

227 Briefly, to identify significant changes in oscillatory activity associated
228 with task performance and task improvements, we performed non-parametric
229 cluster-level 1 sample t-tests for each frequency band. Second, in PRE,
230 we performed non-parametric cluster-level paired t-test on time-frequency
231 epochs (single-trial analysis), contrasting high and low motion coherence as
232 well as correct and incorrect trials. Third, we performed non-parametric

¹<http://surfer.nmr.mgh.harvard.edu/>

²https://github.com/mne-tools/mne-python/blob/master/tutorials/plot_artifacts_correction_ica.py

233 cluster-level paired t-tests on time-frequency epochs, contrasting brain ac-
234 tivity to the same stimuli in PRE and POST blocks. The details of each
235 statistical test is provided below.

236 The oscillatory activity in α , β and γ ranges was established using a
237 univariate time-frequency analytical approach in sensor space (Figure 1.C).
238 Oscillatory activity in the post-stimulus period was contrasted with the pre-
239 stimulus period. Both the duration of the initial incoherent portion of stimu-
240 li (300 to 600 ms) (Figure 1.A) and the decision time reflected in reaction
241 times (RTs) were variable. As such, we locked the epochs according to three
242 different events in the sequence of stimuli, each relevant for our ad-hoc work-
243 ing hypotheses and inherent to our experimental design. A first epoching
244 ranged from -600 ms to $+900$ ms *post-incoherent* motion onset thus fully
245 capturing the incoherent portion of the stimuli. The second epoching fo-
246 cused on the brain activity following the onset of motion coherence *per se*
247 and ranged from 0 ms to $+1500$ ms *post-coherent* motion onset. The third
248 epoching focused on the decision-making analysis and was anchored on RTs
249 from -1000 to $+500$ ms around the *button press* (RT). For all three sets
250 of epochs, the 600 ms interval preceding the incoherence onset served as
251 baseline activity.

252 For each set of epochs, a group-level non-parametric spatio-temporal cluster
253 analysis was computed on single-trial time-frequency transforms obtained
254 with Morlet complex-valued wavelets and averaged in each frequency band
255 of interest. The number of cycles in the Morlet wavelet was defined for each
256 frequency (f) as $f/2$. To assess the statistical significance of the obtained
257 clusters we randomly flipped $r = 10^4$ times the sign of the time-frequency
258 transformed data, and our cluster-level correction for multiple comparisons
259 was based on the maximum statistic method [48]. The spatio-temporal
260 clustering was used to identify the sensors showing significant event-related
261 activity in PRE and in POST. One of these sensors was used for subse-
262 quent univariate analyses to ensure that any inference made on a particular
263 frequency band was first determined independently of our ad-hoc working
264 hypothesis motivating the subsequent contrasts. Specifically, time-frequency
265 cluster analyses were used in PRE to perform group-level statistics ($N = 36$,
266 low *vs.* high MC, and correct *vs.* incorrect trials). Moreover, a statistical
267 contrast was performed between POST and PRE blocks, pooling all par-
268 ticipants together ($N = 36$) as well as considering each group separately
269 ($N = 12$). Statistical significance for all these contrasts was assessed using
270 random permutations as discussed above.

271 To evaluate the extent to which oscillatory activity could significantly con-
272 tribute to the observed behavioral measures (performance, RTs, confidence)

273 and stimulus parameters (strength in visual motion coherence), we used a
 274 post-hoc general linear model (GLM) on single trials over the time intervals
 275 found to be significant in our cluster analyses. The non-parametric approach
 276 to GLM based on random permutations was employed to obtain a robust
 277 and unbiased linear regression [49, 50]. The GLM to test the linear regres-
 278 sion between oscillatory power and the strength of visual motion coherence
 279 and different behavioral parameters followed the equation $y = \mathbf{w}^T \mathbf{x} + \epsilon$.
 280 Here, $y \in \mathbb{R}$ was the MEG mean power in a significant cluster of sensors; \mathbf{x}
 281 was the vector $[1, x_1, x_2, \dots, x_{p-1}]^T \in \mathbb{R}^p$ containing p regressor variables.
 282 To find the best fitting model, we tested different combinations of regressors
 283 including motion coherence, reaction times, correctness, confidence ratings
 284 and their interactions. Each regressor was first tested in an independent lin-
 285 ear model, and significant explanatory variables were subsequently tested in
 286 the same model, together with their interactions in order to identify possible
 287 driving effects.

288 \mathbf{w} contained the p regression coefficients including the constant term, and
 289 ϵ was the error term. Iteratively reweighted least squares were used to obtain
 290 an estimate of \mathbf{w} and a value of the Wald statistic w_{ref} . A non-parametric
 291 approach based on random permutations was used to obtain robust and
 292 unbiased significance levels and confidence intervals. Specifically, to test
 293 the significance of each estimated regression coefficient w_i , $r = 10,000$ ran-
 294 dom permutations of the corresponding regressor variable x_i were generated,
 295 yielding a distribution of Wald statistics w^* for each partial regression coef-
 296 ficient under the null hypothesis $H_0 : w_i = 0$. For each estimated coefficient,
 297 the p-value was calculated as the proportion of w^* greater than or equal to
 298 w_{ref} , in absolute value. Permutation inference for the GLM in common neu-
 299 roimaging applications has been proposed as a non-parametric test to relax
 300 assumptions on data distributions [51]. The 36 participants were pooled
 301 together in PRE ($N = 36$) whereas group-specific analyses ($n = 12$) were
 302 performed on POST data to study the effects of (multi)sensory training.
 303 This analysis was carried out for the three sets of epochs locked to the three
 304 different events (incoherence onset, coherence onset, response).

305 2.7. MRI-MEG coregistration and source reconstruction

306 The coregistration of MEG data with the individual anatomical MRIs
 307 (aMRI) was carried out by realigning the digitized fiducial points with the
 308 markers in MRI slices, using MRILAB (Neuromag-Elekta LTD, Helsinki)
 309 and *mne_analyze* tools within MNE ([44]). Individual forward solutions for
 310 all source reconstructions located on the cortical sheet were computed us-
 311 ing a 3-layers boundary element model constrained by the individual aMRI.

312 Cortical surfaces were extracted with FreeSurfer and decimated to about
313 5,120 vertices per hemisphere with 4.9 mm spacing. The forward solu-
314 tion, noise and source covariance matrices were used to calculate the noise-
315 normalized dynamic statistical parametric mapping (dSPM) ([52]) inverse
316 operator (depth = 0.8). The inverse solution was obtained using a loose
317 orientation constraint on the transverse component of the source covariance
318 matrix (loose = 0.4). The estimates of the reconstructed dSPM time series
319 were interpolated onto the FreeSurfer average brain for group-level source
320 space analysis. Only the radial components of the estimated currents were
321 considered for further analysis.

322 After source estimation, we proceeded by summarizing the results into re-
323 gions of interest (ROIs). When selecting the ROIs, we encountered the
324 well-known trade-off between computational tractability and signal-to-noise
325 ratio: Too small ROIs (e.g., voxel-wise analysis) may increase the noise and
326 at the same time exacerbate the multiple comparisons problem, while too
327 large ROIs may suffer from signal cancellation, especially if multiple sources
328 are captured in one ROI. In MEG and EEG source localization, additional
329 peculiarities have to be considered. First, source reconstructed spatial maps
330 are coarser and more blurred than in fMRI, hence potentially arguing in
331 favor of using coarser parcellations. Second, the sign of the reconstructed
332 signals follows the curvature of the cortex which may induce cancellation
333 during averaging. This may distort resulting time-courses even if only one
334 single source is captured by the ROI. In practice, ROIs are therefore often
335 selected according to specific data analysis goals [53, 54, 55] as is generally
336 recommended for many elements of MEG and EEG analysis [56]. In light
337 of these considerations, we chose the rather coarse Desikan-Killiany parcel-
338 lation [57] from FreeSurfer that covers both hemispheres on each individual
339 cortex with 28 ROIs ³. This set of ROIs has already been established as
340 sufficiently sensitive in previous work from our group. For example, it has
341 been shown to capture multisensory processing, perceptual decision mak-
342 ing and motion discrimination [17]. To mitigate the risk of potential signal
343 cancellation, we used a weighted averaging approach, which explicitly took
344 into account the cortical curvature through the surface normals. The re-
345 sulting ROIs covered the frontopolar regions (FP), frontal eye field (FEF),
346 ventro-lateral prefrontal cortex (vlPFC), premotor cortex and supplemen-
347 tary motor region (BA6), primary motor cortex (PMC), intra-parietal sulcus
348 (IPS), inferior temporal cortex (ITC), auditory cortex (AUD), superior tem-

³<https://surfer.nmr.mgh.harvard.edu/fswiki/CorticalParcellation>

349 poral sulcus (aSTS, mSTS and pSTS), middle temporal visual area (MT),
 350 visual area V4, and primary and secondary visual cortices (V1-V2). The
 351 average activities over all the vertices within each of these cortical regions
 352 (labels) were used for the subsequent functional connectivity analysis.

353 2.8. Functional connectivity analysis

354 2.8.1. Adjacency matrices

355 Functional interaction between brain regions was assessed by evaluating
 356 the similarity of brain activity across remote brain areas, namely functional
 357 connectivity (FC) (Figure 1.D). Several studies have compared a subset of
 358 FC methods with respect to their ability to correctly detect the presence of
 359 simulated connectivity schemes in a multivariate data set [58]. The outcomes
 360 showed that the performance of the measures depended both on the char-
 361 acteristics of the dataset and the methods. No single method outperformed
 362 the others in all cases. A practical and reasonable approach thus consisted
 363 in predetermining the FC method according to the plausible ad-hoc working
 364 hypotheses of the experimental study under scrutiny. To characterize FC
 365 in the absence of *a priori* knowledge about its nature and the generating
 366 model, non-parametric measures could first be used.

The notion of phase coupling derives from the study of oscillatory nonlinear dynamical systems. Based on this notion, Phase Lag Index (PLI) [59] aims at quantifying in a statistical sense the phase delay between such systems from experimental data [60] according to the following formula:

$$PLI_{ij} = |\mathbb{E}\{\text{sign}[\Delta\Phi_{ij}(t_k)]\}|, \in [0, 1] \quad (1)$$

367 where $\Delta_{ij}\Phi(t_k) = \Phi_i(t_k) - \Phi_j(t_k)$ quantifies the instantaneous phase differ-
 368 ence between two source reconstructed time series $s_i(t)$ and $s_j(t)$ at time
 369 point $t = t_k$. In Eq. (1), the expectation is typically replaced by the em-
 370 pirical mean over consecutive time points. PLI was shown to be robust
 371 with respect to instantaneous linear mixing effects which may lead to the
 372 detection of spurious functional couplings not caused by brain interactions
 373 (instantaneous linear mixing effects) [59].

Moreover, PLI has the advantage of not being influenced by the magnitude of phase delays. Weighted PLI (wPLI) also solves the problem of discontinuity around zero [29], by using the magnitude of the imaginary part of the cross-spectrum as weights. To measure pairwise interactions between the extracted cortical labels, we used the definition of wPLI in the frequency domain, exploiting the phase of the Fourier-based cross-spectrum $S_{i,j}(f)$ of

two time series $s_i(t)$ and $s_j(t)$:

$$wPLI_{ij}(f) = \frac{|\mathbb{E}\{|\Im\{S_{ij}(f)\}|\text{sign}(\Im\{S_{ij}(f)\})\}|}{\mathbb{E}\{|\Im\{S_{ij}(f)\}|\}}, \in [0, 1] \quad (2)$$

374 where \Im stands for the imaginary part, and the expectations were replaced
 375 by their empirical estimates averaged over epochs. Here, f usually spans a
 376 specific frequency band such as oscillatory regimes (α , β or γ). Therefore,
 377 each FC observation consisted of a symmetric adjacency matrix of size $28 \times$
 378 28 . 10 instances of FC were obtained for each participant and each block
 379 performing a partition of epochs into 10 non-overlapping subsets. In order to
 380 ensure the balance of the number of epochs used to obtain each FC instance
 381 for the different participants, the total number of epochs was set to the
 382 minimum observed across participants.

383 2.8.2. Statistical analysis of FC

384 A widely employed approach to extract the FC network of interest from
 385 an adjacency matrix consists in applying a threshold to the strength of the
 386 estimated connections (Figure 4.A). The threshold is obtained according
 387 to a suitable criterion [61]. The resulting FC patterns correspond to the
 388 strongest connections, which do not necessarily reflect the most significant
 389 differences between experimental conditions. Additionally, while such ap-
 390 proach is particularly suitable for graph-theoretic network analysis, it does
 391 not allow direct quantitative comparisons, owing to the variability of signif-
 392 icant connections.

393 Here, our goal was to separately investigate the FC changes that were task-
 394 dependent (*i.e.* significant changes in the contrast PRE or POST *vs.* REST)
 395 and the cortical interactions subsequent to (multi)sensory training in each
 396 group. Hence, the comparison between FC estimates obtained for the three
 397 experimental groups (V, AV, CTRL) was addressed using a different ap-
 398 proach. First, adjacency matrices were separately averaged over each fre-
 399 quency band of interest, each block (REST, PRE and POST) and each
 400 participant (Figure 4.A). Second, for each frequency band and each experi-
 401 mental group (V, AV and CTRL), the task-relevant networks were extracted
 402 by performing a group-level permutation t-test between FC estimated in
 403 REST and FC estimated in task blocks (PRE, POST) (Figure 4.B). Third,
 404 considering only the subset of task-related connections common to PRE and
 405 POST blocks (*i.e.* the connections significantly changing both in PRE and
 406 POST as compared to REST), the variability driven by the perceptual his-
 407 tory training (POST *vs.* PRE) was evaluated using a permutation t-test
 408 (Figure 4.C, top).

409 All statistical tests were corrected for multiple comparisons using the max-
 410 imum statistic method [48]. Finally, the reorganization of FC in POST was
 411 addressed by highlighting the emergence of new task-relevant FC in POST,
 412 which were not observed in PRE (Figure 4.C, bottom). Importantly, this
 413 approach considered the FC at REST as the baseline for all other FC anal-
 414 yses. This allowed to better disentangle the different FC patterns and their
 415 changes between PRE and POST. Hence, a linear correlation analysis based
 416 on Pearson’s correlation coefficient was performed between the average in-
 417 crease of post-specific interactions from PRE to POST, and the correspond-
 418 ing increase of confidence ratings, for each frequency band and each training
 419 group separately.

420 2.8.3. Topological analysis of FC

A complementary and conventional topological analysis of FC networks
 was also carried out [62] to investigate the degree of interaction between each
 brain region per oscillatory regime. Specifically, the networks with density
 threshold given by $3/N_{rois}$, where N_{rois} is the number of regions [63], were
 first extracted for each participant, each block and each frequency band.
 The weighted node degree D_i , a topological property which is a conceptually
 simple measure of centrality of a node i within a network, was then computed
 for each label in the extracted networks, according to the formula:

$$D_i = \sum_{k=1}^K r_{i,k} \quad (3)$$

421 where K is the number of nodes in the network (cortical labels), and $r_{i,k}$
 422 is the estimated FC value between nodes i and k . Permutation t-test were
 423 performed to evaluate the differences of node degree values between REST
 424 and task blocks (i.e. PRE or POST) as well as between PRE and POST.
 425 Again, the maximum statistic method was used to correct the statistical
 426 tests for multiple comparisons [48].

427 3. Results

428 We first assessed the broad-band oscillatory activity following the pre-
 429 sentation of visual motion stimuli. For this, we combined single-trials in
 430 PRE, which were evoked by all motion coherence levels in all three exper-
 431 imental groups ($N = 36$), and performed a time-frequency analysis of the
 432 MEG responses. A spatio-temporal clustering permutation test corrected
 433 for multiple comparisons (see Experimental Procedures) on post-stimulus

434 time-frequency activity (Figure 2.A, left panel) revealed a significant de-
435 crease of α (alpha: $7 - 14Hz$) and β ($15 - 30Hz$) power ($p < 0.001$, starting
436 0.09 s post-incoherence onset to 0.31 s post-response; 38 sensors) with a sig-
437 nificant increase in the power of broadband high γ ($60 - 120Hz$, $p < 0.001$,
438 starting 0.04 s post-incoherence onset to 0.62 s post-response; 24 sensors)
439 as compared to baseline. The significant clusters observed for both the sus-
440 tained decrease in α power and the increase in high-frequency γ power were
441 mostly localized in the occipital sensors (Figure 2.A, middle panel). This
442 pattern lasted throughout the presentation of visual motion coherence. Con-
443 sistent with the topographical pattern at the scalp level, source estimations
444 of the α and the high γ responses suggested generators located in bilateral
445 visual cortices (Figure 2.A, right panel). This time-frequency pattern during
446 unisensory visual motion coherence was consistent with previously reported
447 time-frequency responses induced by visual motion stimuli [64, 38]. The
448 significant increase in γ band during visual motion coherence was also con-
449 sistent with a previous report of visual motion eliciting a stronger γ response
450 than stationary visual stimuli [65]. We then asked whether the post-stimulus
451 power changes in α , γ , and β were linked to the strength of visual motion
452 coherence in PRE (for all participants) and in POST (as a function of the
453 experimental group), and then proceeded with the exploration of the β band.

454 3.1. α suppression is independent of sensory evidence and training history

455 In PRE, *i.e.*, prior to any training, we used the grand average data ($N =$
456 36) and assessed changes in α power from the onset of motion coherence
457 (Figure 2.A, left panel, white demarcation lines) as a function of the strength
458 in motion coherence (Figure 2.B) using non-parametric statistics and a
459 GLM. We found no significant relationships between α power and motion
460 coherence. The same regression analysis was performed in the POST data,
461 independently for each experimental group ($N = 12$) in order to preserve
462 the distinct training history of each group. Again, we found no significant
463 relationships between α power and motion coherence, and no significant dif-
464 ferences in α power between PRE and POST experimental blocks. Overall,
465 we found no substantial evidence that α power varied as a function of vi-
466 sual motion coherence strength or perceptual history. While the absence of
467 systematic α modulation limits the functional specificity of α in this task,
468 the general decrease of α power notably seen in posterior sensors during the
469 presentation of visual stimuli was generally consistent with the inhibitory
470 gating of visual information [66, 67] thereby a decrease in α power could be
471 taken as an index of selective attention [68].

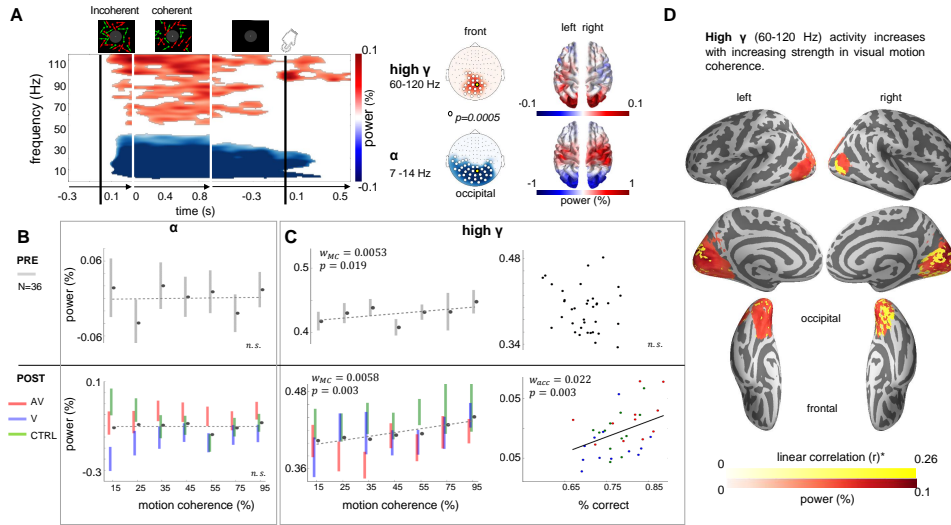


Figure 2: Occipital low-frequency suppression and motion strength (and POST-accuracy) dependent broadband γ increase. (A) Significant occipital time-frequency clusters of low-frequency (< 45 Hz) power suppression and γ (45 – 120 Hz) band increase were found during the presentation of motion coherence (left panel). The time-frequency analysis was locked to the onset of incoherent motion (first black vertical line) and to the coherence motion onset (first white vertical line; the second white vertical line is the offset) as well as response-locked (second black vertical line). The three separate analyses were stacked together to provide the full unfolding of oscillatory activity during the trial. The group average ($N = 36$) time-frequency response of the PRE trials showed a sustained decrease of low-frequency power with an increase in broadband γ power: this is illustrated for one occipital sensor in the obtained spatial clusters (highlighted yellow sensor in the central panel; see also Inline Supp. Mat.A). Source estimates of α (7 – 14 Hz) power and broadband γ revealed the implication of visual and parietal cortices (right panel). (B) In occipital sensors, we found no significant modulations of α power as a function of motion coherence in PRE (top panel) or in POST (bottom panel). Bars are 1 s.e.m. (C) High γ activity increased with motion coherence in PRE (left top panel) and in POST (left bottom). High γ activity also increased with accuracy but only in POST (right bottom). Bars are 1 s.e.m. (D) Source estimates showed a significant linear relationship between high γ and motion coherence in occipital cortices.

472 3.2. Broadband high- γ power increases with the strength in visual motion
473 coherence and post-training performance

474 Before training (PRE, $N = 36$), the occipital broadband high γ follow-
475 ing the presentation of visual motion coherence showed a significant increase
476 with the strength of visual motion coherence ($w_{MC} = 0.0053$, $p < 0.05$; Fig-
477 ure 2.C, left top panel). A similar analysis performed on POST data sepa-
478 rately for each experimental group ($N = 12$) revealed a significant linear
479 relationship between the post-stimulus γ power increase and the increase in
480 stimulus motion coherence. This effect was seen in all three groups irrespec-
481 tive of training history ($w_{MC} = 0.0058$, $p < 0.05$; Figure 2.C, left bottom
482 panel). This observation was consistent with the important role of high γ
483 power during motion discrimination and its modulation by the strength in
484 visual motion ([38]. In PRE, no other effects or interactions were found
485 when adding participants' behavioral correctness (C), reaction times (RT),
486 or confidence ratings (CR) to the GLM (see Experimental Procedures; addi-
487 tional information regarding behavioral outcomes provided in (Figure ??
488 and [17]). To the contrary, in POST, a positive interaction between correct-
489 ness and motion coherence drove the regression analysis on its own ($N = 36$,
490 $w_{MC-C} = 0.0055$, $p < 0.005$). In fact, irrespective of training history, the
491 interaction between the strength of motion coherence and participants' per-
492 formance explained the linear relationship between participants' correctness
493 and occipital broadband high γ power ($w_{C_{tot}} = w_{C:MC} = 0.0055 \times MC$,
494 $p < 0.005$; see Figure 2.C, right panels). Subsequent source estimations
495 (see Experimental Procedures) suggested that the increased modulation of
496 high γ band activity likely originated in visual cortices (Figure 2.D). This
497 observation was in general agreement with previous findings linking local γ
498 band activity to the encoding of sensory evidence [69] during a visual mo-
499 tion discrimination task [38, 25], and suggested that irrespective of sensory
500 history in training, the reliability of visual sensory evidence contributed to
501 successful task performance.

502 In addition to the post-stimulus α and γ effects found in PRE ($N = 36$),
503 we also observed two significant β clusters (15–30Hz) partially overlapping
504 over the frontal sensors during the presentation of coherent motion: a bilat-
505 eral early increase in β band power ($p < 0.005$, from 0.26 s pre-coherence
506 onset to 0.65 s post-coherence onset, 40 sensors) was subsequently followed
507 by a significant decrease ($p < 0.005$, 21 sensors) over the left hemispheric
508 sensors. The decrease in β band power started around 0.57 s following the
509 onset of visual motion coherence (Figure 3.A). The same analysis performed
510 on POST data ($N = 36$) showed, overall, that the decrease in β power was
511 left-lateralized and occurred more strongly over left frontal sensors. In what

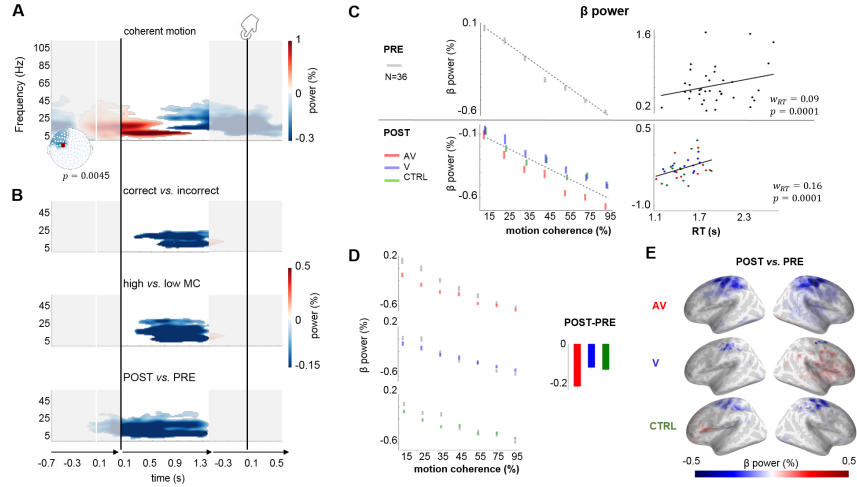


Figure 3: The modulations of β power activity indicate a gain in efficiency. (A) Group average ($N = 36$) time-frequency maps during the PRE block. The analysis was separately performed on trials locked to the incoherent stimulus onset (white vertical line), locked to the coherent motion (first black vertical line) and locked to the response (second black vertical line). All three analyses were stacked for illustration and provided for a left hemispheric sensor (red dot on left topographic map). Time-frequency permutation clustering statistics revealed two β (15 – 30 Hz) components partially overlapping over frontal sensors (topography and represented sensor reported on the bottom right corner) during the presentation of the coherent dot motion: a significant bilateral early increase of β power (red) was followed by a significant decrease solely over the left hemispheric sensors. (B) Statistical contrasts tested the changes in β power between correct *vs.* incorrect trials (top panel), high *vs.* low motion coherence trials (middle panel) and POST *vs.* PRE trials (lower panel). All three contrasts revealed a stronger decrease of β power. See also Inline Supp. Mat.B (C) Consistent with contrasts in (B), β power linearly decreased with increasing motion coherence in PRE and in POST (left top and bottom, respectively) but linearly increased with RT in PRE and POST (right top and bottom, respectively). (D) The AV group showed the strongest β power decrease from PRE (gray) to POST (red) for all strengths of visual motion coherence (left panel). Bars are 1 s.e.m. Thus, during motion coherence stimuli the strongest overall β power decrease from PRE to POST was observed for the AV group (histogram on the right). Source estimates of β power showed a significant decrease in POST as compared to PRE over (E) the motor and parietal cortices. This effect was strongest for the AV group.

512 follows, we thus further investigate changes in β power.

513

514 3.3. Distinct β power effects

515 In a first working hypothesis, we considered prior work showing that changes
516 in β power contribute to perceptual decision-making [37, 70], also that motor
517 β power can be modulated by attention when anticipating motion coherence
518 onset [71] and may index functional inhibition during perceptual discrimi-
519 nation tasks engaging different sensory modalities [72, 73]. To test whether
520 these affected the observed the significant β power suppression in our study,
521 we performed cluster permutations on time-frequency data locked to the
522 onset of motion coherence, and devised three contrasts of interest (Figure
523 3.B): correct *vs.* incorrect trials in PRE as in [37] (top panel), high *vs.* low
524 motion coherence in PRE (middle panel) and PRE *vs.* POST trials (bottom
525 panel). In all three contrasts, we found a significant decrease of β power so
526 that the *a priori* easiest trials yielded a larger suppression of β power com-
527 pared to the more difficult trials. Specifically, we found a systematic late
528 decrease of β power in the correct *vs.* incorrect trials ($p < 0.05$, starting 0.28
529 s post-coherence onset; Figure 3.B, top) and in the high *vs.* low motion co-
530 herence contrast ($p < 0.01$, starting 0.22 s post-coherence onset; Figure 3.B,
531 middle). A similar, yet longer-lasting, left-lateralized frontal β effect was
532 found in the POST *vs.* PRE contrasts ($p < 0.01$, 0.08 s pre-stimulus onset;
533 Figure 3.B, bottom).

534 As the decrease in β power was found locked to the coherence onset but
535 late in the trial – i.e. just before participants’ responses –, it may have re-
536 flected the seminal β suppression preceding movement onset [74] seen when
537 locking epochs to the individuals’ reaction times (RT) (Figure 3.A, second
538 black line). To test for the possibility that the observed β suppression re-
539 flected β event-related desynchronization shaped by motor readiness and
540 action execution [75, 76], we thus locked the trials to participants’ RT and
541 tested the same contrasts as those performed previously on the trials locked
542 to the onset of motion coherence (*i.e.*, correct *vs.* incorrect in PRE data,
543 high *vs.* low motion coherence in PRE data and PRE *vs.* POST). The cor-
544 rect *vs.* incorrect, and the high *vs.* low motion coherence response-locked
545 contrasts did not reveal a decrease but, instead, a small but significant in-
546 crease ($p < 0.05$ starting around 0.6 s before movement onset) of β power
547 before movement preparation. This pattern was only detected when lock-
548 ing the data to the RT (Figure 3.B first two rows on the right) and was
549 distributed over the posterior and frontal sensors. This effect appeared to
550 converge with previous observations [25], in which β power was suggested to

551 mediate stages of decision-making linking sensory evidence encoding with
552 choice-related action execution. We did not observe significant differences
553 when contrasting the PRE and POST activity for this effect (Figure 3.B
554 third row on the right), and thus did not pursue the analysis of this specific
555 effect which had been previously investigated in details [25]. Importantly
556 however, this response-locked β activity did not seem to be shaped by sen-
557 sory history in training, and the changes in β power locked to the onset of
558 visual motion coherence (Figure 3.A and Figure 3.B) were thus considered
559 distinct from the seminal response-locked effect.

560 *3.4. β power is sensitive to integrated evidence during decision-making*

561 Considering that the modulations of β power suppression were not specific
562 to the presentation of visual motion coherence, but rather also sensitive to
563 the correctness and the type of training participants underwent, we tested
564 whether, in the absence of a task, the same β power decrease could be seen.
565 For this, we used the localizer data during which participants passively at-
566 tended the coherent motion stimuli in the absence of a task. We contrasted
567 brain responses elicited by the presentation of coherent motion with those
568 obtained in response to the incoherent motion. We found no significant β
569 power changes in this contrast, suggesting that being engaged in the dis-
570 crimination task was necessary to observe the β suppression effects.

571 We then performed a separate regression analysis (GLM) on the PRE ($N =$
572 36) and the POST data (independently for each experimental group, $N =$
573 12) (Figure 3.C, top and bottom panels, respectively). We used the strength
574 of motion coherence and three behavioral variables (correctness, RT, confi-
575 dence ratings) as regressors. With this approach, we assessed which of the
576 stimulus motion coherence or of the three behavioral outcomes, contributed
577 most to the variance of the observed modulation in β power. We found that
578 β power significantly decreased with increasing strength in motion coher-
579 ence in PRE ($N = 36$, $w = -0.08$, $p < 0.001$), (Figure 3.C, left top panel).
580 We also found a significant positive interaction between motion coherence
581 and RT ($N = 36$, $w = 0.02$, $p < 0.001$; (Figure 3.C, right top panel)): in
582 other words, for a given strength of visual motion coherence, we observed a
583 decrease of β power with faster RT. Altogether, we thus observed that the
584 strongest visual motion coherence and the fastest RT showed the lowest β
585 power.

586 We then applied the same regression analysis on POST data separately for
587 the three experimental groups ($N = 12$). To make the group-specific re-
588 sults comparable, β power from PRE data were separately subtracted from
589 each individual group's POST data. This analysis revealed a decrease in

590 the slope of the regression between β power and the strength of visual mo-
591 tion coherence in all three experimental groups (Figure 3.C, bottom left).
592 This was consistent with the fact that all participants improved their perfor-
593 mance after training with increased accuracy, decreased RT, and increased
594 confidence rating [17]. Similar to the PRE effects, we found a positive in-
595 teraction between the strength of visual motion coherence and RT with β
596 power (Figure 3.C, bottom right). Crucially, an overall decrease of β power
597 from PRE to POST was consistently observed for all levels of visual motion
598 coherence in the AV group as compared to the V and the CTRL groups (Fig-
599 ure 3.D). That motion coherence and RT were the main contributors to the
600 β power variability was consistent with the observation that all experimen-
601 tal groups were faster in POST as compared to PRE. Interestingly however,
602 that the AV group displayed the largest decrease of β power overall after
603 training was also consistent with its overall better performance compared
604 to the other groups (and not with a faster response as the RT were com-
605 parable across groups, [17]). In other words, each group showed an overall
606 decrease of β power as a function of the strength of visual motion coherence,
607 which may indicate an overall gain in stimulus processing efficiency as the
608 regression slopes across groups were comparable (Figure 3.D, left panel).
609 Additionally, this decrease was shifted down for the AV group as indicated
610 by the histogram in Figure 3.D, which shows the overall difference (mean
611 and s.e.m. over subjects) of β power between POST and PRE for each
612 group, separately. Finally, the performance on the task showed a significant
613 correlation with β power but only when using an independent linear regres-
614 sion model, suggesting that motion coherence and RT contributed most to
615 the β power effects, which in turn affected performance.

616 To sum up our observations on β power locked to the onset of visual motion
617 coherence: the task-related decrease in β power over the frontal sensors got
618 generally stronger with integrated evidence to perform the task. Addition-
619 ally, congruent multisensory training (AV) induced a larger (POST-PRE)
620 decrease of β power than other unisensory (V) or conflicting audiovisual
621 (CTRL) trainings. Consistent with the sensor data, the POST *vs.* PRE sta-
622 tistical contrasts of source estimates showed a strong β power decrease over
623 parieto-central regions especially for the AV group; this decrease was also
624 observed in the V and in the CTRL groups to a smaller extent (Figure 3.E).
625 The observed β power suppression during motion coherence discrimination
626 converges with previous literature reporting a central role of β power during
627 perceptual decision making tasks [77, 37, 70].

628 As interim summary for the univariate oscillatory analysis, we observed
629 that α and broadband γ responses during the presentation of visual coher-

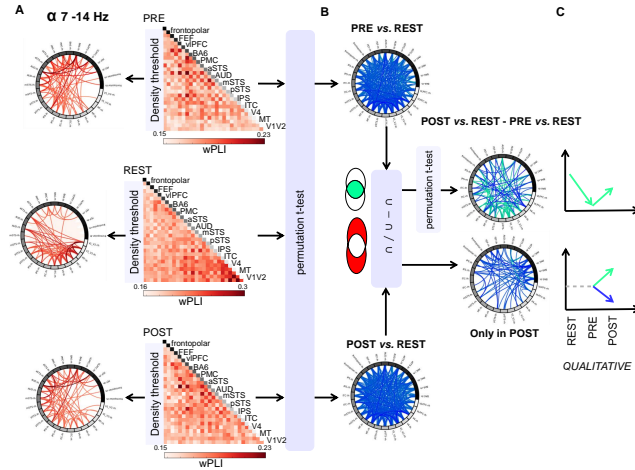


Figure 4: **Overview of statistical contrasts performed to extract functional oscillatory networks.** (A) Functional connectivity (FC) estimates during the presentation of coherent motion, in PRE and in POST, contrasted with resting-state FC patterns (REST). For illustration, we report the full and thresholded α oscillatory networks separately for PRE, REST and POST (top to bottom panels, respectively). Statistical contrasts were based on non-parametric permutation t-tests and performed on the 28 cortical regions. (B) Pairwise phase couplings were contrasted to show significant differences of weighted Phase Lag Index (wPLI) values characterizing the task-related FC network (PRE *vs.* REST and POST *vs.* REST). (C) The FC patterns computed in (B) were compared to assess the variability of the task-related FC in PRE and in POST, as well as to characterize the appearance of new connectivity patterns in POST. FP: frontopolar; FEF: frontal eye field; vLPFC: ventro-lateral prefrontal cortex; PMC: primary motor cortex; BA6: supplementary motor cortex; IPS: intra-parietal sulcus; ITC: inferior temporal cortex; AUD: auditory cortex; aSTS: anterior superior temporal sulcus; mSTS: middle STS; pSTS: posterior STS; MT: middle temporal visual motion area; V4: visual area 4; V1-V2: primary and secondary visual cortices.

630 ent motion were not significantly affected by training history, in contrast to
 631 β oscillatory activity seemingly affected by the degree of integrated evidence
 632 during training. β oscillations may play an important role in (multi)sensory
 633 perceptual discrimination consistent with its role in mediating interactions
 634 across distant structures during perceptual decision-making [25]. To disen-
 635 tangle the possible networks mediating these effects, we turned to multivari-
 636 ate functional connectivity (FC) analysis and investigated whether medium-
 637 and long-range interactions between cortical regions could provide comple-
 638 mentary insights on the specificity of oscillatory regimes as a function of
 639 sensory history in training (Figure 1.E).

640 3.5. *Task-related network synchronization during visual coherent motion dis-*
641 *crimination*

642 To characterize the functional connectivity (FC) induced by (multi)sen-
643 sory training in the different oscillatory regimes, we estimated the PRE
644 and POST activity during the presentation of motion coherence (i.e., ex-
645 cluding the initial incoherence interval of the stimuli) using 28 cortical re-
646 gions (ROIs; Figure 4.A). Hence, the bivariate FC was estimated using the
647 weighted phase-lag index (wPLI) (Figure 4.A) in three main synchroniza-
648 tion regimes (α , β and high γ). ROIs were selected in a manner orthogonal
649 to the contrasts of interest, mainly by performing a source estimation of
650 the grand average data across all experimental conditions ([17], see Meth-
651 ods). All statistical contrasts (Figure 4.B) were based on non-parametric
652 permutation t-tests. Only phase coupling values showing significant differ-
653 ences ($p < 0.01$) were retained in the resulting functional networks herein
654 reported.

655 First, we estimated the functional connectivity pattern during PRE and
656 POST (i.e. during task), which significantly differed from resting-state
657 (PRE *vs.* REST and POST *vs.* REST; Figure 4.B). The subtraction of
658 the resting-state FC from PRE and POST was used as an equivalent of
659 baseline in univariate analyses, and thus was performed to ensure that we
660 characterized the task-relevant FC in both POST and PRE relative to the
661 resting-state network. A direct comparison of POST *vs.* PRE FC without
662 consideration of the initial resting-state FC would be a confounding factor in
663 the interpretation of the results, and could falsely assign significant changes
664 of FC to training effects, when they may in fact simply result from transi-
665 tioning from REST to task. We then considered the task-relevant networks
666 common to PRE and POST (Figure 4.C, top) and explored the effects of
667 training on the changes of cortical interactions and oscillatory couplings.

668 Consistent with the occipital decrease in α band power observed in the uni-
669 variate time-frequency analysis, we found a significant uncoupling of the α
670 oscillatory network in task (both in PRE and in POST) as compared to
671 REST (Figure 5.A, bottom left panel). A relative increase in synchroni-
672 zation modulated by sensory history (Figure 5.A, left column) was also
673 found from PRE to POST, involving a large network comprising occipital,
674 temporal and parietal regions. This relative significant increase in α syn-
675 chronization was observed in the V and in the AV groups, but not in the
676 CTRL group. A similar analysis was performed for the β and the γ oscil-
677 latory regimes. Contrary to the α desynchronization from REST to task
678 (PRE, POST), the β and γ activity showed a strengthening of large-scale

679 coupling between REST and task (PRE, POST) (Figure 5.A, bottom pan-
680 els). The task-related β network present in all groups implicated vIPFC,
681 IPS and MT but showed a significant strengthening from PRE to POST
682 solely in the AV group (5.A, middle column). The significant relative in-
683 crease of task-related FC (POST *vs.* PRE) was also observed for the AV
684 group in the high γ regime implicating the auditory regions and the pSTS.
685 In sum, all three groups displayed a characteristic desynchronization of the
686 α network when engaged in the task, but a higher relative synchronization
687 of the α network in POST as compared to PRE for the AV and V groups.
688 Conversely, an increased synchronization of β and γ networks was found in
689 all three groups from resting-state to task (PRE, POST), but only in the AV
690 group did we see an increase of β and γ synchronization following training.

691 3.6. Brain network analysis and topological differences in regional connec- 692 tivity

693 To investigate the degree of interaction of each brain region, a brain
694 network analysis was carried out using a measure of centrality as index (cf
695 Eq. (3)). This analysis allowed investigating whether specific regions played
696 a central role by assessing the topology of the estimated FC networks based
697 on the number of phase coupling values (connections) over a specific thresh-
698 old for each ROI (*i.e.* node degree, see Experimental Procedures). This
699 quantification revealed distinct patterns for each oscillatory regime (Figure
700 5.B), all corroborating our previous analyses (Figure 5.A). The changes in
701 the node degree within the estimated FC networks were assessed with the
702 statistical contrasts PRE *vs.* REST combining all groups, and POST *vs.*
703 PRE on a per group basis.

704 First, a general task-related decrease of node degree from REST to PRE
705 (Figure 5.B, α blue nodes, top left) was observed in parietal, occipital and
706 temporal regions for the α oscillatory network. This observation was consis-
707 tent with the global α desynchronization during task as compared to REST.
708 The same contrast for the β network (Figure 5.B, β , top middle) showed an
709 increase of node degree in PRE in frontal and parietal regions (red nodes),
710 but a decrease in occipito-temporal regions (blue nodes) as compared to
711 REST networks. This pattern was expected considering that long-range
712 cortical interactions in the β band are known to involve fronto-parietal re-
713 gions during perceptual decision-making [64, 25]. Motor cortices also showed
714 a higher node degree in PRE than in REST, reflecting the information flow
715 during task execution mediated by β oscillatory networks. The same con-
716 trast for the γ network (Figure 5.B, γ , top right) showed mainly a left-
717 lateralized decrease of node degree but an increase in posterior regions.

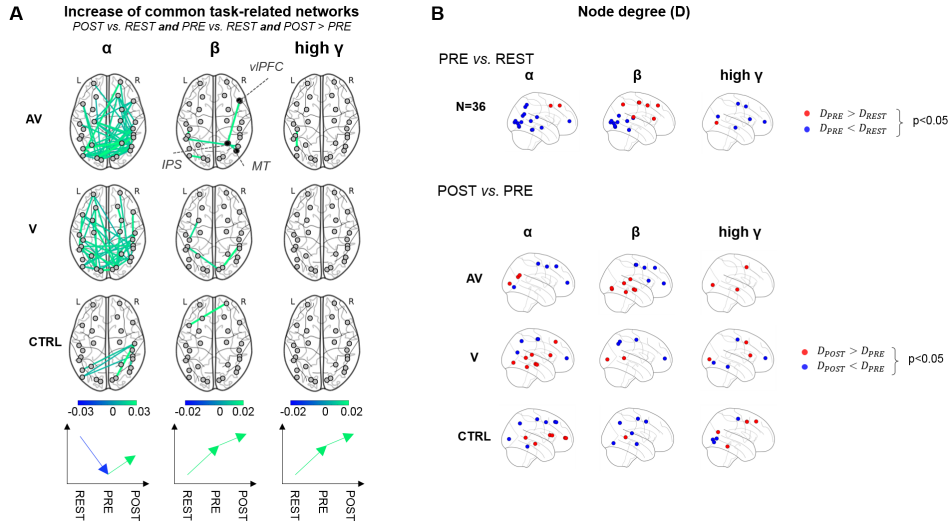


Figure 5: **Fluctuations of the task-related networks in PRE- and POST-training.** (A) Source estimation was performed to obtain cortical activity in 28 regions of interest (see Section 2.7 for details). Pairwise cortical interactions based on wPLI, and averaged in each frequency band of interest, were estimated for each condition (REST, PRE and POST). POST *vs.* PRE contrasts of cortical interactions (lines connecting two regions in the figure) within the task-related FC network common to PRE and POST were separately studied for α (left), β (middle), and γ (right) and for the 3 training groups (AV:top, V: middle; CTRL: bottom). A qualitative description of FC changes (significant increases and decreases of interactions) is provided at the bottom, showing that increases from PRE to POST were relative to REST, with an initial desynchronization of α from REST to task (POST,PRE), and a relative synchronization of β and γ from REST to task (POST,PRE) was found in all three groups. The AV and V groups showed a relative increase of α FC from PRE to POST. Although a significant β phase-coupling in task-related FC network linking IPS, vLPFC and MT was found in all groups, only the AV group showed a significant strengthening of the β network following training. (B) Topological changes in FC networks from REST to PRE (top) and from PRE to POST (bottom). POST *vs.* PRE contrasts were performed for each training group separately. In the β network, the node degree in PRE increased in frontal and parietal regions, whereas it decreased in occipito-temporal regions as compared to REST. The reverse pattern was observed in the β network from PRE to POST in the AV group. See also Inline Supp. Mat.C

718 We then investigated the changes in FC between POST and PRE as
719 a function of training (Figure 5.B, bottom rows). For the AV group, the
720 analysis of β oscillatory networks revealed a clear reversal of the node de-
721 gree pattern in the POST *vs.* PRE contrast as compared to the PRE *vs.*
722 REST contrast: an increase of node degree from PRE to POST was ob-
723 served in occipito-temporal regions (mainly in the right hemisphere), while
724 a decrease was found in frontal regions (mainly in the left hemisphere). The
725 node degree value of β oscillatory networks implicating motor cortices also
726 decreased with training in all three experimental groups. Conversely, the
727 right mSTS region, which showed a decreasing node degree from REST to
728 PRE, now consistently increased from PRE to POST in all three groups.
729 This suggested the implication of the mSTS during actual training, the syn-
730 chronization of which got stronger and more extensive (up to visual regions
731 V4) following training.

732 In the topological analysis of high γ oscillatory networks, frontal regions
733 exhibited opposite dynamics as compared to our observation in the β band.
734 The node degree of the left frontal BA6 region (pre-motor and supplemen-
735 tary motor regions) decreased from REST to PRE, and increased from PRE
736 to POST for the three groups. These results were in line with previous lit-
737 erature [64] showing that high γ and β choice-predictive activities showed
738 opposite changes during perceptual decision-making. In the same study [64],
739 oscillatory activities build up gradually during stimulus evidence encoding
740 to reflect the integration of high γ activity in MT. Here, on the other hand,
741 the node degree in mSTS and MT regions selectively increased after congru-
742 ent multisensory training, consistent with the observed selective implication
743 of these regions in the task [17].

744 3.7. Emergence of β and γ functional networks following training with co- 745 herent audiovisual motion

746 The potential emergence of new functional coupling of cortical brain
747 networks following training (*i.e.*, POST-specific) was addressed on a per
748 group basis (Figure 4.C, bottom). In Figure 6.A, we report cortical in-
749 teractions that were specific to post-training, *i.e.*, phase couplings among
750 brain regions that were not significantly seen in the PRE *vs.* REST contrast
751 but which significantly emerged after training in the POST *vs.* REST con-
752 trast (see Methods). The POST-specific couplings between cortical regions
753 emerged in a training-selective manner in the β band and only for the AV
754 training group (Figure 6.A). This suggested that multisensory training with
755 temporally comodulated audiovisual stimuli could subsequently affect the
756 organization of cortical interactions during a purely visual discrimination

757 task. The observed reorganization notably encompassed long-range interac-
758 tions in POST-specific networks around temporal cortices, consistent with
759 the results of the topological analysis shown in Figure 5.B. Additionally, the
760 emergence of high γ phase-coupling after training was found mainly in the
761 AV and the V training groups, while POST-specific α connectivity emerged
762 in the CTRL group. Intriguingly, the sole behavioral variable relevant to
763 the emergence of the β connectivity was participants' confidence ratings: a
764 significant linear correlation ($N = 12$, $r = 0.72$, $p = 0.011$) was observed
765 so that an increase in POST-specific β band connectivity solely observed
766 in the AV group was commensurate with an increase in these participants'
767 confidence ratings on the task.

768 4. Discussion

769 In this study, we asked how internalized content, established on the basis
770 of temporally coherent audiovisual signals, subsequently benefit the discrim-
771 ination of visual motion coherence. During the presentation of visual motion
772 stimuli, the spectral signatures of brain responses included a decrease in oc-
773 cipital α and frontal β power, and an increase of occipital γ power. While the
774 occipital γ correlated with the strength in visual motion coherence and the
775 post-training performance, α activity showed no functional modulation as
776 a function of stimulus property, sensory evidence, performance or training.
777 Additionally, several contrasts revealed that the local β power captured an
778 integrated aspect of evidence based decision-making as a function of train-
779 ing history. Second, multivariate functional connectivity analysis based on
780 oscillatory phase coupling showed a relative global increase of α (8 – 14 Hz)
781 phase synchronization post-training in the V and AV groups as compared to
782 the CTRL group; this was found in the context of a general decrease of α FC
783 as compared to REST. Third, and importantly, we report the emergence of
784 long-range β (15 – 30 Hz) and γ (60 – 120 Hz) synchronization networks im-
785 plicating temporal, prefrontal, parietal and visual cortices. The emergence
786 of the β and γ networks was essentially observed following congruent (but
787 not incongruent) multisensory training and the β network was indicative
788 of participants' confidence rating in post-training. Despite the limit repre-
789 sented by the number of participants in this study ($N = 36$), altogether, our
790 results suggest that sensory history in training can subsequently strengthen
791 decision-making networks through the regulation of large-scale oscillatory
792 synchronizations. It would thus be beneficial in the future to increase the
793 number of participants for robust estimation of network changes and char-
794 acterization. It would also be interesting to test whether similar pattern of

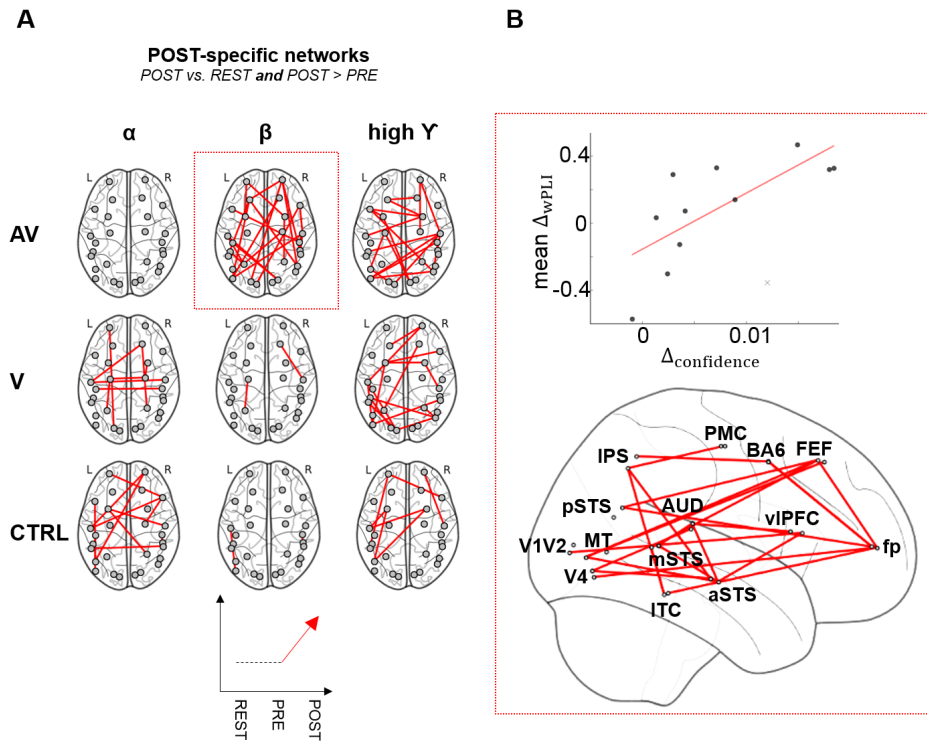


Figure 6: **Emerging oscillatory networks following training.** (A) The phase synchronization based on pairwise wPLI between brain regions (lines connecting two regions in the figure) in α , β , and γ oscillatory regimes was investigated separately as a function of training group. The central finding was the emergence of novel mid- to long-range cortical interactions (POST-specific network, not present during PRE) in the β and γ networks especially in the AV group. The CTRL group trained with incongruent AV stimuli showed the largest synchronization in α . (B) A linear correlation between the average increase of the β band POST-specific interactions from PRE to POST and the increase in participants' confidence ratings was observed solely for the AV group (top panel). The β band POST-specific network was mainly characterized by fronto-occipital and temporo-parietal interactions (bottom panel).

795 beta network can be seen in sensory-impaired populations. The patterns
796 observed in the present study arose from a selected number of cortical re-
797 gions of interest investigated, which represent a second limit to overcome in
798 future research.

799 4.1. Interplay between top-down α and feedforward γ

800 Attending stimuli increases both the local and large-scale synchroniza-
801 tion of rhythmic neuronal activity in the γ band [78, 79, 80, 81, 82]. An in-
802 crease γ power has been reported during binding ([83, 84]), multisensory in-
803 tegration [85, 86] and semantic congruence across sensory modalities [87, 88].
804 Here, we observed an increase in occipital high γ band during the presen-
805 tation of visual motion which, consistent with previous work [89, 38, 25],
806 increased with increasing strength in visual motion coherence. This effect
807 was seen in visual cortices for all three experimental groups, both before and
808 after their respective training. This pattern converged with the notion that
809 γ power provides a spectral index of sensory evidence encoding [38, 25], and
810 here, may further be a significant indicator of participants' correct percep-
811 tual discrimination following training. As expected [79, 90, 91, 66], we also
812 observed a concomitant decrease in occipital α power. Seminal work has
813 suggested that α suppression was stronger for the detection of meaningful
814 objects than for scrambled ones [92], and associated with visuo-spatial [93]
815 and object-based [68] selective attention. An increase in pre-stimulus α
816 power is also known to impair detection [94, 95, 96, 97, 98, 99, 100] and,
817 conversely, an increase in α power is often observed in unattended modal-
818 ities [101, 102, 103]. α oscillations are deemed instrumental for selective
819 attention and the top-down control of information ([104]). The modulation
820 of occipital α was previously shown to correlate with behavioral improve-
821 ments of visual motion discrimination in presence of congruently moving
822 sounds [105]. Here, no systematic changes in the occipital α were found as
823 a function of experimental or behavioral variables, and this was likely due
824 to differences in paradigmatic and methodological approaches: the most
825 notable one being that we did not directly contrast unisensory *vs* multi-
826 sensory stimulations *per se*. Rather, the stable level of occipital α power
827 over experimental conditions parsimoniously indicated that all participants
828 were effectively attentive to the stimuli irrespective of the strength of mo-
829 tion coherence or training history. Recent work has also suggested that γ
830 and α (and β) activity were markers of feedforward and feedback propaga-
831 tion, respectively [106, 81, 107, 108, 109, 110, 111, 112]. Given the pattern
832 of stable α suppression and increased γ power as a function of motion co-
833 herence (and post-training correctness), one possible working hypothesis is

834 that, given a stable and sustained endogenous attentional control exerted in
835 the α range, perceptual training may improve the efficiency with which γ
836 activity propagates sensory evidence up the hierarchy.

837 4.2. *The effect of sensory history in training on α and γ network phase-* 838 *synchronization*

839 In line with the notion that α oscillations actively contribute to the
840 selection of cortical regions during task [113, 114], a decrease of global
841 α phase synchronization was observed from resting-state (REST) to task
842 (PRE, POST) in all groups. Yet, and perhaps more importantly, a relative
843 global increase in α synchronization engaging a parieto-occipital network
844 was observed in post-training as compared to pre-training in both the AV
845 and V groups. This pattern was interestingly not observed in the CTRL
846 group, who was trained with distracting uncorrelated sounds. Rather, the
847 CTRL group (and to some extent, the V group) showed a fronto-parietal α
848 synchronization post-training. The presence of large-scale α synchronization
849 in the CTRL group could be primarily explained by the selective function
850 of α networks, which may help decouple brain regions during conflicting
851 inputs (CTRL). Specifically, at the same time we observed these patterns
852 in the α FC, we also observed a global strengthening of the post-training γ
853 synchronization network. γ -band synchronization in brain networks is fun-
854 damental in cortical communication as phase-coupling across brain regions
855 may promote the transmission of information across large-scale neuronal
856 networks [90, 82, 109]. Global γ synchronization is notably considered to
857 denote “*effective, precise and selective*” communication [82]). In this study,
858 training may have improved long-range γ synchronization with a possible
859 gain in communication efficiency consistent with the general improvement on
860 the task observed in all groups [17]. Sensory history in training affected the
861 general increase of γ phase synchronization so that the group with the largest
862 behavioral improvement, *i.e.* the AV group, also showed the strongest in-
863 crease followed by the V and the CTRL group. Altogether, these results
864 suggest that the type of sensory inputs during a very short training (here a
865 total of 20 minutes) can selectively affect the coordination of brain regions
866 implicated in the endogenous control of information processing.

867 4.3. *β oscillations as integrated evidence*

868 Very recently, β oscillations have been proposed to be markers of inter-
869 nal content [26] and supramodal processing [27]: following learning, rhythms

870 such as β oscillations may regulate the feedback processing of sensory anal-
871 ysis [115] based on abstract categorical representations. These internal net-
872 work dynamics were observed in prefrontal cortices, and operated in the
873 α/β bands [115]. An important finding in our study is the fundamental role
874 of β oscillations, both as local power decrease during sensory encoding and
875 decision-making in all groups, and as an emergent large-scale network fol-
876 lowing congruent multisensory AV training. Several studies have reported
877 an increased coherence or synchronization in the β band associated with
878 multisensory stimulation [116, 117] and, consistent with the implication of
879 the β band in sensorimotor processing [24], β activity was related to par-
880 ticipants response speed in multisensory context. Gleiss and Kayser [118]
881 reported early differences in β band activity but did not find any correlation
882 with behavior. Consistent with another study [117], we found that local
883 modulations of β power were observed when participants were engaged in
884 the task but not during passive viewing, and that RT was the main contrib-
885 utor for this effect: the decrease in local β power was found for contrasts
886 in which evidence-based decisions were most successful (*i.e.*, for strongest
887 as compared to weakest visual motion coherence, for correct as compared
888 to incorrect trials and for post- compared to pre-training trials). Under the
889 working hypothesis that abstract internal content [115, 33] has been learned
890 to drive the processing of incoming sensory information, the strengthening of
891 the large-scale β coupling in the group that has received congruent AV train-
892 ing would further suggest that performing the task with temporally coherent
893 audiovisual events strengthened the ability to predict motion coherence in
894 vision. In other words, the changes in β power and network synchronization
895 may capture endogenous top-down activations of task-relevant (supramodal)
896 cortical representations, which facilitate communication between brain re-
897 gions [119, 25, 26, 27, 28].

898 In this context, recent predictive coding models drawing from audiovisual
899 speech processing [11, 14, 120] and neurophysiological work [112, 28] have
900 pushed forward the notion that prediction errors from one sensory modal-
901 ity to another may be communicated in the γ range, whereas top-down
902 predictions may be mediated by β oscillations [120]. As the emergent β
903 network was solely seen for the AV group in which it was linearly related
904 to confidence rating, we speculate that the hypothesized combined effects of
905 increased communication efficiency in a feedforward γ network, the endoge-
906 nous selective routing in the α network, and the predictive β propagation
907 in the AV group may all contribute to the local selective changes previously
908 reported in the human motion area MT as a change in the neurometric
909 threshold [17]. The notion that internal content (as supramodal or abstract

910 representations) may constrain sensory analysis early on provides additional
911 evidence for the implication of large-scale neural oscillations in integrative
912 and predictive brain functions.

913 *4.4. Limitations*

914 It is perhaps noteworthy that our γ -band results do not necessarily im-
915 ply nor preclude the presence of underlying oscillatory sources. Several
916 studies have cast doubt on the idea that task-related changes or ongoing
917 background activity in γ -band dynamics are consistently due to oscilla-
918 tions [121, 122, 123]. Accordingly, the power spectrum does not always
919 show a distinct peak that could unequivocally index oscillations. Instead
920 broad-band power changes are often observed that may exhibit 1/f scale-free
921 behavior [124] and may be accounted for in terms of short-lived stochastic
922 spiking [125]. We want to emphasize that our study does not possess the
923 requisite statistical power or experimental paradigm to tell apart these con-
924 current interpretations. We, therefore, carefully suggest to view our γ -band
925 findings as neuronal activity in the wider sense, leaving open the precise
926 physiological generative mechanism. Our phase-based analysis in the γ -band
927 may therefore suffer from specificity, and has to be regarded as pragmatic
928 approximation that may get revised in the future upon the availability of
929 more precise computational tools and an extended study-design.

930 *4.5. Conclusion*

931 Taken together, our results support the notion that cortical computa-
932 tions encompass sensory-based processing and that, consistent with the role
933 of prefrontal cortices shifting activity from feedforward inputs to internal
934 dynamics [115], the internal content shaped by multisensory inputs during
935 short training can strengthen the selectivity of large-scale oscillatory net-
936 works for later adaptive purposes.

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