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1 **NeuroReport (2020), in press**

2
3 **Causally Linking Neural Dominance to Perceptual Dominance**
4 **in a Multisensory Conflict**

5
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21 **Running Head:** Neuronal to perceptual dominance

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27 **Abstract**

28 When different senses are in conflict, one sense may dominate the perception of other sense, but it is
29 not known whether the sensory cortex associated with the dominant modality exerts directional
30 influence, at the functional brain level, over the sensory cortex associated with the dominated modality;
31 in short, the link between sensory dominance and neuronal dominance is not established. In a task
32 involving audio-visual conflict, using magnetoencephalography recordings in humans, we first
33 demonstrated that the neuronal dominance – auditory cortex functionally influencing visual cortex –
34 was associated with the sensory dominance – sound qualitatively altering visual perception. Further, we
35 found that pre-stimulus auditory-to-visual connectivity could predict the perceptual outcome on a trial-
36 by-trial basis. Subsequently, we performed an effective connectivity-guided neurofeedback
37 electroencephalography experiment and showed that participants who were briefly trained to increase
38 the neuronal dominance from auditory to visual cortex showed higher sensory, i.e. auditory, dominance
39 during the conflict task immediately after the training. These results shed new light into the interactive
40 neuronal nature of multisensory integration and open up exciting opportunities by enhancing or
41 suppressing targeted mental functions subserved by effective connectivity.

42

43 *Key Words:* multisensory, crossmodal, illusion, brain oscillations, pre-stimulus, connectivity, neuronal
44 causality, neurofeedback

45

46 **Introduction**

47 We continuously encounter with visual and auditory information, processed by distinct sensory cortical
48 areas, which are eventually integrated to produce a conscious behavioural unique response [1, 2].
49 However, when visual and auditory information is incongruent or in conflict, one sensory modality may
50 dominate the other, leading towards a multisensory illusion [3]. A critical question remains whether
51 sensory dominance is linked to neuronal causality, i.e. sensory cortex of the dominant modality would
52 causally influence, at the functional level, the activities of the sensory cortex of the subordinate modality.
53 We tested this specific prediction in the framework of an audio-visual conflict – sound-induced flash
54 illusion [4-6]: a multisensory illusion, when a single flash in the visual periphery is accompanied by
55 two beeps, the single flash is often misperceived as two flashes. Individual differences in proneness to
56 the illusion are reflected in the neurochemical [7] (GABA concentration in superior temporal sulcus),
57 structural [8] (grey matter volume in early visual cortex), and functional excitability [9, 10] (visual
58 event-related responses to sound) differences. However, these findings do not explain the trial-by-trial
59 variability, i.e. observers perceive the illusion sometimes, but not always, even though the physical
60 stimuli remain identical and supra-threshold across trials. Since the auditory information dominates
61 over the visual information for this illusion to occur, neural activity in the auditory cortex is predicted
62 to exert a causal influence on the activity in the visual cortex, not the other way around.

63 We addressed this question by recording MEG signals from healthy humans in the sound-induced flash
64 paradigm (Fig. 1A). We compared the effective connectivity between auditory to visual cortical regions
65 for illusion and non-illusion trials, differing only in terms of the qualitative nature of visual perception,
66 and verified our prediction. Next, to establish a causal mechanism, we performed a separate experiment
67 involving EEG based neurofeedback in which participants were briefly trained to regulate their auditory
68 to visual effective connectivity spontaneously and found that such connectivity-based neurofeedback
69 training significantly increased the probability of auditory stimulus qualitatively altering the visual
70 perception. MEG was used to quantify the trial-by-trial effective connectivity between auditory and
71 visual cortical regions due to its high sensitivity, and EEG was used as a neurofeedback tool to modulate
72 the effective connectivity due to its practicality.

73

74 **Materials and methods**

75 *Ethics statement*

76 All participants provided written informed consent before the experiments and were paid for their
77 participation. The MEG study was approved by the Internal Review Board of National Institute of
78 Advanced Industrial Science and Technology, Osaka, Japan, and the EEG study were approved by the
79 Internal Review Board at California Institute of Technology, Pasadena, USA; both studies were
80 conducted following the Declaration of Helsinki.

81

82 *Participants*

83 For the MEG study, 11 adults (3 females, ages ranging between 22-40 years; mean±S.D. of 30.5±6.88
84 years) participated. For the EEG study, 27 adults (11 females, ages ranging between 22-40 years;
85 mean±S.D. of 27.3±4.43 years) participated. The sample sizes were comparable to previously published
86 related studies [5, 11]. The two sets of participants were completely independent. All participants were
87 healthy, had no history of neurological or psychiatric disorders, and had normal or corrected to normal
88 visual acuity, and normal hearing.

89

90

91 *MEG study: Design, procedure, and materials*

92 We recorded MEG signals with a 122-channel whole-scalp planar-gradiometer (Neuromag 122, Elekta-
93 Neuromag Oy, Helsinki, Finland) in a magnetically shielded room. The instrument measured two
94 orthogonal tangential derivatives of the magnetic field at 61 scalp locations. In the examined bimodal
95 condition, the event trigger was synchronized with the onset of the flash. The participants were seated
96 upright with their heads comfortably resting against the inner wall of the helmet and were instructed to
97 fixate on a cross on the screen, and not to blink during trials.

98

99 The experiment consisted of four conditions: (i) a visual flash, (ii) a flash accompanied by two auditory

100 beeps, (iii) two beeps and no flashes, and (iv) two flashes. The flashing stimulus was a uniform white
101 disk subtending a visual angle of 2° in the periphery at 8.5° eccentricity for a duration of 20 ms. The
102 auditory stimulus consisted of two brief beeps each lasting 10 ms and separated by 50 ms. The sound
103 stimulus (1 kHz frequency at 70 dB SPL) was presented by headphones. In the bimodal condition, the
104 flash onset was 14 ms after the onset of the first beep. There were 80 trials for each condition, and the
105 order of the trials was random. The inter-trial interval was varied randomly between 1500 and 2000 ms.
106 The participant's task was to judge the number of flashes they perceived at the end of each trial in a
107 three-response-category paradigm – zero, one, or two flashes.

108

109 The continuous MEG signals were band-pass filtered at 0.01 - 100 Hz, digitized at 550 Hz and stored
110 for off-line analysis. To remove the contamination due to spurious oscillations (~ 40 Hz) of Helium
111 cylinders, we applied a further band-pass (0.05-30 Hz) Butterworth filter of order 3. The epochs
112 containing eye blinks or excessive movements were excluded based on amplitude criteria. Here, we
113 considered only one experimental condition, a flash accompanied by two beeps that have two possible
114 behavioural outcomes: (i) no-illusion - perceiving one flash, (ii) illusion: perceiving two flashes.

115

116 We used partial directed coherence, PDC [12] to identify the direction of information flow. Multivariate
117 autoregressive models were adaptively estimated using overlapped time-windows (60 ms time-
118 windows with 40 ms overlap) to make the estimated model parameters varying smoothly. The optimal
119 model order was determined by locating the minimum of the Akaike Information Criterion (AIC) [13]
120 across time and was set to 6. Statistical significance of PDC values was determined by independently
121 shuffling the trial order across participants for each sensor. Thus, we obtained PDC values that were
122 due to chance by pooling over participants. We shuffled the data 200 times and used a nonparametric
123 rank test as a qualitative measure of significance. Only for those PDC values that passed this
124 nonparametric test, we expressed significant PDC values in terms of standard deviations of the shuffled
125 distribution to have better visual clarity of the degree of causal interdependence.

126

127 For predicting the perception of one ($\theta = 1$, i.e. no-illusion) or two flashes ($\theta = 2$, i.e. illusion), we
128 applied a Bayesian classifier with a uniform prior probability. Input data for this classifier was the
129 directed influence from the auditory cortex, AC (4 sensors) to the visual cortex, VC (5 sensors) (see
130 Figure 1B). For predicting perceptual outcome on a trial-by-trial basis, we estimated PDC on each trial.
131 Here, we considered bivariate autoregressive models (with optimal AIC model order of 3) and longer
132 (i.e. 100 ms) time-windows to get reliable estimates. The immediate pre-stimulus time-window was -
133 114 ms to -14 ms, and the post-stimulus time-window was 0 to 100 ms.

134 The random variable y represents the classification input data vector of PDC values in alpha and beta
135 bands. Bayes' Theorem gives us the posterior probability of θ given the information that y occurred:

$$136 \quad p(\theta_i|y) \propto p(y|\theta_i)p(\theta_i), \quad i \in \{1,2\}$$

137 where $p(\theta_i)$ is the prior probability of θ_i , which is uniform by design and $p(y|\theta_i)$ is the probability
138 distribution of y , which we estimated by a Gaussian mixture model with two components. The predicted
139 post-stimulus response was subsequently chosen to be the one with maximum probability. We repeated
140 10-fold cross-validation 100 times to assess the performance of the classification accuracy.

141

142 *EEG study: Design, procedure, and materials*

143 Each participant was seated in front of the computer screen. The EGI (Electrical Geodesics Inc., Eugene,
144 OR) cap was used for the EEG recording and analysis. The experiment consists of three sessions: pre-
145 training, neurofeedback training, and post-training sessions. First, in the pre-training session,
146 participants were instructed to answer using a keypad how many flashes they perceived, and they
147 performed 100 trials of sound-induced visual illusion tasks. In the centre of a 15-inch black computer
148 screen, 20x20 mm sized white crosshair (+) was shown across all the trials, and participants were asked
149 to look at the crosshair during all the tasks. On each trial, a 67 mm diameter white circle appeared at
150 the bottom of the screen for 16 ms. The first beep was played 14 ms before the white circle appeared.
151 Then the second beep was randomly played 46 ms after the white circle appeared. Inter-trial interval
152 randomly varied between 1 s to 3 s.

153

154 Next, participants were randomly assigned to one of the two groups: $A \rightarrow V$ and $V \rightarrow A$ training groups.
155 Participants of $A \rightarrow V$ training group were shown a bar graph displaying the real-time processed $A \rightarrow V$
156 connectivity of their brains. They were asked to try to figure out how to increase the height of the bar
157 graph. The participants of $V \rightarrow A$ group were shown the bar graph displaying $V \rightarrow A$ connectivity. In
158 essence, the participants were only instructed to “control” their brain connectivity voluntarily and
159 heighten the bar graph on the computer screen. The neurofeedback training lasted for a brief period of
160 5 min. Subsequently, participants performed the post-training tasks that were the same as they did before
161 the EEG neurofeedback training.

162

163 EEG was recorded at a sampling rate of 1000 Hz using 128-channels EGI cap. The EEG activities at 7
164 channels (T3, T4, T5, T6, O1, O2, and Oz) between 8-12 Hz were used for PDC computation. The
165 impedance of the electrodes was kept below 50 k Ω . Real-time frequency filtering to extract alpha
166 frequency band (8-12 Hz) and the PDC computation were performed. The processing latency was
167 223ms +- 26ms. The detected EEG signal was both recorded for analysis and fed back to the subject
168 forming a feedback loop. Computed connectivity using PDC from auditory (T3, T4, T5, T6) to visual
169 cortical regions (O1, O2, Oz) was represented as the height of the bar graph, and its sign was reversed
170 at the bar graph shown to the control group. While participants tried to heighten the bar graph, their
171 brain connectivity was modulated and in turn, formed the feedback loop.

172

173 **Results**

174 **Experiment 1: MEG study linking neural dominance to perceptual dominance**

175 **Auditory to visual connectivity was associated with the double-flash illusion:** Flash illusion was
176 reported for 62% of trials (i.e. out of 687 trials, participants reported perceiving two flashes on 424
177 trials), while stimulus parameters remained identical with 2 beeps and 1 flash (Fig 1A). We used partial
178 directed coherence [12], a frequency domain representation of Granger’s causality [14], to measure the
179 effective connectivity (i.e. the explicit and directional flow of information) between auditory and visual

180 cortical regions. We focused our analysis in the alpha (8-12 Hz) and the beta (13-21 Hz) band neuronal
181 oscillations after previous studies [11, 15]. With the adaptive multivariate autoregressive modelling
182 approach for short window spectral analysis [13], we determined the connectivity from the nine selected
183 MEG sensors located approximately over the auditory cortex (AC) and visual cortex (VC) (Fig 1B). We
184 observed a robust flow of information from auditory to the visual cortex for the illusion trials in both
185 alpha (Fig 1C) and beta (Fig 1D) oscillations; on the other hand, such directional flow of information
186 from auditory to visual cortex remained mostly non-significant (except around 70 ms after flash-onset).
187 The timings of the peaks of auditory to visual connectivity at 40 to 100 ms [16, 17] and 110 to 170 ms
188 [16] for illusion trials are in close agreement with the reported time-intervals of previous studies on
189 multisensory integration. However, in contrast to earlier findings [16, 17] which compared
190 multisensory to unisensory conditions, we compared two identical multisensory conditions, differing
191 only in the quality of the subjective perception. Therefore, our results establish a clear link between the
192 brain's specific connectivity pattern and conscious awareness. This potentially causal functional
193 influence on the visual cortex by the auditory cortex at such an early stage of information processing
194 may be indicative of direct communication between these two sensory areas at a functional level.

195

196 **Directedness and asymmetrical nature of auditory to visual connectivity:** To validate that these
197 causal modulations were possibly direct at the functional level but not via other multisensory areas, we
198 repeated the connectivity analysis after including sensors from other multisensory regions including
199 parietal, frontal, and temporal cortex in our information flow model (see Figure 2A-B; left panel) while
200 omitting some sensors from AC and VC areas. Results for different model configurations are shown in
201 Figs. 2A, B for alpha and beta band, respectively. Despite the variations in the temporal profiles from
202 AC to VC connectivity across model configurations, we observed that overall the degree of AC to VC
203 was larger and more sustained in the illusion trials than no-illusion trials, thereby confirming our earlier
204 findings. Thus, the reported early AC to VC connectivity was unlikely to be influenced by the higher-
205 order multisensory areas.

206 Next, we inspected the connectivity in the reverse direction, i.e., the influence of the visual

207 cortex onto the auditory cortex. In the flash illusion, sound dominates vision, but not vice versa. Aligned
208 with this inherent nature of the illusion, we found that the information flow from the visual cortex to
209 the auditory cortex was comparable between illusion and non-illusion trials (see Figure S1,
210 Supplemental Digital Content). Therefore, we suggest that the effective connectivity from the AC to the
211 VC, but not the other way round, is crucial to alter the qualitative nature of visual perception in the
212 sound-induced flash illusion.

213

214 **Pre-stimulus auditory to visual connectivity predicting perceptual outcomes:** Given the early nature
215 of the causal interactions, and the recently reported evidence of pre-stimulus brain states shaping post-
216 stimulus responses [18-20], we investigated the immediate pre-stimulus period (100 ms before flash-
217 onset) and found robust differences between illusion and non-illusion trials (Figure 1C, D). In illusion
218 trials only, we found strong causal influence exerted by the auditory cortex onto the visual cortex in the
219 pre-stimulus period. We suggest, therefore, that the spontaneous fluctuations of this causal interaction
220 between two sensory cortical regions in the pre-stimulus period might bias sensory perception in
221 ambiguous or sensory-conflicting situations

222 If the effective connectivity from auditory to visual cortex has a causal role in biasing decisions,
223 it would be possible to predict, above chance, the behavioural response from the connectivity values on
224 a trial-by-trial basis. We tested this by applying a machine-learning technique. Using PDC values in the
225 alpha and beta frequency bands (estimated from 100 ms long time-windows) as features in a Bayesian
226 classifier, we predicted the behavioral response (either illusion or no-illusion). Using the pre-sound
227 onset time window only gave an accuracy of 55.3 % (one-sided exact binomial test, $n = 68700$,
228 successes = 37998, H_0 : probability of success = .5; $p < 0.0001$), whereas using the immediate post-flash
229 onset time-window decreased (Mann-Whitney, $p < 0.0001$ with respect to pre-stimulus time-window)
230 accuracy to 53 % (successes = 36247, $p < 0.0001$). However, when using the joint information from
231 that pre- and post-stimulus onset time-window, the mean prediction accuracy improved to 61.4 %
232 (successes = 42184, $p < 0.0001$). Although this classification accuracy is relatively moderate (possibly
233 due to our simple model excluding brain regions other than AC and VC, a brief period, and less robust

234 estimation of PDC values at the single-trial level), the prediction improvement, after including the
235 immediate pre-stimulus period, remained statistically significant.

236 These results, altogether, provide robust and consistent evidence that the effective connectivity
237 from the auditory to the visual cortex significantly induces a qualitative alteration of visual perception
238 by sound in the sound-induced flash illusion.

239

240 **Experiment 2: EEG based effective connectivity guided neurofeedback causally modulating** 241 **perceptual dominance**

242 To establish a piece of further causal evidence for this link between neural dominance and perceptual
243 dominance, we subsequently performed an effective connectivity-guided neurofeedback EEG
244 experiment ($n=27$) consisting of three sessions: pre-training, training, and post-training. In the pre-
245 training session, participants were presented with 100 trials each of the four conditions: 1 flash with 1-
246 4 beeps; participants had to report the number of perceived flashes on each trial. In the brief training
247 session (5 min [21]), the participants were shown a bar graph displaying the real-time effective
248 connectivity measure, either auditory to the visual cortex, $A \rightarrow V$, or visual to the auditory cortex, $V \rightarrow A$,
249 as measured by PDC in the alpha band. The participants were instructed to increase the height of the
250 bar graph by voluntarily “controlling” the level of spontaneous audio-visual alpha band cortical
251 connectivity. The EEG activities at 7 electrode locations (auditory: T3/4, T5/6; visual: O1/2, Oz) were
252 used for PDC calculation in the alpha band (8-12 Hz) after previous studies [15] and our MEG findings.
253 Half of the participants increased $A \rightarrow V$ cortical connectivity and the other half increased $V \rightarrow A$
254 connectivity. The post-training session was immediately after the training sessions, and the participants
255 were presented with the same task as in the pre-training session.

256 Next, we investigated whether this information flow indeed occurred during the sound-induced
257 flash illusion and whether information flow changes after connectivity-based neurofeedback training.
258 The PDC of $A \rightarrow V$ connectivity in illusion trials was significantly larger than in non-illusion trials
259 ($t(26)=2.21$, $p=0.036$), while PDC of $V \rightarrow A$ connectivity did not differ significantly between illusion
260 and non-illusion trials ($t(26)=0.062$, $p=0.95$) (Figs. 3C,D). So, our earlier MEG findings of linking

261 neural dominance, from auditory to the visual cortex, to perceptual dominance, sound modulating vision,
262 was replicated using EEG from an independent sample.

263 Next, we investigated whether the effective connectivity guided neurofeedback ($A \rightarrow V$ or
264 $V \rightarrow A$) could significantly modulate the sound-induced flash illusion at the behavioural level. We found
265 that after a brief $A \rightarrow V$ connectivity guided neurofeedback training, participants indeed showed an
266 increased rate of sound-induced visual illusion (Fig. 4). After the $A \rightarrow V$ neurofeedback training,
267 participants reported significantly higher sound-induced visual illusions in post-training trials with 3
268 beeps ($t(26)=8.2$ $p<0.00001$) and 4 beeps ($t(26)=3.0$ $p=.006$) (Figs. 4A,B). Further, $A \rightarrow V$ effective
269 connectivity increased after $A \rightarrow V$ training ($t(26)=4.25$, $p=.0002$) and decreased after $V \rightarrow A$ training
270 ($t(26)=6.66$, $p=0.00001$), and this was reflected by an interaction between pre-post and $A \rightarrow V/V \rightarrow A$
271 training, $F(1,7)=31.6$, $p=0.001$. Of note, the number of perceived flashes change after training was
272 marginally correlated with the changes in the $A \rightarrow V$ cortical PDC values ($R^2=0.468$, $p=0.06$) (Fig. 4C),
273 yet no such correlation was observed with the changes in the $V \rightarrow A$ cortical PDC values ($R^2=0.247$,
274 $p=0.21$) (Fig. 4D).

275

276 **Discussion**

277 In this study, we demonstrated a robust link between neural dominance and perceptual
278 dominance using sound-induced flash illusion as an experimental paradigm. We showed that effective
279 connectivity from auditory to visual cortical regions significantly increased in illusion trials compared
280 to non-illusion trials using both EEG and MEG independently. Further, by designing a novel effective
281 connectivity guided neurofeedback protocol, we provided causal evidence that the dominance of the
282 auditory cortex over the visual cortex, but not the other way around, critically influences the reported
283 perceptual dominance of auditory over visual information. Our findings also confirmed the previous
284 findings of increased pre-stimulus auditory and visual connectivity in sound-induced illusion [11]. Our
285 findings also extended the previous findings by providing trial-specific variations, in terms of
286 connectivity between auditory and visual cortical regions, for identical stimulus configurations, and
287 thereby, establishing a direct link between sensory interactions at the neural level and perceptual

288 outcomes on a trial-by-trial basis. The incorporation of MEG allows a better sensitivity to reveal the
289 connectivity correlates of the sound-induced flash illusion, and the EEG was adopted for the
290 neurofeedback protocol for its practicality and ease of implementation.

291 Our findings provided evidence for a simple neural mechanism underlying sound-induced visual
292 illusion. Because of the nature of the PDC, which is primarily sensitive to direct functional connections
293 [12], we suggest that connections from auditory cortical areas to the visual cortical areas underlie sound-
294 induced flash illusion. But what could be the anatomical basis of such functional associations between
295 two sensory cortical regions? Is it anatomically a direct one or mediated by other brain regions (s)? A
296 previous study [22] used retrograde tracers in macaques to identify structural connectivity between the
297 primary auditory cortex (A1) and the primary visual cortex (V1 or area 17) and reported some (9.5%)
298 neuronal projections from A1 to V1. Another study [23] used anterograde tracers in macaques and
299 reported direct structural projections from auditory to V1 and V2 in the calcarine fissure. Of particular
300 relevance in this context is that both studies reported that these projections target the peripheral visual
301 field representation in the visual cortex, which matches with our earlier results [4] that the sound-
302 induced flash illusion is stronger if the visual flash is presented in the periphery than in the fovea.
303 However, we are mindful of the lack of similar anatomical evidence in humans, and more importantly,
304 our results are based on purely functional data while the structure-functional relationship(s) remains
305 elusive. Therefore, concluding direct connectivity between two cortical regions from EEG/MEG data
306 would remain problematic, and we cannot be sure about the anatomical directness of the reported
307 connectivity between the auditory and the visual cortical regions. Furthermore, our sensor selections
308 (i.e. mainly the temporal ones) might not reflect activities of purely sensory cortical regions (i.e.
309 auditory cortex), and the temporal resolution of the frequency domain connectivity, as measured by
310 PDC, should be treated with caution [24]. Nevertheless, we would argue that the ongoing spontaneous
311 functional interaction between distant cortical regions, as reported here, could explain the sound-
312 induced visual illusion, and it is possible to alter the qualitative nature of illusory experience by
313 dynamical modulation of the spontaneous effective connectivity between two cortical regions.

314 Importantly, we observed a crucial asymmetry between two different directions of

315 neurofeedback training ($A \rightarrow V$, $V \rightarrow A$). At the neural level, both $A \rightarrow V$ and $V \rightarrow A$ training changed the
316 connectivity. However, at the behavioural level, only $A \rightarrow V$ training led to a significant change. It is
317 consistent with our earlier findings that the sound-induced visual illusion was resistant to feedback
318 training [25]. In other words, the fact that there was only enhancement, but no suppression effect might
319 be due to a flooring effect and/or inherent hard connectivity between sensory cortical regions. Our
320 findings also critically implicate the role of the neural oscillations and effective connectivity, especially
321 in the alpha frequency range [26], subserving multisensory processing [2].

322 Additionally, we showed that not only can specific regions of the brain be modulated by EEG
323 neurofeedback [21], the connectivity between the regions can also be modulated by the same technique.
324 The connectivity-based neurofeedback is especially useful for establishing a causal relationship
325 between neural activity and behaviour. More importantly, this would open ample possible applications
326 whereby training neural connectivity using the feedback technique, and we may enhance (or suppress)
327 various mental functions not just limited to multisensory and/or conscious perception.

328 Summing up, we showed that the spontaneous information flow between sensory cortical
329 regions as recorded by large scale brain oscillations could be reliably linked with behavioural outcomes,
330 and further, it might be possible to self-regulate this connectivity. These results altogether suggest a
331 more connected and less modular nature of cortical information processing.

332

333 **References**

334

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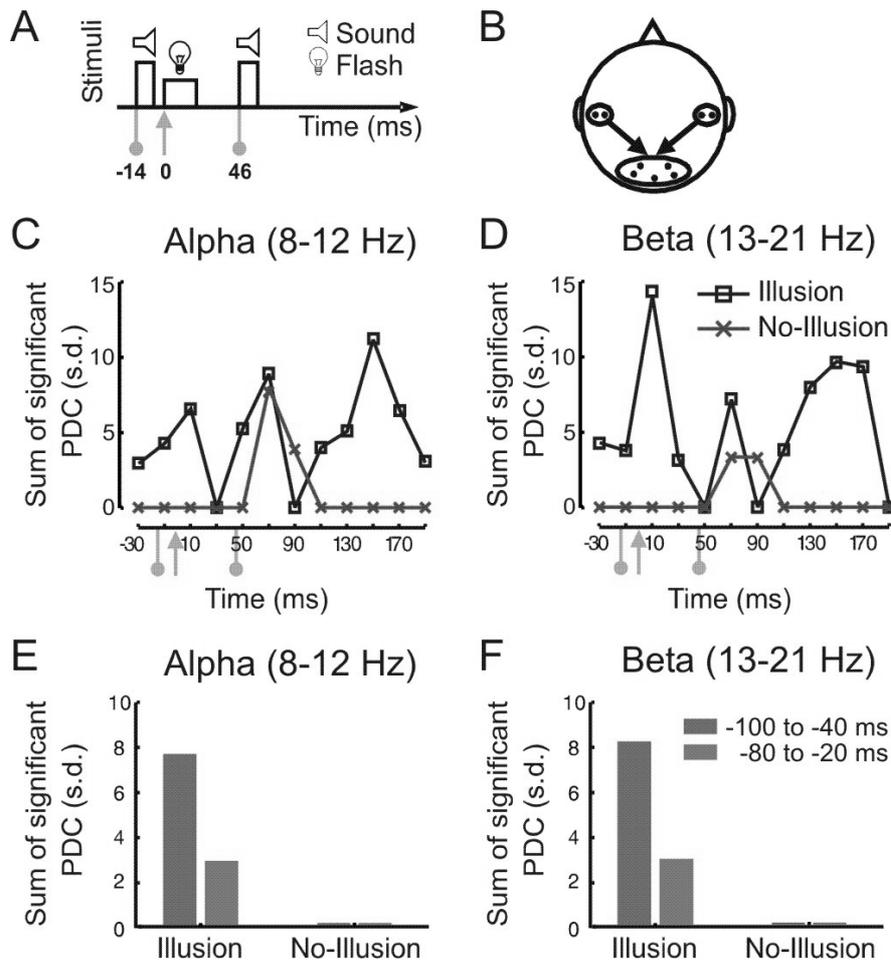
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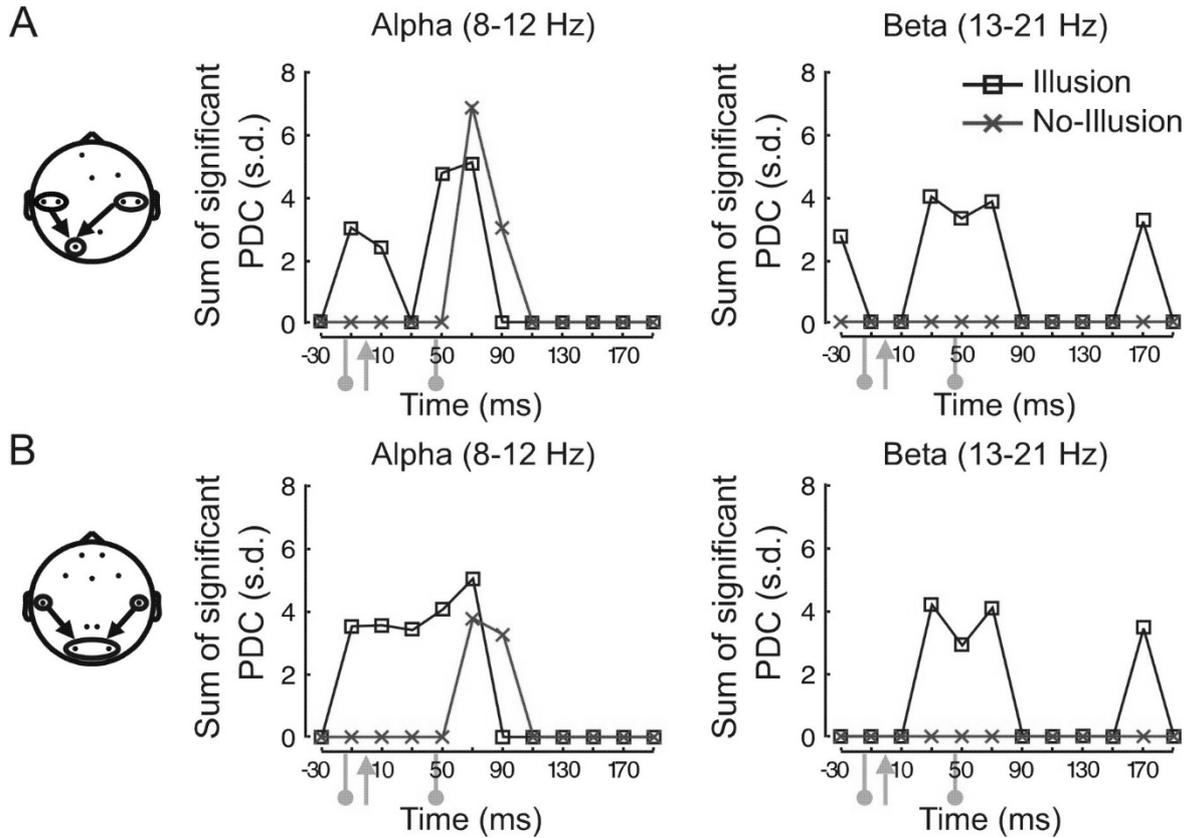
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408 **Figure 1. Experimental setting of sound-induced flash illusion, and strong partial directed**
 409 **coherence from auditory to the visual cortex, but primarily in illusion trials.** (A) Sound-
 410 induced flash illusion stimuli parameters. The auditory stimulus consisted of two brief beeps
 411 each lasting 10 ms and separated by 50 ms. The flashing stimulus was a uniform white disk
 412 appearing in the periphery (8.5° eccentricity) for a duration of 20 ms. (B) Considered sensors
 413 and direction of information flow. (C)-(D) Sum of significant partial directed coherence, PDC
 414 values (rank test; $p < 0.005$, see Experimental procedures), expressed in s.d., displaying the
 415 degree of the causal influence of auditory cortex onto visual cortex in (C) alpha (8-12 Hz) and
 416 (D) beta band (13-21 Hz) as a function of time. Each time point corresponds to a time-window
 417 spanning ± 30 ms. For example, the first time-point at -30 ms spans a time-window from -60
 418 to 0 ms with respect to flash onset. Gray markers indicate flash and auditory beep onsets (see
 419 (A)). (E)-(F) Sum of significant PDC values (rank test; $p < 0.005$) from the auditory cortex to
 420 the visual cortex in the -100 to -40 ms and -80 to -20 ms pre-flash-onset time window in (E)
 421 alpha and (F) beta band.



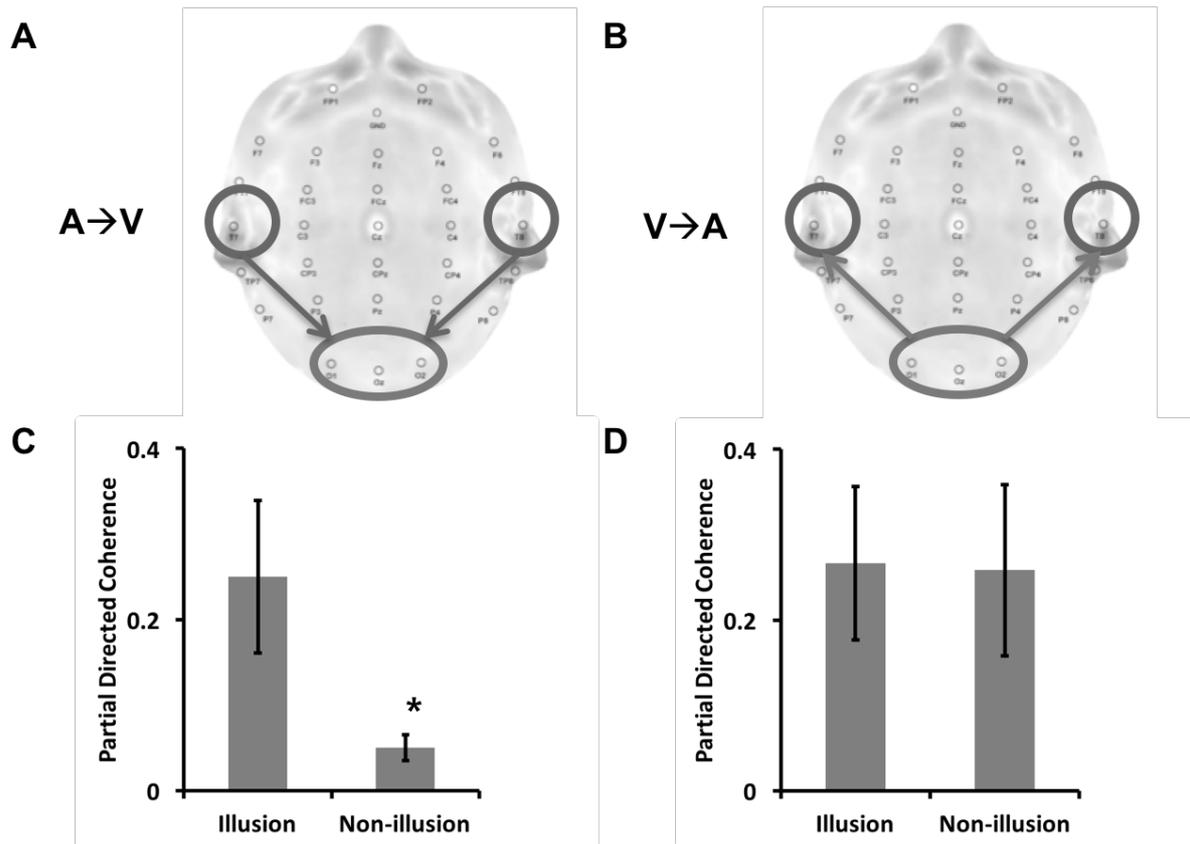
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425 **Figure 2. Two control sensor settings to investigate potentially directed nature of the**
 426 **influence from the auditory (A) to visual (V) cortex.** (A) Left, considered sensors and
 427 direction of information flow. Some temporal and/or occipital sensors were omitted to
 428 incorporate some frontal sensors into the model in order to constrain the dimension of the
 429 multivariate autoregressive model. Sensors that showed the strongest responses in the evoked-
 430 related-field analysis [9] were included. Right, the sum of significant (rank test; $p < 0.01$) PDC
 431 values, expressed in s.d., display degree of the causal influence of auditory cortex onto visual
 432 cortex in alpha (8-12 Hz) and beta band (13-21 Hz) as a function over time. (B) As in (A) but
 433 for second sensor setting incorporating bilateral sensors.

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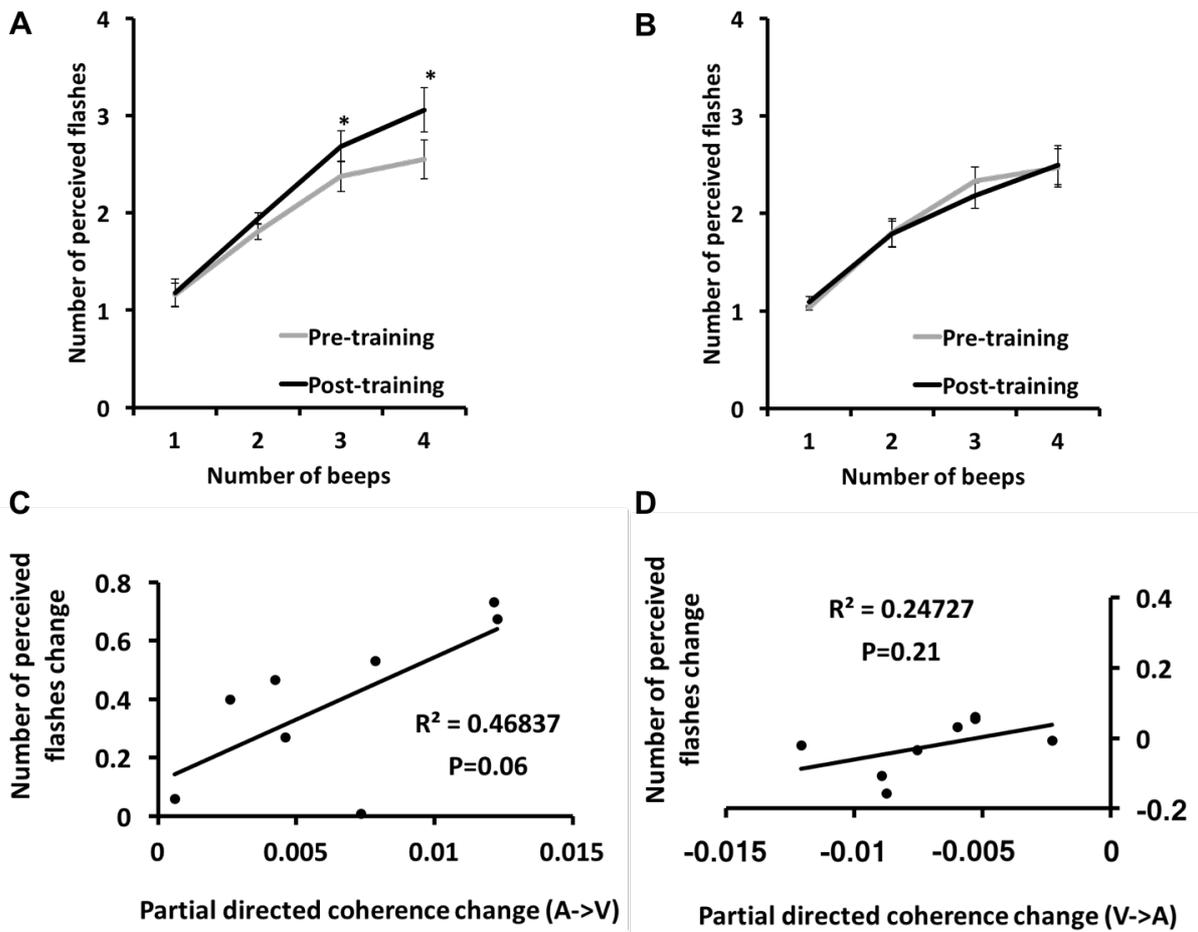
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438 **Figure 3. Replication of MEG findings by an independent EEG study, demonstrating**
 439 **higher PDC values from auditory to visual cortical regions in illusion trials.** (A) Partial
 440 directed coherence from auditory to the visual cortex ($A \rightarrow V$), and (B) partial directed
 441 coherence from visual to auditory cortex ($V \rightarrow A$), in the alpha frequency range (8-12Hz). (C)
 442 Partial directed coherence of non-illusion trials decreased significantly compared to that of
 443 illusion trials in $A \rightarrow V$ ($*p < 0.05$). (D) They were not different in $V \rightarrow A$.

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448 **Figure 4. Effective connectivity guided neurofeedback training increases sound-induced**

449 **visual illusion.** (A) Auditory-to-visual training ($*p < 0.05$), (B) visual-to-auditory training.

450 Correlations between partial directed coherence change and the number of perceived flashes

451 change in (C) auditory to visual training and in (D) visual to auditory training.

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456 Supplementary Information for:

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458 **“Causally Linking Neural Dominance to Perceptual Dominance in a Multisensory Conflict”**

459 Kyongsik Yun^{1,2,3*}, Joydeep Bhattacharya^{4*,#}, Simone Sandkuhler⁵, Yong-Jun Lin¹, Sunao Iwaki⁶, and

460 Shinsuke Shimojo^{1,2,7}

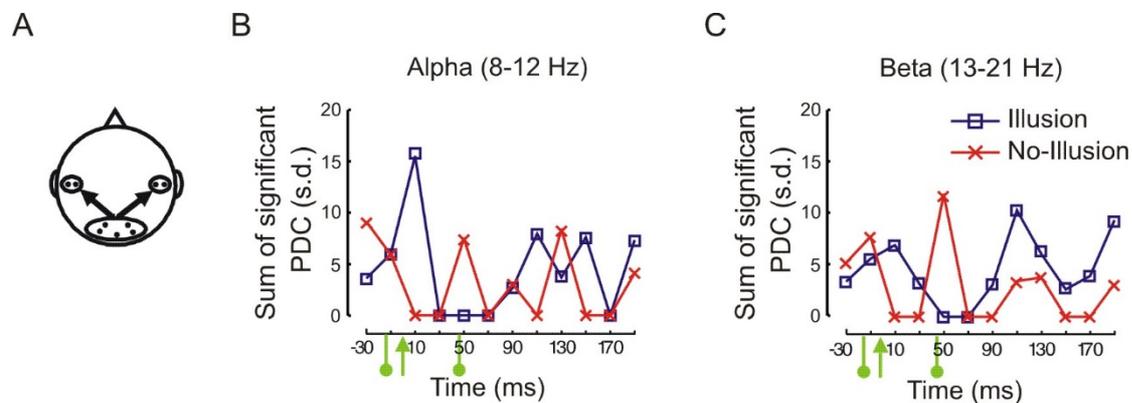
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468 **Figure S1. Modulation of auditory cortex by visual cortex.**

469 (A) Considered sensors (as in Figure 1B) and direction of information flow. (B)-(C) As in Figure 1C-

470 D, for the causal influence of VC onto AC. As expected (unlike the modulation of the visual cortex

471 by auditory cortex (Figure 1C-D)), no systematically directional influence was observed.

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