

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

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20 **Running Head:** Neuronal to perceptual dominance

21 **Funding:** This work was partially supported by the ERATO “Implicit Brain Function” project,  
22 Japan Science and Technology Agency.

23 **Conflict of Interest:** None declared.

24

## 25 **Abstract**

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

42

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

45

## 46 **Introduction**

47 We continuously encounter with visual and auditory information, processed by distinct  
48 sensory cortices, which are eventually integrated to produce a conscious behavioral unique  
49 response [1, 2]. However, when visual and auditory information is incongruent or in conflict,  
50 one sensory modality may dominate the other, leading towards a multisensory illusion [3]. A  
51 critical question remains whether sensory dominance is linked to neuronal causality, i.e.  
52 sensory cortex of the dominant modality would causally influence, at the functional level, the  
53 activities of the sensory cortex of the subordinate modality.

54 We tested this specific prediction in the framework of an audio-visual conflict – sound-  
55 induced flash illusion [4, 5]: a multisensory illusion, when a single flash in the visual  
56 periphery is accompanied by two beeps, the single flash is often misperceived as two flashes.  
57 Individual differences in proneness to the illusion are reflected in the neurochemical [6]  
58 (GABA concentration in superior temporal sulcus), structural [7] (grey matter volume in  
59 early visual cortex), and functional excitability [8, 9] (visual event-related responses to sound)  
60 differences. However, these findings do not explain the trial-by-trial variability, i.e. observers  
61 perceive the illusion sometimes, but not always, even though the physical stimuli remain  
62 identical and supra-threshold across trials. Since the auditory information dominates over the  
63 visual information for this illusion to occur, neural activity in the auditory cortex is predicted  
64 to exert a causal influence on the activity in the visual cortex, not the other way around.

65 We addressed this question by recording MEG signals from healthy humans in the sound-  
66 induced flash paradigm (Fig. 1A). We compared the effective connectivity between auditory  
67 to visual cortices for illusion and non-illusion trials, differing only in terms of the qualitative  
68 nature of visual perception, and verified our prediction. Next, to establish a causal mechanism,  
69 we performed a separate experiment involving EEG based neurofeedback in which

70 participants were briefly trained to spontaneously regulate their auditory to visual effective  
71 connectivity and found that such connectivity-based neurofeedback training significantly  
72 increased the probability of auditory stimulus qualitatively altering the visual perception.  
73 MEG was used to quantify the trial-by-trial effective connectivity between auditory and  
74 visual cortices due to its high sensitivity, and EEG was used as a neurofeedback tool to  
75 modulate the effective connectivity due to its practicality.

76

## 77 **Materials and methods**

### 78 *Ethics statement*

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

84

### 85 *Participants*

86 For the MEG study, 11 adults (3 females, ages ranging between 22-40 years) participated. For  
87 the EEG study, 27 adults (11 females, ages ranging between 22-40 years) participated. The  
88 sample sizes were comparable to previously published related studies [5, 10]. Two sets of  
89 participants were completely independent. All participants were healthy, had no history of  
90 neurological or psychiatric disorders and had normal or corrected to normal visual acuity, and  
91 normal hearing.

92

93

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

95 The MEG signals were recorded with a 122-channel whole-scalp planar-gradiometer  
96 (Neuromag 122, Elekta-Neuromag Oy, Helsinki, Finland) in a magnetically shielded room.

97 The instrument measured two orthogonal tangential derivatives of the magnetic field at 61  
98 scalp locations. In the examined bimodal condition, the event trigger was synchronized with  
99 the onset of the flash. The subjects were seated upright with their heads comfortably resting  
100 against the inner wall of the helmet and were instructed to fixate on a cross on the screen, and  
101 not to blink during trials.

102

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

113

114 The continuous MEG signals were band-pass filtered at 0.01 - 100 Hz, digitized at 550 Hz  
115 and stored for off-line analysis. To remove the contamination due to spurious oscillations (~  
116 40 Hz) of Helium cylinders, a further band-pass filtered was applied at 0.05 - 30 Hz using a  
117 Butterworth filter of order 3. The epochs containing eye blinks or excessive movements were

118 excluded based on amplitude criteria. Here, we considered only one experimental condition, a  
119 flash accompanied by two beeps that have two possible outcomes: (i) no-illusion -  
120 perceiving one flash, (ii) illusion: perceiving two flashes.

121

122 We used partial directed coherence, PDC [11] to identify the direction of information flow.  
123 Multivariate autoregressive models were adaptively estimated using overlapped time-  
124 windows (60 ms time-windows with 40 ms overlap) to make the estimated model parameters  
125 varying smoothly. The optimal model order was determined by locating the minimum of the  
126 Akaike Information Criterion (AIC) [12] across time and was set to 6. Statistical significance  
127 of PDC values was determined by independently shuffling the trial order across participants  
128 for each sensor. Thus, we obtained PDC values that were due to chance by pooling over  
129 participants. The data were shuffled for 200 times, and we used a nonparametric rank test as a  
130 qualitative measure of significance. Only for those PDC values that passed this  
131 nonparametric test, we expressed significant PDC values in terms of standard deviations of  
132 the shuffled distribution to have better visual clarity of the degree of causal interdependence.

133

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

141 The random variable  $y$  represents the classification input data vector of PDC values in alpha  
142 and beta bands. Bayes' Theorem gives us the posterior probability of  $\theta$  given the information  
143 that  $y$  occurred:

$$144 \quad p(\theta_i|y) \propto p(y|\theta_i)p(\theta_i), \quad i \in \{1,2\}$$

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

150

### 151 *EEG study: Design, procedure, and materials*

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

163

164 Next, participants were randomly assigned to one of the two groups:  $A \rightarrow V$  and  $V \rightarrow A$

165 training groups. Participants of  $A \rightarrow V$  training group were shown a bar graph displaying the  
166 real-time processed  $A \rightarrow V$  connectivity of their brains. They were asked to try to figure out  
167 how to increase the height of the bar graph. Participants of  $V \rightarrow A$  group was shown the bar  
168 graph displaying  $V \rightarrow A$  connectivity. In essence, the participants were only instructed to  
169 “control” their brain connectivity voluntarily and heighten the bar graph on the computer  
170 screen. The neurofeedback training lasted for a brief period of 5 min. Subsequently,  
171 participants performed the post-training tasks that were the same as they did before the EEG  
172 neurofeedback training.

173

174 EEG was recorded at a sampling rate of 1000 Hz using 128-channels EGI cap. The EEG  
175 activities at 7 channels (T3, T4, T5, T6, O1, O2, and Oz) between 8-12 Hz were used for  
176 PDC computation. The impedance of the electrodes was kept below 50 k $\Omega$ . Real-time  
177 frequency filtering to extract alpha frequency band (8-12 Hz) and the PDC computation were  
178 performed. The processing latency was 223ms +- 26ms. The detected EEG signal was both  
179 recorded for analysis and fed back to the subject forming a feedback loop. Computed  
180 connectivity using PDC from auditory (T3, T4, T5, T6) to visual cortices (O1, O2, Oz) was  
181 represented as the height of the bar graph and its sign was reversed at the bar graph shown to  
182 the control group. While participants tried to heighten the bar graph, their brain connectivity  
183 was modulated and in turn, formed the feedback loop.

184

## 185 **Results**

### 186 **Experiment 1: MEG study linking neural dominance to perceptual dominance**

187 **Auditory to visual connectivity was associated with the double-flash illusion:** Flash  
188 illusion was reported for 62% of trials (i.e. out of 687 trials, participants reported perceiving



189 two flashes on 424 trials), while stimulus parameters remained identical with 2 beeps and 1  
190 flash (Fig 1A). We used partial directed coherence [11], a frequency domain representation of  
191 Granger's causality [13], to measure the effective connectivity (i.e. the explicit and  
192 directional flow of information) between auditory and visual cortices. We focused our  
193 analysis in the alpha (8-12 Hz) and the beta (13-21 Hz) band neuronal oscillations after  
194 previous studies [10, 14]. With the adaptive multivariate autoregressive modeling approach  
195 for short window spectral analysis [12], we determined the connectivity from the nine  
196 selected MEG sensors located approximately over the auditory cortex (AC) and visual cortex  
197 (VC) (Fig 1B). We observed a robust flow of information from auditory to the visual cortex  
198 for the illusion trials in both alpha (Fig 1C) and beta (Fig 1D) oscillations; on the other hand,  
199 such directional flow of information from auditory to visual cortex remained mostly non-  
200 significant (except around 70 ms after flash-onset). The timings of the peaks of auditory to  
201 visual connectivity at 40 to 100 ms [15, 16] and 110 to 170 ms [15] for illusion trials are in  
202 close agreement with the reported time-intervals of previous studies on multisensory  
203 integration. However, in contrast to earlier findings [15, 16] which compared multisensory  
204 to unisensory conditions, we compared two identical multisensory conditions, differing only  
205 in the quality of the subjective perception. Therefore, our results establish a direct link  
206 between the brain's specific connectivity pattern and conscious awareness. This potentially  
207 causal influence on the visual cortex by the auditory cortex at such an early stage of  
208 information processing may be indicative of direct communication between these two  
209 sensory areas at a functional level. Of note, earlier studies [17, 18] suggest direct structural  
210 connectivity between these two sensory areas, especially between the primary cortices. Both  
211 studies reported that these projections target the peripheral visual field representation in the  
212 visual cortex, which matches with our earlier results [4] that the sound-induced flash illusion

213 is stronger if the visual flash is presented in the periphery than in the fovea.

214

215 **Directedness and asymmetrical nature of auditory to visual connectivity:** To validate that  
216 these causal functional modulations were possibly direct and not via other multisensory areas,  
217 we repeated the connectivity analysis after including different sensors from other  
218 multisensory regions including parietal, frontal, and temporal cortex in our information flow  
219 model (see Figure 2A-B; left panel) and by omitting some sensors from AC and VC areas.  
220 Results for different model configurations are shown in Figs. 2(A-B) and Figs. 2(C-D) for  
221 alpha and beta band, respectively. Despite the variations in the temporal profiles from AC to  
222 VC connectivity across model configurations, we observed that overall the degree of AC to  
223 VC was larger and more sustained in the illusion trials than no-illusion trials, thereby  
224 confirming our earlier findings. Thus, the reported early AC to VC connectivity was unlikely  
225 to be influenced by the higher-order multisensory areas.

226       Next, we inspected the connectivity in the reverse direction, i.e., the influence of the  
227 visual cortex onto the auditory cortex. In the flash illusion, sound dominates vision, but not  
228 vice versa. Aligned with this inherent nature of the illusion, we found that the information  
229 flow from the visual cortex to the auditory cortex was comparable between illusion and non-  
230 illusion trials (see Figure S1, Supplemental Digital Content). This suggests that the effective  
231 connectivity from AC to VS, but not the other way round, is crucial to alter the qualitative  
232 nature of visual perception in the sound-induced flash illusion.

233

234 **Prestimulus auditory to visual connectivity predicting perceptual outcomes:** Given the  
235 early nature of the causal interactions, and the recently reported evidence of pre-stimulus  
236 brain states shaping post-stimulus responses [19-21], we investigated the immediate pre-

237 stimulus period (100 ms before flash-onset) and found robust differences between illusion  
238 and non-illusion trials (Figure 1C, D). In illusion trials only, we found strong causal influence  
239 exerted by the auditory cortex onto the visual cortex in the pre-stimulus period. We suggest,  
240 therefore, that the spontaneous fluctuations of this causal interaction between two sensory  
241 cortices in the prestimulus period might bias sensory perception in ambiguous or sensory-  
242 conflicting situations

243         If the effective connectivity from auditory to visual cortex has a causal role in biasing  
244 decisions, it would be possible to predict, above chance, the behavioral response from the  
245 connectivity values on a trial-by-trial basis. We tested this by applying a machine-learning  
246 technique. Using PDC values in the alpha and beta frequency bands (estimated from 100 ms  
247 long time-windows) as features in a Bayesian classifier, we predicted the behavioral response  
248 (either illusion or no-illusion). Using the pre-sound onset time window only gave an accuracy  
249 of 55.3 % (one-sided exact binomial test,  $n = 68700$ , successes = 37998,  $H_0$ : probability of  
250 success = .5;  $p < 0.0001$ ), whereas using the immediate post-flash onset time-window  
251 decreased (Mann-Whitney,  $p < 0.0001$  with respect to pre-stimulus time-window) accuracy to  
252 53 % (successes = 36247,  $p < 0.0001$ ). However, when using the joint information from that  
253 pre- and post-stimulus onset time-window, the mean prediction accuracy improved to 61.4 %  
254 (successes = 42184,  $p < 0.0001$ ). Although this classification accuracy is relatively moderate  
255 (possibly due to our simple model excluding brain regions other than AC and VC, a brief  
256 period, and less robust estimation of PDC values at the single-trial level), the prediction  
257 improvement, after including the immediate pre-stimulus period, remained statistically  
258 significant.

259         These results, altogether, provide robust and consistent evidence that the effective  
260 connectivity from the auditory to the visual cortex significantly induces a qualitative

261 alteration of visual perception by sound in the sound-induced flash illusion.

262

263 **Experiment 2: EEG based effective connectivity guided neurofeedback causally**  
264 **modulating perceptual dominance**

265 To establish a piece of further causal evidence for this link between neural dominance and  
266 perceptual dominance, we subsequently performed an effective connectivity-guided  
267 neurofeedback EEG experiment ( $n=27$ ) consisting of three sessions: pre-training, training,  
268 and post-training. In the pre-training session, participants were presented with 100 trials each  
269 of the four conditions: 1 flash with 1-4 beeps; participants had to report the number of  
270 perceived flashes on each trial. In the brief training session (5 min [22]), the participants were  
271 shown a bar graph displaying the real-time effective connectivity measure, either auditory to  
272 the visual cortex,  $A \rightarrow V$ , or visual to the auditory cortex,  $V \rightarrow A$ , as measured by PDC in the  
273 alpha band. The participants were instructed to increase the height of the bar graph by  
274 voluntarily “controlling” the level of spontaneous audio-visual alpha band cortical  
275 connectivity. The EEG activities at 7 electrode locations (auditory: T3/4, T5/6; visual: O1/2,  
276 Oz) were used for PDC calculation in the alpha band (8-12 Hz) after previous studies [14]  
277 and our MEG findings. Half of the participants increased  $A \rightarrow V$  cortical connectivity and the  
278 other half increased  $V \rightarrow A$  connectivity. The post-training session was immediately after the  
279 training sessions, and the participants were presented with the same task as in the pre-training  
280 session.

281 Next, we investigated whether this information flow indeed occurred during the  
282 sound-induced flash illusion and whether information flow changes after connectivity-based  
283 neurofeedback training. The PDC of  $A \rightarrow V$  connectivity in illusion trials was significantly  
284 larger than in non-illusion trials ( $t(26)=2.21$ ,  $p=0.036$ ), while PDC of  $V \rightarrow A$  connectivity did

285 not differ significantly between illusion and non-illusion trials ( $t(26)=0.062, p=0.95$ ) (Figs.  
286 3C,D). So, our earlier MEG findings of linking neural dominance, from auditory to the visual  
287 cortex, to perceptual dominance, sound modulating vision, was replicated using EEG from an  
288 independent sample.

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

302

## 303 Discussion

304 In this study, we demonstrated a robust link between neural dominance and  
305 perceptual dominance using sound-induced flash illusion as an experimental paradigm. We  
306 showed that effective connectivity from auditory to visual cortices significantly increased in  
307 illusion trials compared to non-illusion trials using both EEG and MEG independently.  
308 Further, by designing a novel effective connectivity guided neurofeedback protocol, we

309 provided causal evidence that the dominance of the auditory cortex over the visual cortex, but  
310 not the other way around, critically influences the reported perceptual dominance of auditory  
311 over visual information. Our findings also confirmed the previous findings of increased pre-  
312 stimulus auditory and visual connectivity in sound-induced illusion [10]. Our findings also  
313 extended the previous findings by providing trial-specific variations, in terms of connectivity  
314 between auditory and visual cortices, for identical stimulus configurations, and thereby,  
315 establishing a direct link between sensory interactions at the neural level and perceptual  
316 outcomes on a trial-by-trial basis. The incorporation of MEG allows a better sensitivity to  
317 reveal the connectivity correlates of the sound-induced flash illusion, and the EEG was  
318 adopted for the neurofeedback protocol for its practicality and ease of implementation.

319 Our findings provided evidence for a simple neural mechanism underlying sound-  
320 induced visual illusion. Because of the nature of the PDC, which is primarily sensitive to  
321 direct functional connections [11], we suggest that the connection from auditory to visual  
322 cortices underlies sound-induced flash illusion. However, concluding direct connectivity  
323 between two brain regions from EEG/MEG data would remain problematic, so we cannot be  
324 certain about the directness of the reported connectivity between the auditory and the visual  
325 cortical regions. Further, our sensor selections (i.e. especially the temporal ones) might not  
326 reflect activities of purely sensory cortices (i.e. auditory cortex), and the temporal resolution  
327 of the frequency domain connectivity, as measured by PDC, should be treated with caution  
328 [23]. Nevertheless, we would argue that the ongoing spontaneous interaction of distant  
329 cortices, as reported here, could explain the sound-induced visual illusion, and it is possible  
330 to alter the qualitative nature of illusory experience by dynamical modulation of the  
331 spontaneous effective connectivity between two cortices.

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

333 neurofeedback training ( $A \rightarrow V$ ,  $V \rightarrow A$ ). At the neural level, both  $A \rightarrow V$  and  $V \rightarrow A$  training  
334 changed the connectivity. However, at the behavioral level, only  $A \rightarrow V$  training led to a  
335 significant change. It is consistent with our earlier findings that the sound-induced visual  
336 illusion was resistant to feedback training [24]. In other words, the fact that there was only  
337 enhancement but no suppression effect might be due to a flooring effect and/or inherent hard  
338 connectivity between sensory cortices. Our findings also critically implicate the role of the  
339 neural oscillations and effective connectivity, especially in the alpha frequency range [25],  
340 subserving multisensory processing [2].

341           Additionally, we showed that not only can specific regions of the brain be modulated  
342 by EEG neurofeedback [22], the connectivity between the regions can also be modulated by  
343 the same technique. The connectivity-based neurofeedback is especially useful for  
344 establishing a causal relationship between neural activity and behavior. More importantly,  
345 this would open ample possible applications whereby training neural connectivity using the  
346 feedback technique, we may enhance (or suppress) various mental functions not just limited  
347 to multisensory and/or conscious perception.

348           Summing up, we showed that the spontaneous information flow between sensory  
349 cortices as recorded by large scale brain oscillations can be reliably linked with behavioural  
350 outcomes, and further, it might be possible to self-regulate this connectivity. These results  
351 altogether suggest a more connected and less modular nature of cortical information  
352 processing.

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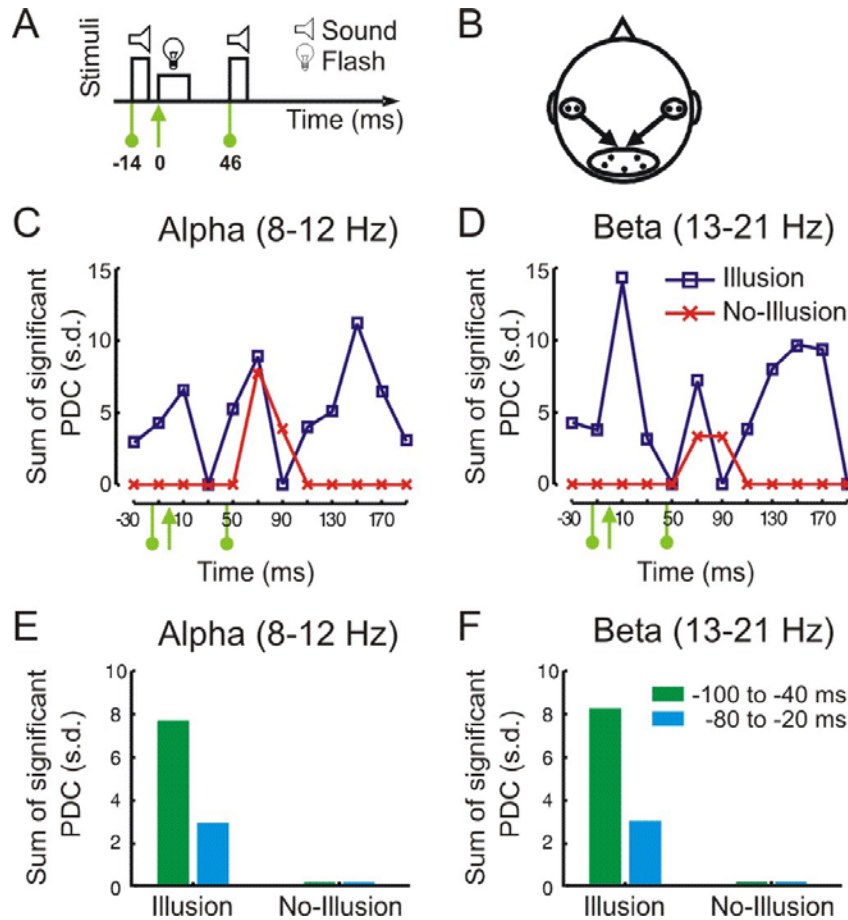
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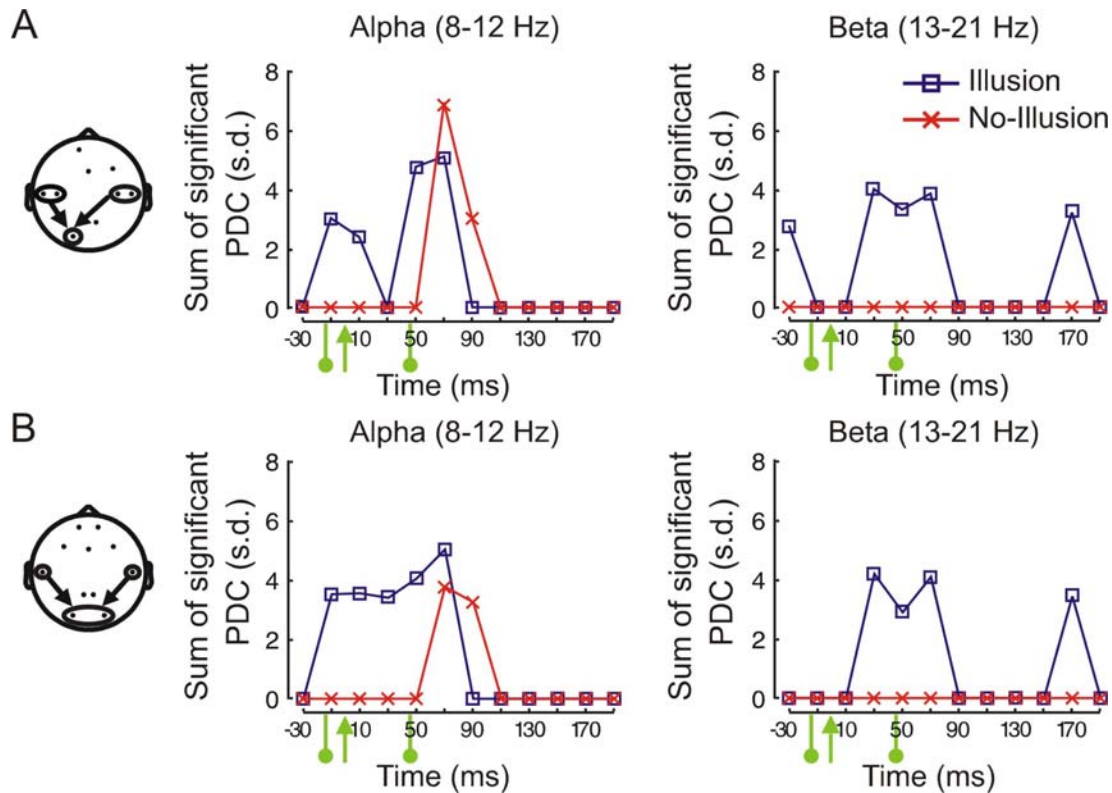
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422 **Figure 1. Experimental setting of sound-induced flash illusion, and strong partial**  
 423 **directed coherence from auditory to the visual cortex, but primarily in illusion trials.** (A)  
 424 Sound-induced flash illusion stimuli parameters. The auditory stimulus consisted of two brief  
 425 beeps each lasting 10 ms and separated by 50 ms. The flashing stimulus was a uniform white  
 426 disk appearing in the periphery (8.5° eccentricity) for a duration of 20 ms. (B) Considered  
 427 sensors and direction of information flow. (C)-(D) Sum of significant PDC values (rank test;  
 428  $p < 0.005$ , see Experimental procedures), expressed in s.d., displaying the degree of the  
 429 causal influence of auditory cortex onto visual cortex in (C) alpha (8-12 Hz) and (D) beta  
 430 band (13-21 Hz) as a function of time. Each time point corresponds to a time-window  
 431 spanning  $\pm 30$  ms. For example, the first time-point at -30 ms spans a time-window from -60  
 432 to 0 ms with respect to flash onset. Green markers indicate flash and auditory beep onsets  
 433 (see (A)). (E)-(F) Sum of significant PDC values (rank test;  $p < 0.005$ ) from auditory cortex  
 434 to the visual cortex in the -100 to -40 ms and -80 to -20 ms pre-flash-onset time window in (E)  
 435 alpha and (F) beta band.

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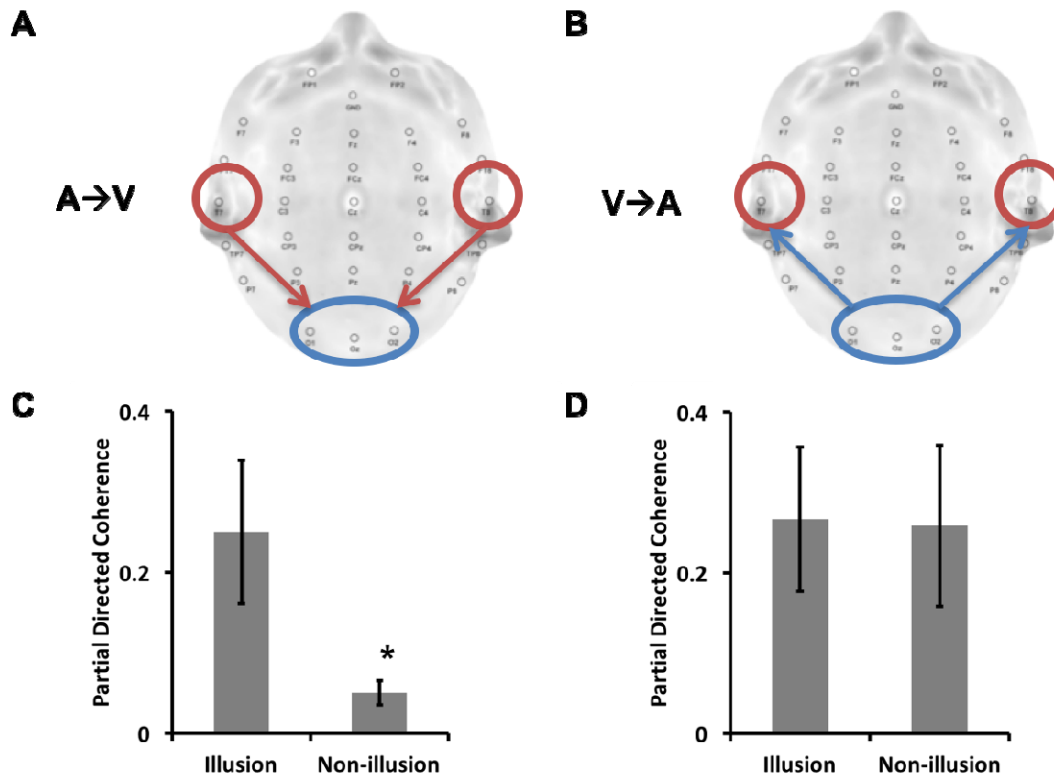
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439 **Figure 2. Two control sensor settings to investigate potentially directed nature of the**  
440 **influence from AC to VC.** (A) Left, considered sensors and direction of information flow.  
441 Some AC and/or VC sensors were omitted for both settings to constrain the dimension of the  
442 multivariate AR model. Sensors that showed the strongest responses in ERP analysis were  
443 included. Right, the sum of significant (rank test;  $p < 0.01$ ) PDC values, expressed in s.d.,  
444 display degree of the causal influence of AC onto VC in alpha (8-12 Hz) and beta band (13-  
445 21 Hz) as a function over time (see Figure 1C-D). (B) As in (A) for second sensor setting  
446 incorporating bilateral sensors.

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451 **Figure 3. Replication of MEG findings by an independent EEG study, demonstrating**

452 **higher PDC values from auditory to visual cortices in illusion trials.** (A) Partial directed

453 coherence from auditory to visual cortices ( $A \rightarrow V$ ), and (B) partial directed coherence from

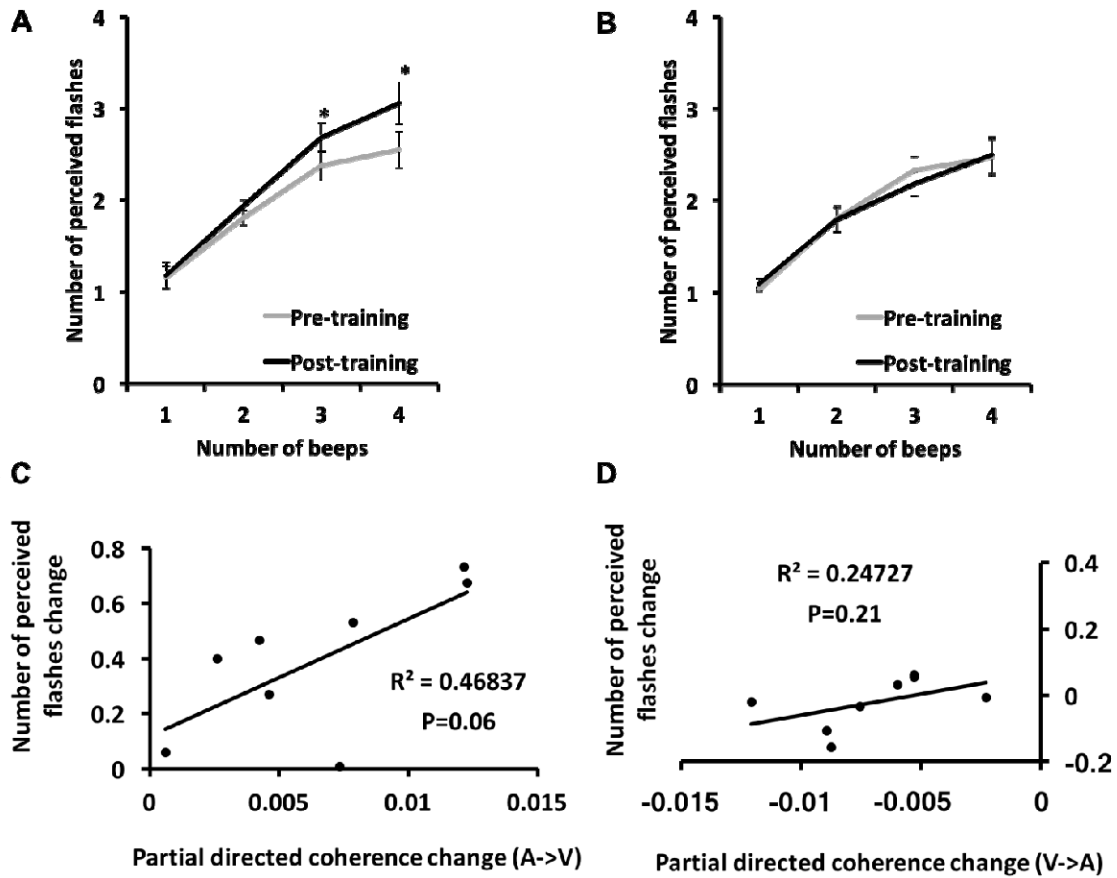
454 visual to auditory cortices ( $V \rightarrow A$ ), in the alpha frequency range (8-12Hz). (C) Partial

455 directed coherence of non-illusion trials decreased significantly compared to that of illusion

456 trials in  $A \rightarrow V$  (\* $p < 0.05$ ). (D) They were not different in  $V \rightarrow A$ .

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

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

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

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

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473 [Supplementary Information for:](#)

474

475 “Causally Linking Neural Dominance to Perceptual Dominance in a Multisensory

476 Conflict”

477 Kyongsik Yun<sup>1,2,3\*</sup>, Joydeep Bhattacharya<sup>4\*,#</sup>, Simone Sandkuhler<sup>5</sup>, Yong-Jun

478 Lin<sup>1</sup>, Sunao Iwaki<sup>6</sup>, and Shinsuke Shimojo<sup>1,2,7</sup>

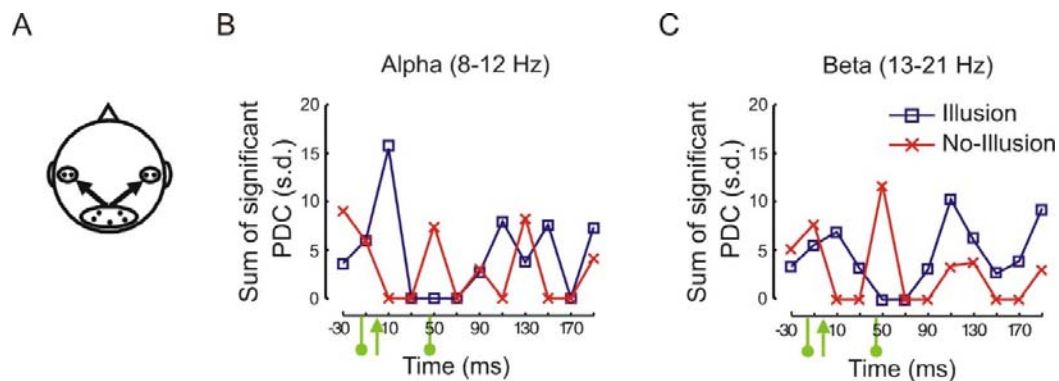
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486 **Figure S1. Modulation of auditory cortex by visual cortex.**

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

488 Figure 1C-D, for the causal influence of VC onto AC. As expected (unlike the modulation

489 of the visual cortex by auditory cortex (Figure 1C-D)), no systematically directional influence

490 was observed.

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