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Oscillatory properties of functional connections between sensory areas mediate crossmodal illusory perception

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1 **Oscillatory properties of functional connections between sensory areas mediate**
2 **crossmodal illusory perception**

3

4 **SHORT TITLE:** Oscillatory networks mediate crossmodal illusions

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25

26 **Abstract**

27 The presentation of simple auditory stimuli can significantly impact visual processing
28 and even induce visual illusions, such as the auditory-induced Double Flash Illusion (DFI).
29 These crossmodal processes have been shown to be driven by occipital oscillatory activity
30 within the alpha band. Whether this phenomenon is network specific or can be generalized to
31 other sensory interactions remains unknown. The aim of the current study was to test whether
32 crossmodal interactions between somatosensory-to-visual areas leading to the same (but
33 tactile-induced) DFI share similar properties to the auditory-DFI. We hypothesized that if the
34 effects are mediated by the oscillatory properties of early visual areas per se then the two
35 versions of the illusion should be subtended by the same neurophysiological mechanism (i.e.
36 the speed of alpha frequency). Alternatively, if the oscillatory activity in visual areas
37 predicting this phenomenon is dependent on the specific neural network involved, then it
38 should reflect network-specific oscillatory properties. In line with the latter, results recorded
39 in humans (both genders) show a network-specific oscillatory profile linking the auditory-
40 DFI to occipital alpha oscillations, replicating previous findings, and tactile-DFI to occipital
41 beta oscillations, a rhythm typical of somatosensory processes. These frequency-specific
42 effects are observed for visual (but not auditory or somatosensory) areas and account for
43 auditory-visual connectivity in the alpha band and somatosensory-visual connectivity in the
44 beta band. We conclude that task-dependent visual oscillations reflect network-specific
45 oscillatory properties favouring optimal, directional neural communication timing for sensory
46 binding.

47
48 **Significant Statement:** Cooke and colleagues investigate the oscillatory correlates of
49 the auditory- and tactile-induced double flash illusion (DFI), a phenomenon where two
50 interleaved beeps (taps) set within 100ms apart and paired with one visual flash induce the

51 sensation of a second illusory flash. Results confirm previous evidence that the speed of
52 individual occipital alpha oscillations predict the temporal window of the auditory-induced
53 illusion. Importantly, they provide novel evidence that the tactile-induced DFI is instead
54 mediated by the speed of individual occipital beta oscillations. These task-dependent occipital
55 oscillations are shown to be mediated by the oscillatory properties of the neural network
56 engaged in the task to favour optimal temporal integration between the senses.

57

58 **Introduction**

59 Our senses act as temporal gateways to our environment, allowing continuous
60 information streams within and across senses to be coded into discrete information units
61 (VanRullen & Koch, 2003, VanRullen, 2016; Chakravarthi & VanRullen., 2012). The
62 temporal resolution of such mechanisms may allow the brain to temporally bind sensory
63 input over time and across senses into meaningful objects and events (Cecere et al., 2015)
64 reducing the complexity of our environment (Wutz et al., 2016; 2018).

65 This Bayesian mechanism (Beierholm et al., 2009; Barakat et al., 2013; Kayser &
66 Shams 2015; Cuppini et al., 2017) generally leads to prompt, efficient readouts of the
67 experienced environment. However, when presented with incongruent sensory information, it
68 often gives rise to illusory phenomena. One such example is the Double Flash Illusion (DFI).
69 Shams and colleagues (2000) first discovered that when two shortly interleaved beeps are
70 paired with a single flash, participants often perceive a second illusory flash (Shams et al.,
71 2000; 2002). Such illusion may possibly represent the best coherent perceptual resolution of
72 otherwise conflicting sensory information (Cecere et al., 2015). By systematically
73 manipulating temporal intervals between paired “beeps”, it is possible to define the temporal
74 window of this illusion (TWI); i.e. the time interval in which the illusory flash is perceived.
75 This TWI, first characterised by Shams and colleagues (2002) and detailed by Cecere et al.,

76 (2015), demonstrates that the illusion decays when the average time between stimuli exceeds
77 100ms. Cecere et al., (2015) argued that these TWIs, variable across individuals, are
78 reminiscent of the temporal profile of posterior oscillatory activity in the alpha band (8-
79 12Hz). Employing both correlational and causal approaches, Cecere et al., (2015) found a
80 tight correlation between individual TWI and individual alpha frequency peak (IAF) with
81 faster IAFs predicting shorter TWIs, and slower IAFs predicting larger TWIs.

82 Yet, we are unaware whether this mechanism is determined by local network rules per
83 se, i.e. local occipital oscillatory resonance activity (typically alpha) (Rosanova et al., 2009),
84 or whether it depends on long-range communication networks (Fries, 2015), i.e. the way in
85 which a sensory modality (e.g. auditory) impacts on visual cortex activity (Romei et al.,
86 2012). In other words, are crossmodal visual illusions determined strictly by typically visual
87 oscillatory constraints, or do visual oscillations mediating these effects reflect the oscillatory
88 properties of the functional connection between sensory modalities?

89 An elegant way to tease apart these hypotheses is to investigate the temporal profile
90 and neural underpinnings of a DFI induced by a sensory modality other than audition and
91 compare it with the auditory-DFI. Here, we utilised the tactile-DFI (Violentyev et al., 2005),
92 whereby replacing paired “beeps” with “taps” upon the index finger elicits a similar illusory
93 experience. No previous report of a temporal profile for the tactile-DFI exists. If the induced
94 illusory flash is determined by local resonance frequency of the visual cortex (alpha),
95 irrespective of paired modality, then similar illusory phenomena should also be mediated by
96 occipital IAF. Alternatively, if functional connections between auditory/somatosensory and
97 visual cortices determine the fate of the illusory experience, then occipital oscillations
98 accounting for auditory- and tactile-DFI may depend on communication-specific mechanisms
99 influencing visual cortical processing at the speed of their typical resonance frequency.

100 According to the “Communication Through Coherence” framework (Fries, 2005;
101 2015), neural communication subserved by oscillatory synchronization between remote but
102 functionally interconnected areas would be the result of the alignment of post-synaptic neural
103 activity (visual cortex) to pre-synaptic input (auditory/somatosensory cortex), creating
104 temporal windows of optimal communication.

105 This hypothesis would not contradict evidence that auditory-induced TWI is mediated
106 by alpha oscillations as auditory processing (pre-synaptic), which is typically associated with
107 alpha activity (Weisz et al., 2011), phase-aligns alpha oscillations in visual cortex (post-
108 synaptic) (Romei et al., 2012). Crucially, this would predict somewhat faster waves to
109 influence the tactile-TWI, since tactile processing (pre-synaptic) is often associated with beta
110 frequency oscillations (Salenius & Hari, 2003; Foffani, et al., 2005; Engel & Fries, 2010;
111 Baumgarten, et al., 2015).

112

113 **Materials and Methods**

114 **Participants**

115 A total of 62 participants volunteered to take part in the study which was approved by
116 the ethics committee of the University of Essex. Eleven participants were excluded from data
117 analysis as their perceived illusion could not be fitted to the sigmoid function curve.

118 All but 3 participants (of whom 2 were left handed and 1 ambidextrous by self-report
119 were right handed (mean age: 25, range: 18 – 44, 31 females).

120 Prior to taking part, participants completed a screening questionnaire ensuring they
121 had no psychiatric or neurological history and normal (or corrected) vision, as well as normal
122 hearing and somatosensation by self-report.

123

124 **Materials and Apparatus**

125 All visual stimuli were presented on a 17.5" cathode ray tube monitor via a Dell
126 Optiplex 960 computer (Windows XP, resolution: 1280x1024) with a refresh rate of 85Hz.
127 Auditory stimuli were delivered via a pair of speakers placed either side of the monitor
128 (perceived by the participants as originating from the centre of the screen, close to the visual
129 stimuli). Volume was set so stimuli were approximately 50 dB (SPL) at the location of the
130 participants' head. The tactile stimulation was provided via a tactile controller and
131 mechanical solenoid stimulator (Heijjo Research Electronics, London, UK). This would
132 deliver a suprathreshold tap (on the left index finger tip) by pushing a blunt plastic tip against
133 the participant's skin whenever a current was passed through the solenoid. During the tactile
134 stimulation, white-noise (approximately 50db) was played to participants through speakers to
135 mask and ensure that the mechanic noise produced by the tactile stimulator was not heard by
136 the participants. Experimental stimuli were presented via E-prime (version 2.0; Psychology
137 Software Tools, Pittsburgh, PA).

138 We piloted the experiment in the first 15 participants and electroencephalography
139 (EEG) was recorded with a restricted number of electrodes including Electrodes Oz, O2, O1,
140 FP1, FPz and FP2, alongside the ground electrode (location: AFz) and the reference electrode
141 placed over the right mastoid bone.

142 In the remaining participants (N=36), the EEG was recorded from 64 sintered
143 Ag/AgCl electrodes mounted on an elastic cap (Easycap, Herrsching, Germany) alongside the
144 ground electrode (position: AFz) and the reference electrode (placed upon the right mastoid
145 bone). The EEG signals were digitized at 500Hz and amplified using BrainVision
146 Professional BrainAmp amplifier through the BrainVision Recorder programme
147 (BrainProducts GmbH, Gilching, Germany). Before the recording began we ensured that all
148 electrodes were set on the participant's scalp at an impedance not exceeding 10k Ω .

149 In all trials, participants were presented with a flashing disc, displayed just below a
150 central fixation cross (this disc always flashed once for a duration of 12ms and had a diameter
151 of 2cm). During the auditory DFI task the disc was always paired with a double-beep with
152 each beep having a frequency of 3500Hz and a duration of 7ms. During the tactile DFI task
153 disc presentation was paired with a double tactile stimulation to the left index finger.

154 The two brief tones (and the two tactile stimulations) were spaced apart by varying
155 Stimulus Onset Asynchronies (SOAs) ranging between 36 and 204ms with increments of
156 12ms, resulting in 15 different SOAs. Each SOA was presented 10 times, resulting in 150
157 randomly ordered trials per task.

158 The time between trials included the presentation of the stimuli (as described above)
159 plus a varying interval. The interval corresponded to the elapsed time following the
160 experimenter inputting on the keyboard the participant's vocal response plus an interval
161 ranging between 1000ms and 1800ms (there were 5 different inter-trial delays in steps of
162 200ms, each occurring 30 times).

163

164 **Experimental Design**

165 Upon EEG fitting completion, participants were seated 57cm away from the screen.
166 EEG recording was manually started prior to trial commencement. Participants were
167 instructed to fixate on a cross situated at the centre of the screen while 150 flashing discs
168 were presented in a first block of trials paired with two auditory (or tactile) stimuli, followed,
169 after a brief resting period, by a second block of 150 flashing discs paired with two tactile (or
170 auditory) stimuli. To control for order effects (including fatigue or boredom), the order of the
171 blocks was counterbalanced, with half of the participants performing the tactile DFI first, and
172 the other half performing the auditory DFI first. For the tactile DFI block, participants were

173 asked to place their left index finger immediately below the presentation of the flashing disc
174 to maximise spatial co-occurrence of the visual and tactile stimuli processing.

175 In all trials participants were required to verbally report whether they perceived one or
176 two flashes, to avoid motor interference from participants using their resting hand to respond
177 to the stimuli, especially with the tactile version of the experiment. Participants were
178 instructed to provide unspeeded, accurate responses. The verbal report was then input by the
179 examiner via the “1” and “2” key on the keyboard which prompted the new trial to start after
180 a variable inter-trial interval.

181

182 **Statistical Analysis**

183 **Behavioural data analysis**

184 The participants’ perceived illusory flashes across the different SOAs were used to separately
185 calculate for the auditory- and tactile-DFI the temporal window in which the visual illusion
186 was maximally perceived. Therefore, we calculated the percentage of illusory trials (i.e. two
187 flashes perceived) and plotted them as a function of SOAs separately for the auditory- and
188 tactile-DFI. A psychometric sigmoid function [$y = a+b/(1+\exp(-(x-c)/d))$]; a = upper
189 asymptote; b = lower asymptote; c = inflection point; d = slope] was then fitted to each
190 percentage distribution returning a corresponding inflection point (centre c) of the fitted
191 sigmoid representing the point of decay of the illusion, taken as an index of the TWI. If data
192 would not fit to the sigmoid function, participants’ performance was deemed unreliable and
193 discarded. Following this procedure, 11 of the 62 participants were not enrolled in the full
194 experiment procedure and therefore excluded from data analysis.

195

196 **EEG data analysis**

197 **Sensor space analysis**

198 EEG activity concurrently recorded during task execution was analysed to calculate
199 individual alpha and beta frequency peaks, for each participant performing the auditory- and
200 tactile-DFI tasks.

201 In the first 15 participants, EEG analysis was performed on electrode Oz only.
202 Depending on the band of interest the data was band pass filtered as follows: for alpha, a high
203 pass filter of 3Hz and a low pass filter of 40Hz were used (identical to Cecere et al., 2015);
204 for beta, given the lower power relative to alpha, a more stringent criterium was used: a high
205 pass filter of 12Hz and a low pass filter of 25Hz were used. The EEG signal was segmented
206 in equal epochs of 2000ms. As data in this first sample of participants was not synched to
207 stimulus presentation (no trigger was recorded for each stimulus onset and response), the
208 2000ms epochs corresponded to consecutive non-overlapping segments independent of the
209 stimulus onset (for a total of ~170 epochs on average). The potential confound of induced and
210 evoked oscillatory responses was controlled for in the second group of 36 participants, where
211 64 channel EEG was recorded at a sampling rate of 500Hz. In this group the EEG signal was
212 re-referenced offline to the average of all scalp electrodes. EEG data was subsequently
213 segmented into 2000ms epochs time-locked to and preceding the visual stimulus onset. This
214 resulted in 150 epochs of pre-stimulus oscillatory activity for each of the three frequency
215 bands assessed both for the tactile and auditory DFI task. Each single epoch was visually
216 inspected for artefacts (from eye blinks and muscle contractions), and manually rejected
217 where necessary. For each participant and for all the recorded electrodes a full power
218 spectrum was obtained through Fast Fourier Transform (FFT) with zero padded window
219 (nominal frequency resolution 0.125Hz). Finally, for each participant, task and frequency
220 band, EEG segments were averaged for calculation of the average peak frequency in the
221 visual cortex, as calculated at the electrode Oz. For each frequency band, the peak frequency
222 was determined for each participant as the value corresponding to the maximum peak

223 frequency within their frequency range: alpha, 7-12Hz; beta, 12-25Hz. Finally, for each
224 participant the speed (in ms) of one single oscillatory cycle was calculated using the peak
225 frequency data (in Hz) obtained in the alpha and beta bands over Oz in the first 15
226 participants and over 64 channels in the other 36 participants.

227

228 **Source Space analysis**

229 All source space analyses were performed on the second group of 36 participants for whom
230 the signal had been recorded from a full set of 64 EEG channels.

231

232 **Frequency peak analysis in virtual electrodes**

233 Virtual electrodes were computed for three different cortical areas (visual cortex, auditory
234 cortex and somatosensory cortex) using the linearly constrained minimum variance scalar
235 beamformer (Sekihara et al., 2004) implemented in Fieldtrip. First, a 10 mm three-
236 dimensional grid was fitted to the MNI standard brain. Then, the forward model was created
237 using a standardized realistic head model. The spatial filters were computed for each DFI task
238 using a 2-s pre-stimulus and a 0.5-s post second stimulus covariance window, with the
239 regularization parameter set to 10%. Single trial time series were projected to the cortical
240 surface by multiplying them by the spatial filters weights. The source volume was
241 interpolated with the MNI standard brain to define three regions of interest: right calcarine
242 gyrus (visual-cortex), right superior temporal gyrus (auditory cortex), and the right
243 postcentral gyrus (somatosensory cortex). For each participant the IAF and IBF were
244 calculated in the voxel inside each of the three ROIs that showed a clear peak with the
245 maximal amplitude. Finally, for each participant and selected voxel we calculated the speed
246 (in ms) of one single oscillatory cycle for each peak frequency data (in Hz).

247

248 **Phase locking value analysis**

249 To quantify the frequency specificity synchronization between the visual and the
 250 somatosensory cortex in the tactile-DFI condition, and between the visual and the auditory
 251 cortex in the auditory-DFI condition, we computed the phase locking value (PLV) centred in
 252 each participant specific IAF and IBF (Lachaux et al. 1999). The time series in each virtual
 253 electrode was filtered with Fc of IAF and IBF +/- 1Hz. The instantaneous phase complex
 254 representation of the filtered signal was calculated as follows: $e^{i\phi(t)} = s_a(t)/|s_a(t)|$, where $s_a(t)$ is
 255 the signal's analytic representation. The phase alignment between the two virtual electrodes
 256 was computed as follows:

$$257 \quad PLV_{i,j}(t) = \frac{1}{N} \left| \sum_{n=1}^N e^{-i(\varphi_i(t,n) - \varphi_j(t,n))} \right|$$

258

259

260 where N is the number of trials.

261 PLVs were computed separately for trials within each participant's TWI and for trials outside
 262 each participant's TWI, and rescaled with respect to a 100-ms pre-stimulus window.

263 Nonparametric statistics were used to compute significant differences between each condition
 264 (Maris & Oostenveld, 2007). First, temporal clusters of PLVs were calculated based on time-
 265 points that were significant in paired t-tests. Then, Monte-Carlo randomisation was
 266 performed to obtain the empirical distribution of the maximum cluster statistic, computed as
 267 the sum of within-cluster t-values. The observed cluster was considered significant if its
 268 cluster statistic value was above the 95% of the empirical distribution.

269

270 **Correlation analyses on behavioural data**

271 First, we looked at the behavioural data obtained in the 51 participants for the
 272 auditory- and tactile-DFI, to compare performance in the two tasks and characterise for the

273 first time the temporal profile of the tactile DFI. Second, we assessed the relationship
274 between the known auditory-DFI and the previously unexplored tactile-DFI temporal
275 profiles.

276 To investigate this relationship, we also utilised the robust skipped correlation method
277 as described by Pernet et al. (2013).

278

279 **Correlation analyses between behavioural and electrophysiological data (sensor space)**

280 Next, we performed correlational analyses between the individual speeds (in ms) of each
281 oscillatory cycle and the individual width (in ms) of the TWI separately for the auditory- and
282 tactile-DFI.

283 Our behavioural and electrophysiological data were used to test the following predictions.

284 Firstly, we aimed to replicate data from Cecere et al., (2015) providing evidence suggesting
285 that occipital IAF is selectively predictive of TWI size. Secondly, we wanted to test the
286 hypothesis that occipital IAF is predictive of both the size of the auditory and tactile TWI or
287 alternatively that the size of TWI is differently accounted for by the occipital IAF in the
288 specific instance of the auditory DFI and by the Individual Beta Frequency (IBF) in the
289 specific instance of the tactile DFI. We tested these hypotheses first in the initial 15
290 participants over Oz (with epochs unlocked to stimulus onsets) and again in the sample of 36,
291 this time using a full array of electrodes allowing for a topographical distribution of Pearson's
292 r (and stimulus-locked epochs). As the preliminary analyses of both behavioural and EEG
293 data showed comparable results between groups, notably excluding at the EEG level the
294 potential confounds of evoked responses in the calculation of individual frequency peaks,
295 data from both groups were pooled together for behavioural and EEG analyses at sensor Oz.
296 Furthermore, we utilised the robust skipped correlation method as described by Pernet, et al.,
297 (2013).

298

299 **Multiple regression analyses between behavioural and electrophysiological data (source**
300 **space)**

301 To test whether any relationship between behavioural and oscillatory data was
302 specific to the visual cortex a multiple linear regression analysis was used to assess the
303 relationship between: 1) the TWI in the auditory-DFI and the IAF and IBF of visual and
304 auditory virtual electrodes; 2) the TWI in the tactile-DFI and the IAF and IBF of visual and
305 somatosensory virtual electrodes (Keil et al., 2016). A forward step procedure was adopted to
306 fit the regression model.

307

308

309 **Results**

310 **Auditory-induced vs. tactile-induced DFI**

311 We first determined the temporal profile for the auditory- and tactile-DFI. For the
312 auditory-DFI we replicated previous reports (Cecere et al., 2015) of an average TWI just
313 around 100ms. The temporal profile of the tactile-induced DFI was very similar to the
314 auditory-induced DFI in the same participants and did not significantly differ from each other
315 (auditory-induced TWI: 99.02ms (S.E.M.: 3.08); tactile-induced TWI: 102.80ms (S.E.M.:
316 3.23); $t(50) = -1.02$; $p = 0.31$). We then tested whether these two measures were correlated.
317 We found a significant correlation between the two versions of the DFI (Pearson's $r = 0.31$ p
318 $= 0.03$) which also survived the robust skipped correlation method ($r = 0.31$, $CI = [0.02\ 0.55]$)
319 (See Figure 1).

320

321 We further compared the two sensory versions of the illusion by contrasting the
322 goodness of fit across the two versions of the DFI. Specifically, measurements were taken for
322 the R^2 value (as an indicator of the goodness of fit) for each curve across participants and

323 conditions. We found that the goodness of fit for the tactile illusion ($R^2=0.70$) was
324 significantly lower compared to that of the auditory illusion ($R^2=0.83$, $p < .001$), suggesting
325 the tactile illusion is inherently noisier than the auditory version.

326 Overall, a first interpretation of these behavioural findings is that the auditory and
327 tactile version of the DFI might be driven by similar neurophysiological mechanisms.

328

329 **EEG correlates of auditory- and tactile-DFI**

330 **Sensor space**

331 We found that occipital IAF (in ms) positively correlates with the size of the TWI in
332 the auditory-DBI (Pearson's $r = 0.52$; $p < .001$), which also survives robust skipped
333 correlations ($r = 0.41$, $CI = [0.18\ 0.59]$), such that faster IAFs accounted for shorter TWIs,
334 essentially replicating the results of Cecere et al., (2015). Pearson's correlation topography
335 (calculated on 36 participants) suggests that this effect is maximal over posterior regions and
336 is frequency-specific as no significant correlations could be found for IBF (calculated on
337 51 participants: $r = -0.06$; $p = .69$) (See Figure 2). Crucially, when looking at the tactile-DFI, a
338 different pattern of results emerged. IAF did not correlate with TWI when the TWI was
339 induced by tactile stimuli ($r = -0.13$; $p = .38$). Instead we found that occipital IBF positively
340 correlated with the size of the TWI in the tactile-DFI (Pearson's $r = 0.54$; $p < .001$), which
341 also survives robust skipped correlations ($r = 0.54$, $CI = [0.32\ 0.69]$), such that faster IBFs
342 accounted for shorter TWIs (See Figure 3B).

343

344 **Source Space**

345 Multiple linear regression analysis showed that, for the TWI of the auditory-DFI task,
346 the visual IAF (Beta = 0.751, $p < .01$) was a significant predictor (in line with recent findings
347 by Keil & Senkowski (2017)), while the auditory IAF (0.040, $p > 0.05$), the visual IBF

348 (Beta=0.020, $p>0.05$) and the auditory IBF (Beta=-0.05, $p>0.05$) were not significant. The
349 overall model fit was $R^2 = 0.184$.

350 For the TWI of the tactile-DFI task, the visual IBF (Beta = 0.984, $p < .05$) was a
351 significant predictor, while the somatosensory IBF (-0.141, $p>0.05$), the visual IAF (Beta=-
352 0.020, $p>0.05$), and the somatosensory IAF (Beta=0.104, $p>0.05$) were not significant. The
353 overall model fit was $R^2 = 0.16$.

354

355 **Phase locking value**

356 Next, we explored whether the frequency-specific effects observed at the level of the
357 visual cortex for the auditory-DFI and the tactile-DFI can be best explained by a network
358 specific mechanism. For this purpose, we measured the Phase Locking Value (PLV) in alpha
359 and beta oscillatory activity for auditory-visual and somatosensory-visual networks
360 depending on: 1) the performed task (auditory- and tactile-DFI) and 2) the individual TWI,
361 thus contrasting trials within and outside the TWI respectively.

362 Non-parametric statistical analysis revealed significant differences between trials
363 within and outside the TWI (see Figure 3). Specifically, IAF PLVs between the auditory and
364 visual cortices in the auditory-DFI were significantly greater for the trials outside the TWI in
365 a temporal cluster comprised between 310 and 400 ms post stimulus ($p=0.046$). IBF PLVs
366 between the visual and somatosensory cortices in the tactile-DFI differed between conditions
367 in two temporal clusters, between 210 and 260 ms and between 280 and 360 ms post stimulus
368 ($p=0.015$ and $p=0.03$, respectively).

369

370

371 **Discussion**

372 In the current study we characterised for the first time the temporal profile of the
373 tactile-DFI directly comparing it to the temporal profile of the auditory-DFI. We found that
374 these temporal profiles are comparable; they do not significantly differ and positively
375 correlate, suggesting that similar mechanisms may be at play in determining these effects. We
376 thus tested which neurophysiological mechanism might best account for the auditory- and
377 tactile-DFI.

378 EEG results demonstrated that oscillatory processes relate to the two illusions in a
379 frequency- and network-specific manner. Whilst replicating previous findings demonstrating
380 a relationship between IAF and auditory-DFI (Cecere, et al., 2015; Keil & Senkowski, 2017),
381 we could not replicate this relationship between IAF and tactile-TWI. Instead, a positive
382 correlation between TWI and IBF was found, such that faster IBF predicted shorter TWI.
383 This was found both at sensor and source space, over early visual areas. Moreover, in source
384 space we found that visual (but not auditory or somatosensory) IAF explained the audio-
385 visual TWI (in line with a recent report by Keil & Senkowski, 2017) and similarly only
386 visual-IBF explained the tactile-visual TWI.

387 To test for the specific interpretation that oscillatory correlates of the auditory- and
388 tactile-DFI represent not just a local occipital phenomenon but rather a reliable marker of the
389 specific crossmodal network engendering the illusion we have looked at an index of
390 connectivity between nodes of the network, namely PLV. Specifically, we investigated the
391 modulation of signal strength between auditory-visual and somatosensory-visual networks in
392 alpha and beta bands following stimulus presentation.

393 We found enhanced PLV in alpha (but not beta) oscillations between auditory-visual
394 (but not tactile-visual) nodes, while the same was found in beta (but not alpha) oscillations
395 between tactile-visual (but not auditory-visual) nodes, confirming that oscillatory tuning to
396 the particular version of the illusion reflects a marker of network-specific activation.

397 This frequency and network specific PLV enhancement was found for trials not
398 inducing the illusion. This finding might reflect temporal alignment to coherent temporal and
399 quantity information across the senses within the temporal binding unit defined by the
400 oscillatory cycle (Romei et al., 2012). This same mechanism may be time-sensitive to
401 quantity-disparity information presented within the temporal binding unit defined by the
402 oscillatory cycle, leading to altered integration processes across the senses, ultimately
403 resulting in an illusory percept.

404 What neurophysiological mechanism might be in place to account for this set of
405 results? A relevant model which might explain the current data is the “Communication
406 Through Coherence” framework (Fries, 2005; 2015). Here, neural communication is
407 subserved by neural synchronization between remote but functionally interconnected areas.
408 Specifically, such neural synchronization is the result of alignment of post-synaptic neural
409 activity to pre-synaptic input, creating temporal windows of optimal, preferred
410 communication between involved areas. In this case, such temporal profiles observed in our
411 study related to the auditory and tactile-DFI may be the result of top-down directed alpha and
412 beta (7-25 Hz) influences (feedback connections) on primary sensory input (Fries, 2015),
413 shaping the final illusory perceptual outcome.

414 From this perspective, if a crossmodal stimulus (auditory/tactile) phase-aligns
415 oscillatory activity (alpha/beta) in visual areas, it will define the temporal windows
416 corresponding to such oscillatory cycle lengths (alpha/beta) within which two consecutive
417 stimuli may give rise to the illusory percept (i.e. the TWI). The illusory phenomenon will be
418 engendered by a second crossmodal phase alignment attempt induced by the second cross-
419 sensory stimulus reactivating the visual trace being still processed by the ongoing phase
420 alignment induced by the first multisensory pair. Thus, individual frequency peaks would

421 characterize the temporal resolution of interregional synchronization within which the TWI
422 phenomenon arise.

423 A closely related reference framework has been introduced by Klimesch et al., (2007),
424 who proposes that communication between remote, but interconnected areas can be achieved
425 through travelling waves, that is neural oscillations allowing information transference as
426 measured through propagation between electrodes via a neural network (Klimesch et al.,
427 2007, Muller et al., 2018). According to this framework, local oscillatory activity (i.e.
428 resonance frequency) in auditory (alpha) or somatosensory (beta) cortices will propagate
429 towards the visual cortex accounting for the specific differential impact of alpha and beta
430 oscillations on the auditory- and tactile-DFI, respectively. This mechanism allows prompt
431 rescaling of temporal sampling across the senses, optimizing cross-sensory communication
432 efficiency.

433 Under these circumstances, one expects the respective size of observed TWIs to
434 reflect the length of the oscillatory cycle determining it, i.e., ~100ms when alpha oscillations
435 mediate the auditory-TWI and ~70ms when beta oscillations mediate the tactile-TWI. While
436 the case for the auditory-DFI, the tactile-DFI instead shows a TWI comparable to the
437 auditory-DFI rather than one significantly shorter.

438 Here several issues may combine to account for the lack of one-to-one
439 correspondence between beta cycle length and the length of tactile-TWI. First, it simply takes
440 longer for signals from the hand to reach the brain than it does for signals from the ears (von
441 Békésy, 1959). Such conduction time differences could total 10-15ms which may in part
442 account for the longer than expected tactile-TWI. Second, the tactile-DFI was far noisier than
443 its auditory counterpart, with its overall goodness of fit being significantly lower. A possible
444 caveat accounting for noisier fitting may lie on the asymmetry in our experimental design.
445 White-noise was continuously played in the tactile- but not auditory-DFI in order to cancel

446 out the spiky noise induced by the tactile stimulator. One potential solution could have been
447 to use white-noise across both versions of the illusion, or even better, intermix both versions
448 within the same block while continuously playing white-noise. Additionally, this might have
449 taken care of a potentially induced bias in the allocation of intersensory attention (Pomper et
450 al., 2015) across the two versions of the illusion.

451 However, it should be noted that by pairing white-noise with the auditory-DFI,
452 participants may have relied more on visual information (Hartcher-O'Brien et al., 2014),
453 which may hamper the auditory-DFI.

454 Moreover, several reports have shown the DFI to be resistant to feedback training
455 (Rosenthal et al., 2009) and that participants perceive the illusion independently of
456 crossmodal spatial congruence (Innes-Brown & Crewther, 2009) or even with prior
457 awareness of the illusion itself (Rosenthal et al., 2009), suggesting a minor role played by
458 intersensory attention allocation in this particular task.

459 Therefore, given the comparative nature of our design looking at possible differences
460 of the impact of auditory and tactile stimuli on DFI, it was imperative to control for the
461 specific contribution of each sensory modality.

462 Playing white-noise in the tactile-DFI might have contributed to the tactile-TWI being
463 more skewed towards slower durations due to noisier curve fitting, leading to a less efficient
464 temporal profile calculation of the tactile-DFI. These aspects may in part provide an
465 explanation as to the lack of a one-to-one relationship between TWI and the beta cycle
466 length. Nevertheless, they would not affect or alter the relationship between TWI and the
467 oscillatory marker as they represent a fixed-level noise to be accounted for in the calculation
468 of the absolute size of the tactile-TWI.

469 The specific mechanism subtending this outcome may be comparable across sensory
470 modalities but simultaneously reflects the peculiarity of each sensory modality, including

471 temporal resolution. In other words, auditory and tactile crossmodal induced visual illusions
472 might have been caused by the specific oscillatory properties of each sensory signal's pairing.
473 The different oscillatory tuning could be explained as the specific computational speed
474 needed by the cross-sensory network to efficiently integrate information, thus representing
475 the optimal quantum for temporal binding between a given cross-sensory pair when
476 impacting visual processing specifically. In this respect, there is ample evidence that, in
477 isolation, visual and auditory sensory processing are governed by oscillatory activity in the
478 alpha band (e.g. Ergenoglu et al., 2004; Hanslmayr et al., 2007; van Dijk et al., 2008; Romei
479 et al., 2008a,b; Dugue' et al., 2011; Romei et al., 2010; Weisz et al., 2011; Frey et al., 2014),
480 while somatosensory processing typically occurs within the beta band (Salenius & Hari,
481 2003; Foffani, et al., 2005; Engel & Fries, 2010; Baumgarten, et al, 2015). While there is
482 abundant documentation of the relationship of visual processing with alpha oscillations, and
483 with the speed of alpha frequency (e.g. Samaha and Postle 2015; Wutz et al., 2016, 2018;
484 Ronconi et al., 2018; Minami & Amano 2017; Gulbinaite et al., 2017), there is little empirical
485 evidence highlighting the specific oscillatory nature of the interaction between multiple
486 senses. We and other groups have shown that the impact of simple auditory stimulation on
487 visual processing seems to be governed by the way sounds phase aligns alpha oscillatory
488 activity in the occipital cortex (Teplan, Krakovská, & Štolc, 2003; Romei et al., 2012;
489 Mercier et al., 2013; Gleiss & Kayser, 2014; Frey, et al., 2014). Yet, it was unclear whether
490 this was a general feature of crossmodal interactions within the visual system or whether the
491 specific cross-sensory input determines the fate of the visual response to the visual
492 processing. In the current study we provide the first evidence highlighting the relevance of
493 neural communication at the network level through frequency-specific oscillatory activity.
494
495

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621

622 **Figure legends**

623 **Figure 1. Behavioral data.** Sigmoid curve represents the best fit of the average probability
624 of perceiving the double flash illusion (DFI) plotted as a function of inter-beep (red) and
625 inter-tap (blue) delays. Each individual point represents the average TWI at each SOA. Upper
626 inset represents the significant positive correlation between respective TWIs for each illusion.
627 Lower inset displays the absolute values of the average TWIs for the auditory-induced (red)
628 and the tactile-induced (blue) TWI, respectively.

629

630 **Figure 2. EEG correlates of auditory- and tactile-DFI.**

631 **A. Auditory-DFI.** Whilst viewing the flashing disc (12ms duration) participants also
632 experienced two 3500Hz tones (both with a 7ms duration). These auditory
633 stimulations were separated by a variable SOA (36ms - 204ms). Participants were
634 asked to ignore the sound and state aloud whether they perceived one or two flashes.

635 **B. Tactile-DFI.** Whilst viewing the flashing disc (12ms duration) participants also
636 experienced two brief taps to their left index finger (both with a 7ms duration). These
637 tactile stimulations were separated by a variable SOA (36ms - 204ms). In addition,
638 white-noise was continuously played in order to mask the noise induced by the tactile
639 stimulation. Participants were asked to ignore the tactile stimulation and state aloud
640 whether they perceived one or two flashes.

641 **C. Correlation plots** (upper panels) for occipital regions (electrode Oz) and **Pearsons' r**
642 **topographic distributions** (lower panels) between auditory-TWI and alpha (leftmost
643 panel) or beta (rightmost panel) bands. A selective, positive and significant
644 relationship between the auditory-induced TWI and the speed of alpha oscillations

645 was found suggesting that faster alpha speed accounts for shorter TWI, replicating
646 previous evidence (Cecere et al., 2015; Keil & Senkowski, 2017).

647 **D. Correlation plots** (upper panels) for occipital regions (Electrode Oz) and **Pearsons' r**
648 **topographic distributions** (lower panels) between tactile-TWI and alpha (leftmost
649 panel) or beta (rightmost panel) bands. A selective, positive and significant
650 relationship between the tactile-induced TWI and the speed of beta oscillations was
651 found suggesting that faster beta speed accounts for shorter TWI.

652

653 **Figure 3. Phase Locking Value (PLV) Analysis in Source space.**

654 Phase Locking Value (PLV) in the alpha (leftmost quadrants) and beta (rightmost
655 quadrants) oscillatory activity for auditory-visual (upper quadrants) and somatosensory-visual
656 (lower quadrants) networks. For each quadrant, trials within (blue trace) and outside (red
657 trace) each individual TWI are depicted as a function of time (ms) from visual stimulus onset.

658 In the auditory-DFI, trials outside the TWI showed significantly higher PLVs in the
659 alpha band for the auditory-visual (but not somatosensory-visual) network between 310 and
660 400 ms poststimulus.

661 In tactile-DFI, trials outside the TWI showed significantly higher PLVs in the beta
662 band for the somatosensory-visual (but not auditory-visual) network between 210 and 260 ms
663 and again between 280 and 360 ms poststimulus.

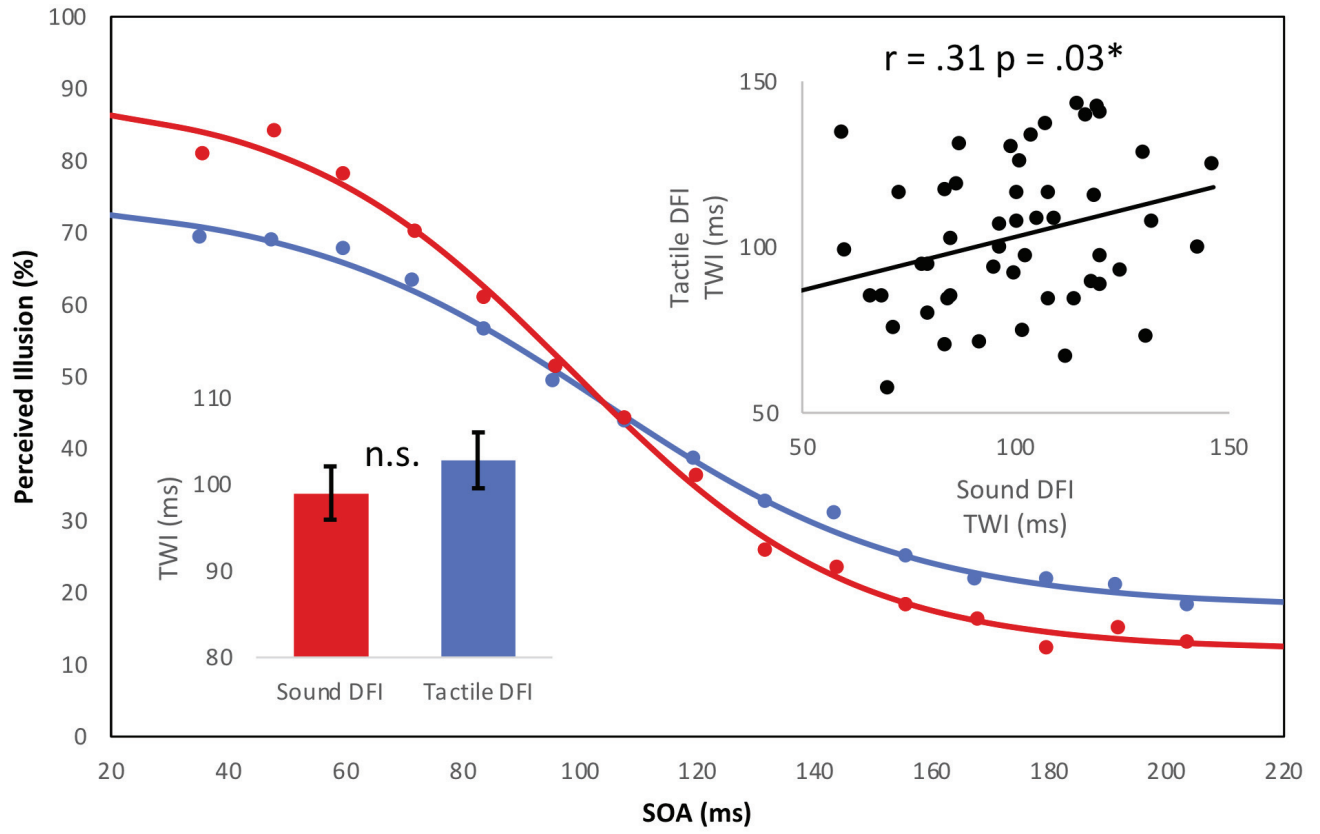
664 PLV differences between trials within or outside the TWI occurred at a late time
665 following stimuli presentation. However, it should be noted that by nature of experimental
666 design, the second crossmodal stimulus was not locked to the first one but jittered by tens of
667 milliseconds (different SOAs), which might have masked an early differential PLV onset.

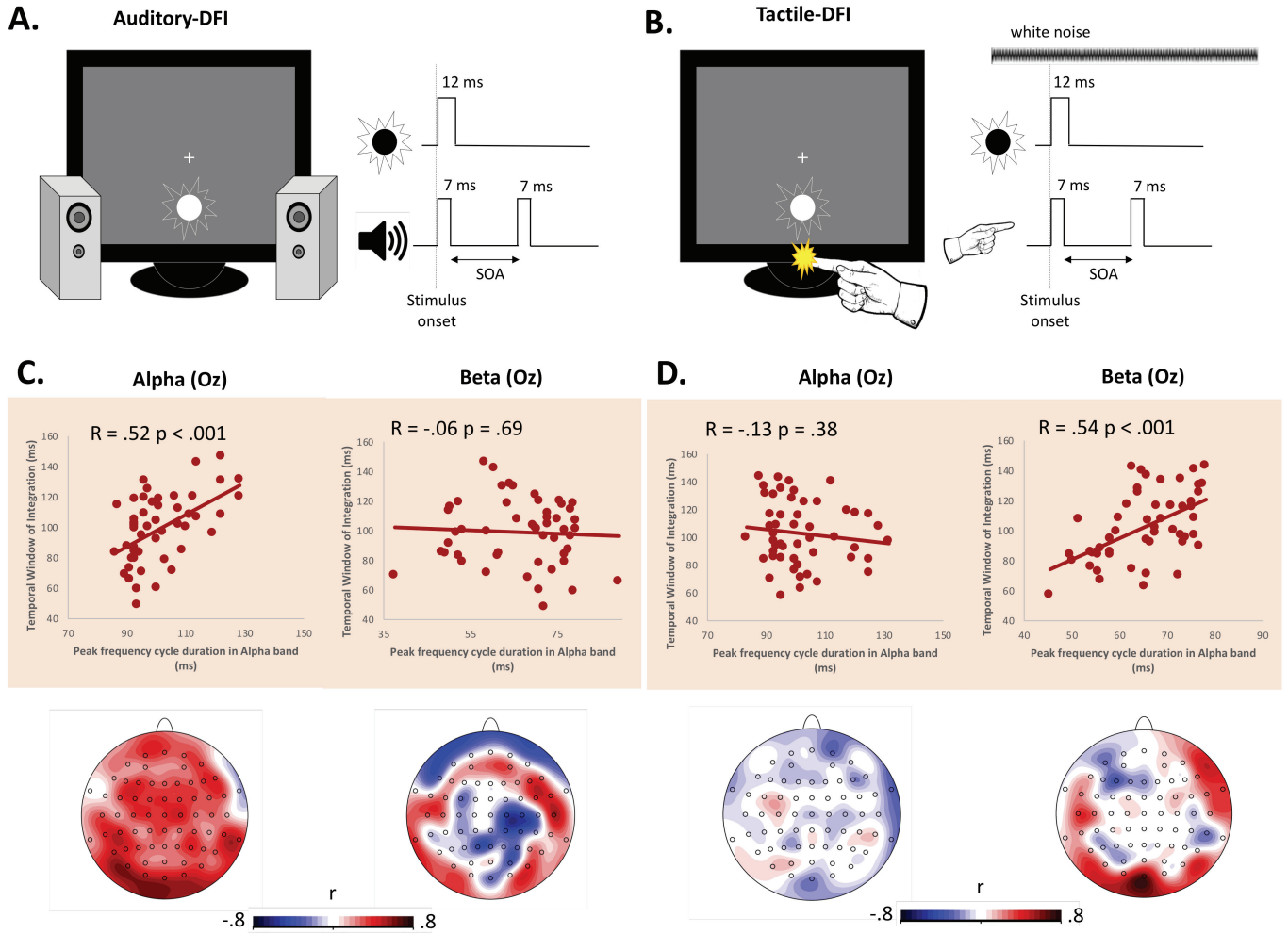
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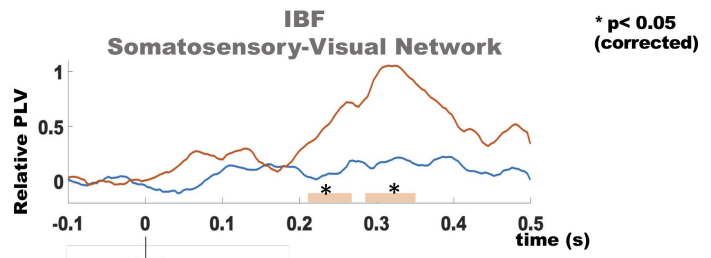
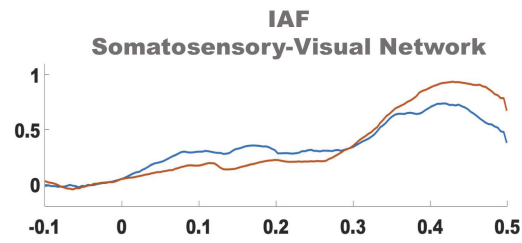
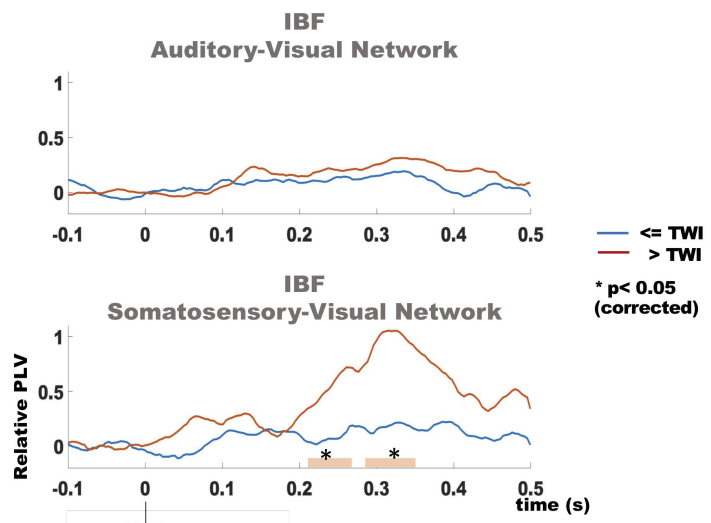
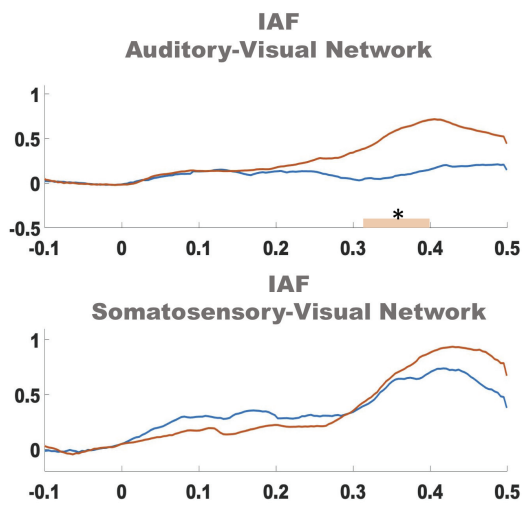
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— $\leq TWI$
— $> TWI$
* $p < 0.05$
(corrected)

