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The neural correlates of coloured music: A functional MRI investigation of auditory–visual synaesthesia

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ABSTRACT

In auditory–visual synaesthesia, all kinds of sound can induce additional visual experiences. To identify the brain regions mainly involved in this form of synaesthesia, functional magnetic resonance imaging (fMRI) has been used during non-linguistic sound perception (chords and pure tones) in synaesthetes and non-synaesthetes. Synaesthetes showed increased activation in the left inferior parietal cortex (IPC), an area involved in multimodal integration, feature binding and attention guidance. No significant group-differences could be detected in area V4, which is known to be related to colour vision and form processing. The results support the idea of the parietal cortex acting as sensory nexus area in auditory–visual synaesthesia, and as a common neural correlate for different types of synaesthesia.

1. Introduction

In synaesthesia the perception of a certain stimulus ('inducer') results automatically in an additional internally generated sensation ('concurrent'). The main characteristics of synaesthesia are its consistency (Baron-Cohen, Wyke, & Binnie, 1987; Cytovic, 2002; Simner & Logie, 2007) and automaticity (Lupianez & Callejas, 2006; Mills, Boteler, & Oliver, 1999): one inducer always triggers the same concurrent sensation, which cannot be suppressed or altered voluntarily. The most investigated form is grapheme-colour synaesthesia, in which achromatic letters, words or numbers are perceived in specific colours. In auditory–visual synaesthesia, all kinds of sound (e.g. music or single tones) can induce additional visual experiences, as for example colours, forms and textures (Cytovic, 2002; Ward, Huckstep, & Tsakanikos, 2006). Investigating the neural basis of acoustically induced synaesthesia is of particular interest as it is a condition, in which visual experiences can be elicited without any external visual input. Further, a better understanding of this phenomenon may help to shed more light on the mechanisms of audio–visual integration.

Two types of models are discussed to explain the mechanisms of synaesthesia: a model of direct cross-activation (Ramachandran & Hubbard, 2001) and a disinhibited feedback model (Grossenbacher & Lovelace, 2001). The former model propagates a direct linkage between the areas of inducer- and concurrent-representation, e.g. in grapheme-colour synaesthesia the area of grapheme representation and the adjacent colour processing region V4 in the fusiform gyrus, while the latter proposes an unusual activation of concurrent-areas via disinhibition of feedback coming from a "multisensory nexus" area.

There is growing evidence from several neuro-imaging studies for an involvement of V4 (Brang, Hubbard, Coulson, Huang, & Ramachandran, 2010; Hubbard, Arman, Ramachandran, & Boynton, 2005; Nunn et al., 2002) and the parietal cortex (Rouw & Scholte, 2007, 2010; van Leeuwen, Petersson, & Hagoort, 2010; Weiss & Fink, 2009; Weiss, Zilles, & Fink, 2005) in grapheme-colour synaesthesia. However, it is not clear if the same neural mechanisms are involved in different types of synaesthetes or different forms of synaesthesia. One possibility is that there is one common factor and additional variable factors which depend on individual differences (Hubbard, 2007; Rouw & Scholte, 2010). A recent investigation using dynamic causal modelling (DCM) of fMRI data (van Leeuwen, den Ouden, & Hagoort, 2011) found evidence for different mechanisms underlying synaesthesia depending on the type of synaesthetes. According to their data, disinhibited feedback from the parietal cortex to V4 is more relevant for associator synaesthetes (who perceive synaesthetic colours evoked by graphemes

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Table 1
Mean values, standard deviations (SD) and *T*-statistics of demographic data.

	Synaesthetes	Controls	Statistics
N (male)	14 (5)	14 (5)	
Age (SD)	38.00 (13.77)	36.79 (12.64)	$t = 0.215$; $p = 0.832$
MWT-B[a] right answers (SD)	30.79 (3.87)	30.00 (4.13)	$t = 0.519$; $p = 0.608$
OMSI[b] probability in % (SD)	43.45 (27.66)	36.54 (26.76)	$t = 0.671$; $p = 0.508$
Years of music lessons (SD)	7.64 (5.92)	8.36 (8.85)	$t = 0.251$; $p = 0.804$
Years of instrumental training (SD)	8.21 (10.53)	7.36 (9.46)	$t = 0.227$; $p = 0.822$
Handedness: right (left)	13 (1)	13 (1)	
Grapheme-colour synaesthesia[c]	11	–	
Coloured month/week-days[c]	10	–	
Other forms of synaesthesia[c]	11	–	

[a] Mehrfach Wortschatz Test B according to Lehrl et al.
[b] Ollen Musical Sophistication Index according to Ollen et al.
[c] Additionally reported forms of synaesthesia.

in their 'mind's eye'), while a cross-activation mechanism between V4 and the 'letter shape area' is more relevant for projector synaesthetes (who see the colour directly projected to the written letter). The results found by van Leeuwen et al. fit also to a combined model of synaesthesia (Hubbard, 2007) integrating the cross activation idea together with a parietal 'hyperbinding' mechanism (Esterman, Verstynen, Ivry, & Robertson, 2006).

While 'coloured-hearing' was a very popular topic of the scientific literature from the 18th to the 20th century (Marks, 1975), few recent studies have investigated auditory–visual synaesthesia depending on non-linguistic inducer stimuli. A recent investigation demonstrated that on the one hand this form of synaesthesia shows the characteristics of genuine synaesthesia (consistency and automaticity) and on the other hand that it seems to recruit mechanisms which are also used in normal cross-modal perception (Ward et al., 2006). A recent electrophysiological event related potential study on auditory–visual synaesthesia revealed differences in early as well as late components between synaesthetes and controls due to tone perception, but no evidence for an auditory evoked potential over occipital sites (Goller, Otten, & Ward, 2009). The authors proposed an involvement of audio–visual integration areas which lay close to regions normally involved in auditory perception.

The current study investigates the neural correlates of auditory–visual synaesthesia induced by single tones and chords. It is to our knowledge the first group study on this form of synaesthesia using fMRI. Our aims were two folded: first to identify brain areas which show differences in activation according to inducing stimuli in synaesthetes compared to controls. Second to test the hypothesis that V4 is involved in auditory–visual synaesthesia, as it has been reported for grapheme-colour synaesthesia, by comparing brain activation in this area as a region of interest (ROI) between groups.

2. Methods

2.1. Participants

Fourteen auditory–visual synaesthetes and fourteen control subjects, who did not report synaesthesia, participated in the study. The controls were matched for age, sex, handedness, IQ as measured by the MWT-B (Mehrfach-Wortschatz-Intelligenztest B) (Lehrl, 1995) and musical expertise as measured by the Ollen Musical Sophistication Index (OMSI) (Ollen, 2006) and years of music lessons (Table 1). The local ethics committee approved the study and written informed consent was obtained from all participants.

Synaesthetes were asked (directly prior to the scanning procedure) to rate the strength of their synaesthesia induced by sounds on a 10 point scale (1 = very weak, 10 = very strong).

2.2. Consistency of synaesthesia

All participants performed a consistency test (Eagleman, Kagan, Nelson, Sagaram, & Sarma, 2007), a modification of the offline version of the Synaesthesia Test Battery (http://www.synesthete.org/) of Eagleman and colleagues, on a PC. Thirty-six pure tones of 12 different timbres were presented, with three different pitches for each instrument. Every stimulus was presented separately and three times in a randomized order, so that there were 108 stimuli in total. The stimuli were generated on an apple computer using the EXS24 sampler of the audio sequencer software 'Logic Audio Pro' (Emagic). They were edited for length and loudness and presented via standard headphones.

Subjects were instructed to adjust loudness to a comfortable listening level and to select for every stimulus a colour by moving a cross hair cursor over a colour matrix. Synaesthetes were asked to choose the colour which matched their experienced synaesthetic colour induced by the tone best, non-synaesthetes were asked to select the colour which they thought to fit best to the tone. Every tone could be played as often as needed until participants confirmed their choice by pressing a button. Consistency was calculated via the geometric distance of the RGB (red green blue) values between the three repetitions as described in (Eagleman et al., 2007).

2.3. Functional magnetic resonance imaging (fMRI) procedure

2.3.1. Experimental design

To avoid habituation, different sound stimuli were presented in a pseudo randomized order. There were six sound conditions: major, minor and dissonant piano chords and pure piano, sine and bassoon tones (each stimulus group in 12 different pitches: C', Cis', D', Dis', E', F', Fis', G', Gis', A' Ais' H'). Stimuli were presented via pneumatic headphones in an event-related design with three sessions and 48 stimuli per session (8 stimuli per condition per block; 24 stimuli per condition in total), with a stimulus duration of 2 s and an inter-stimulus interval of 13 s. Between the sessions the participants had the opportunity to relax to avoid tiring and attention diminishment. To achieve a better signal to noise ratio of acoustic stimuli against the scanner noise, the sound level was adjusted individually for each subject during a test scan in which some of the stimuli were presented and sound level was adjusted until the stimuli were clearly audible and tones and chords were clearly discriminable for the subject. All participants held a response device in their right hand and performed a task during measurement to guaranty that they fully attended the stimuli. They were asked to press the right button (with their right middle finger) when hearing a chord and the left one (with their right index finger) when hearing a tone. Subjects were instructed to keep their eyes closed during the sessions to avoid visual deflection. All synaesthetes reported that they perceive synaesthesia with open as well as with closed eyes.

2.3.2. Image acquisition

Functional images were acquired on a 1.5 T General Electrics scanner (Signa Horizon; GE Medical Systems, Milwaukee, WI) equipped with a standard head coil, at the Institute of Diagnostic and Interventional Neuroradiology, Medical School Hannover. T2* functional scans covering the whole brain were acquired by using a multislice two-dimensional echo-planar imaging (EPI) sequence (acquisition matrix 64×64 pixels, 26 axial slices, TR = 3000 ms, echo-time (TE) = 40 ms, Field of view (FOV) = 26 cm, slice thickness = 5 mm, flip angle = 90°). Measurements were acquired in three sessions of 12 min. Each fMRI time series consisted of 244 images; the first 4 of them were discarded to allow the scanner to reach a steady state.

2.3.3. Image processing and data analysis

Image processing and statistical analysis was conducted with spm5 (Statistical Parametric Mapping software version 5, Wellcome department of Imaging Neuroscience, London, UK, http://www.fil.ion.ucl.ac.uk) using MATLAB7.0 release 14 (The Mathworks Inc., Natrick, MA). Images were realigned to the 1st volume to correct for inter-scan movements by means of a rigid body transformation with three rotation and three translation parameters. Further, the EPI volumes were spatially normalized to a standard template of the Montreal Neurological Institute (MNI, Canada), resulting in a voxel size of $2\,mm \times 2\,mm \times 2\,mm$, and smoothed (with a Gaussian smoothing kernel of 8 mm) to create statistical maps of changes in relative regional BOLD responses corresponding to the six experimental conditions.

Data analysis was performed on the single subject level by modelling the six stimulus conditions (major, minor and dissonant piano chords and piano, bassoon

Table 2
Mean values, standard deviations (SD) and group comparisons of behavioural data.

	Synaesthetes	Controls	Statistics
Dimensionless consistency score[a] (SD)	1.26 (0.55)	1.85 (0.50)	$t = 2.981$; $p = 0.006^{**}$
% correctly identified tones[b] (SD)	92.13 (5.57)	86.11 (17.64)	$t = 1.095$; $p = 0.312$
Reaction time[b] in s	1.39 (0.30)	1.31 (0.45)	$t = 0.266$; $p = 0.793$

$^{**}p < 0.01$
[a] Tone-Colour Consistency Test: smaller scores indicate a higher tone-colour consistency.
[b] Tone-Chord Discrimination Task conducted during fMRI.

and sine tones) using a set of temporal basis functions including the canonical hemodynamic response function (HRF), as well as its temporal and dispersion derivates, to account for inter-regional and between-subject variability in the shape of the HRF. Periods in which no stimuli were presented (13 s after each stimulus presentation) were modelled as an implicit baseline. Six vectors representing the parameters from the realignment procedure were included as regressors of no interest. The resulting random effects single-subject t-contrasts were then entered into a full-factorial analysis of variance (ANOVA) model in spm5 with main between factor 'group' (two levels: synaesthetes and controls) and main within factor 'stimulation' (six levels: different sound conditions). The statistical threshold was set to $p_{FWE} < 0.05$ (extend threshold > 10 voxels) for the *F*-Tests for the main effect of 'group' and 'stimulation', as well as the post hoc *T*-Test for the main effect of 'group'. After coordinates were transformed to Talairach space using the mni2tal function in MATLAB7.0 (http://www.mrc-cbu.cam.ac.uk/Imaging/mnispace.html), corresponding brain areas were retrieved from the Talairach Deamon database server (Lancaster et al., 2000) and verified with the spm Anatomy toolbox version 1.7 (Eickhoff et al., 2005).

Regions of interest (ROI) analysis was conducted to detect whether or not there was increased brain activation in synaesthetes compared to controls in bilateral colour area V4 (Talairach coordinates (*xyz*) = −29, −68, −14/30, −75, −19 (McKeefry & Zeki, 1997). The ROI-analysis was conducted using MarsBaR (Brett, Anton, Valabregue, & Poline, 2002) with ROIs defined as spheres around the V4 coordinates with a 10 mm radius.

3. Results

3.1. Behavioural data

Similar as shown by Ward et al. (2006), auditory–visual synaesthetes were significantly more consistent compared to controls in the Tone-Colour Consistency-Test. No significant differences were detected between synaesthetes and controls in the numbers of correctly identified tones, as well as reaction times in the Tone-Chord Discrimination Task conducted during fMRI (Table 2).

By rating the strength of their synaesthesia on a ten point scale, synaesthetes indicated values between 2 and 10 (mean = 6.8 ± 2.34). For all synaesthetic subjects, all stimuli categories elicited synaesthetic sensations during the scan: in 13 of the 14 synaesthetes coloured forms and in one synaesthete only colours. None of the controls reported perceiving any synaesthetic experiences during the scan or at any other time point.

3.2. Imaging data

3.2.1. Group comparison

The analysis of the group data by means of ANOVA at a significance level of 0.05 (FWE corrected for multiple comparisons, extend threshold > 10 voxels) revealed only one significant cluster of 41 voxels for the main between factor 'group' (*F*-Test) with the centre of mass at the location of MNI (*xyz*) −46, −54, 58. This site corresponds to inferior parietal cortex (Brodmann area 40). The post hoc *T*-Test revealed a cluster of 61 voxels with a centre of mass at the same location as brain site responding stronger to the stimulation in the synaesthetes-group (Fig. 1A). The inverse contrast (controls > synaesthetes) did not show significant brain activation in any region, even when a low threshold of 0.01 uncorrected was chosen. There also was no significant interaction effect between the factor 'group' and the factor 'stimulation'.

ROI analysis in left and right colour processing area V4 did not reveal significant differences in brain activation between synaesthetes and controls.

3.2.2. Effect of stimulation

The *F*-Test with the main within factor 'stimulation' at a significance level of 0.05 (FWE corrected for multiple comparisons, extend threshold > 10 voxels) revealed two significant clusters in the right and left temporal gyrus (Fig. 1B). The cluster in the right superior temporal gyrus (194 voxels) had the centre of mass at the location of MNI (*xyz*) 58, −16, −4, the cluster in the left middle temporal

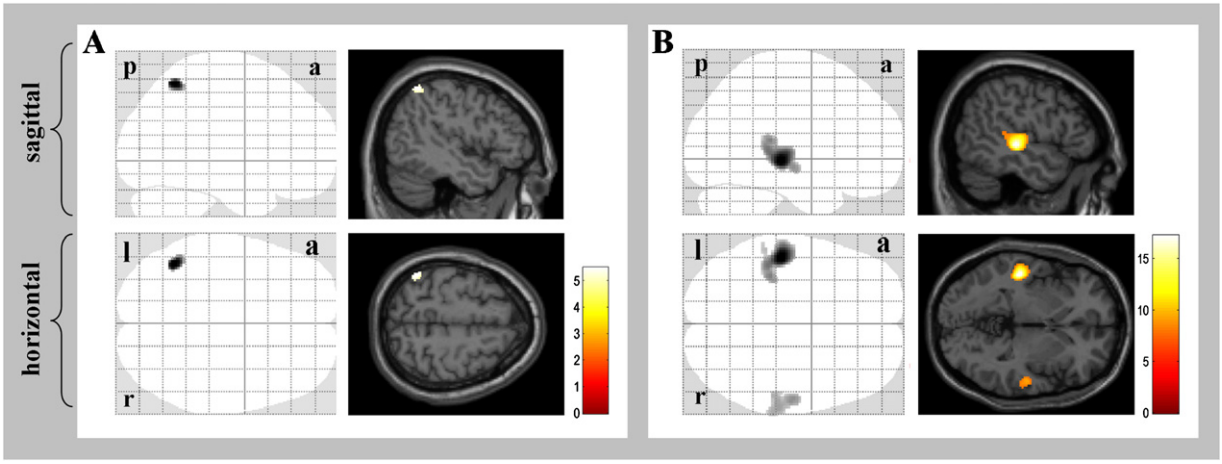

Fig. 1. Significant brain activation differences on the whole-brain level revealed by the multi-factorial ANOVA with the factors "group" and "stimulation" ($p_{FWE} < 0.05$, extent threshold > 10 voxels). (A) Effect of the main between factor "group" (*T*-Test): one cluster is significantly more activated during auditory stimulation in synaesthetes in the left inferior parietal cortex (IPC). MNI-coordinates of the centre of mass of this cluster: $x = -46$, $y = -54$, $z = 58$. (B) Effect of the main within factor "stimulation" (*F*-Test): in both subject groups differences between stimulation conditions revealed two significant clusters in left and right temporal cortex. MNI-coordinates of the centre of mass of these clusters are: $x = -50$, $y = -24$, $z = -2/x = 58$, $y = -16$, $z = -4$. p = posterior, a = anterior, r = right, l = left, colour bars show strength of activation.

gyrus (664 voxels) had the centre of mass at the location of MNI (*xyz*) −50, −24, −2.

4. Discussion

In the current fMRI-study a group of auditory–visual synaesthetes and a group of matched controls was investigated during the perception of speech unrelated sounds (tones and chords) which all evoked synaesthesia in the synaesthete-group. The results showed that at the whole brain level the IPC was significantly more activated in the synaesthete-group compared to the control-group. Differences in brain activation according to different stimulation conditions were detected in bilateral temporal gyrus, but there was no significant interaction between stimulation condition and synaesthesia.

4.1. The role of the inferior parietal cortex (IPC)

Synaesthetes show significantly more brain activation compared to controls in the left IPC. This area is known to have many different functions: it is involved in spatio-dynamic processing as well as in cross-modal (e.g. audio–visual) integration (Calvert, 2001), polymodal object processing (Grefkes, Weiss, Zilles, & Fink, 2002; Shen, Hu, Yacoub, & Ugurbil, 1999), mental imagery (Ganis, Thompson, & Kosslyn, 2004; Knauff, Kassubek, Mulack, & Greenlee, 2000) and non-synaesthetic feature-binding (Robertson, 2003). Further, it is part of a network of frontal and parietal areas which is essential for attention guidance and visuo-motor control (Astafiev et al., 2003; Corbetta & Shulman, 2002; Grefkes, Ritzl, Zilles, & Fink, 2004). Specifically its functions in cross modal integration and feature binding have led to the hypothesis that this area induces a synaesthetic "hyperbinding" (Robertson, 2003), serving as a "sensory nexus" between inducer- and concurrent-areas, e.g. by coupling them with each other via disinhibited feedback (Grossenbacher & Lovelace, 2001). The results of the current investigation support this hypothesis. Furthermore they are in line with the findings of several previous studies dealing with different forms of synaesthesia, like grapheme-colour and number-form synaesthesia, which also revealed increased parietal activation according to synaesthesia (Rouw & Scholte, 2010; Tang, Ward, & Butterworth, 2008; van Leeuwen et al., 2010; Weiss et al., 2005), structural differences in the parietal cortex between synaesthetes and controls (Rouw & Scholte, 2007; Weiss & Fink, 2009) and a disruption of synaesthesia by TMS (transcranial magnetic stimulation) over parietal sites (Esterman et al., 2006; Muggleton, Tsakanikos, Walsh, & Ward, 2007; Rothen, Nyffeler, von, Muri, & Meier, 2010). Together with reports of different forms of synaesthesia within one family/one synaesthete (Ward & Simner, 2005), the fact that similar findings are reported for different types of synaesthesia speaks in favour for a general mechanism, depending on the parietal cortex.

4.2. Involvement of visual areas

In synaesthesia research, one central question is, if visual areas – and especially the colour area V4 in the fusiform gyrus – are involved in synaesthetic perception. Some studies reported activation in or near this area in synaesthetes during the presentation of inducers versus non-inducing stimuli (Nunn et al., 2002; Rouw & Scholte, 2007; Sperling, Prvulovic, Linden, Singer, & Stirn, 2006; Steven, Hansen, & Blakemore, 2006) or significantly more brain activation according to inducing stimuli in synaesthetes compared to controls (Hubbard et al., 2005; van Leeuwen et al., 2010), while others did not (Paulesu et al., 1995; Tang et al., 2008; Weiss et al., 2005). Further, structural differences between synaesthetes and controls have been detected in or adjacent to the fusiform gyrus (Jaencke, Beeli, Eulig, & Haenggi, 2009; Rouw & Scholte, 2007; Weiss & Fink, 2009). As this area is not only involved in processing of colour information (Bartels & Zeki, 2000), but also other object properties like shape or texture (Gallant, Shoup, & Mazer, 2000; Gustavsen & Gallant, 2003) it would be a perfect candidate for processing the synaesthetically perceived photisms induced by sound, which often consist of colour, shape and texture. In the present study there were no differences found in brain activation between synaesthetes and controls in V4. However, it has been pointed out previously that the absence of significant group differences in V4 cannot be considered as proof against its involvement in synaesthesia (Hubbard, 2007). For example, it may be that the involvement of visual areas in general is different in different types of synaesthetes. Earlier visual areas (e.g. primary visual cortex) have been found to be activated according to inducing stimuli in single cases of synaesthesia (Aleman, Rutten, Sitskoorn, Dautzenberg, & Ramsey, 2001; Steven et al., 2006) or showed anatomical differences in synaesthetes compared to controls (Jaencke et al., 2009). Further, some studies found increased activation in synaesthetes not in V4, but more associative visual areas as in the inferior temporal cortex (Aleman et al., 2001; Paulesu et al., 1995) or an area in the lingual gyrus which is thought to process colour knowledge (Rich et al., 2006). Therefore it is possible that while in some synaesthetes rather early visual areas are involved, more associative areas may be recruited in others. This would explain why no group difference in V4 activation could be detected by the present study and former investigations.

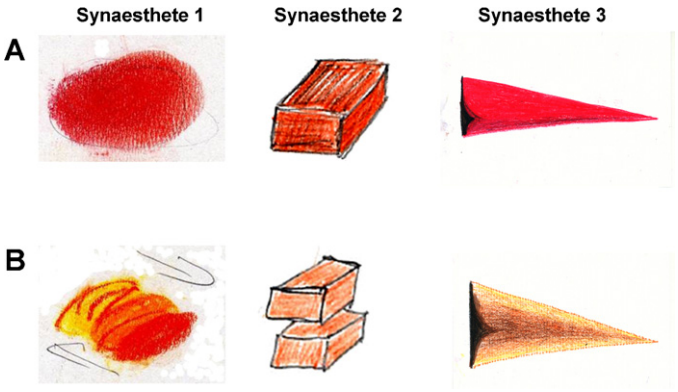

Fig. 2. Acoustically induced synaesthetic photisms: the photisms induced by (A) a piano tone in A' and (B) a major piano chord in A' painted by the same three synaesthetes are shown exemplarily. Arrows indicate the direction of movement of the photism.

4.3. Effect of stimulation conditions

Differences in brain activation according to different stimulation conditions were detected in bilateral temporal gyrus. The differences between stimulus conditions in auditory cortex activation might result mainly from the different complexity of the sound stimuli: as a recent meta-analysis of functional neuroimaging studies has shown, increasing complexity of auditory stimuli results in increased auditory cortex activation—in particular in the superior temporal gyrus (Samson, Toussaint, & Belin, 2011). However, there was no significant interaction between the factors 'group' and 'stimulation', which leads to the interpretation that the brain activation induced by synaesthesia did not depend on the stimulation condition. This fits to the statements of the synaesthetes, who did not report stronger synaesthetic sensations for a particular stimulus group. For some subjects, chords and tones differed in the complexity of the perceived photisms but this was not at all consistently found in all subjects (Fig. 2).

5. Conclusions

The involvement of the IPC as a multimodal integration area in synaesthesia, which is supported by the present study and also by studies dealing with other forms of synaesthesia, speaks against cross-activation as the only mechanism underlying synaesthesia. The results are more in line with the idea of the IPC as a sensory nexus, leading to synaesthesia by disinhibited projections to visual areas. Alternatively, visual areas might first be activated via cross activation and inducer and concurrent are bound together in a second step by the IPC (Hubbard, 2007). No evidence for an involvement of V4, nor any other visual area, has been found in this study—a fact which could be the result of individual differences amongst synaesthetes concerning the recruitment of visual brain areas. The results are in line with the findings of Rouw and Scholte in grapheme colour synaesthetes, who also observed increased activation in left parietal cortex in the whole group of synaesthetes, while activation in visual areas and connectivity in the inferior temporal cortex as measured by diffusion tensor imaging (DTI) depended on individual differences between synaesthetes (Rouw & Scholte, 2007, 2010). The similarity between the findings of the current study to previous investigations on other forms of synaesthesia points to similar mechanisms across different forms of synaesthesia.

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