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Research report

# The neural correlate of colour distances revealed with competing synaesthetic and real colours

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ABSTRACT

Synaesthetes claim to perceive illusory colours when reading alphanumeric symbols so that two colours are said to be bound to the same letter or digit (i.e., the colour of the ink, e.g., black, and an additional, synaesthetic, colour). To explore the neural correlates of this phenomenon, we used a Stroop single-letter colour-naming task and found that distances in colour space between the illusory and real colours of a letter target (as computed from either the RGB or CIExyY coordinates of colours) systematically influenced the degree of neuronal activation in colour-processing brain regions. The synaesthetes also activated the same fronto-parietal network during the classic colour-word Stroop task and single-letter tasks. We conclude that the same neural substrate that supports the conscious experience of colour, as triggered by physical wavelength, supports the experience of synaesthetic colours. Thus, two colour attributes (one that is wavelength-dependent and one that is illusory) can be bound to the same stimulus position and simultaneously engage the colour areas in proportion to their similarity in colour space.



A minority of people in the normal population report a phenomenon, called synaesthesia, which seems to entirely escape the possibility of ''knowing what it is like'' either through shared physical stimulation or by reference to past experience. Most synaesthetes (Rich et al., 2005; Simner et al., 2005) report the intrusion of colour sensations that are systematically triggered by stimuli that are not coloured per se (e.g., black-printed alphanumeric symbols). This has been labeled grapheme-colour synaesthesia. Specifically, a synaesthete may report seeing the letter A as generating the sensation of two colours, one being that of the ink (or pixels), which depends on physical wavelengths, and the other being an illusory colour that only the synaesthete experiences. Differently from the illusory experiences of colour afterimages, which can be easily verified by any normal observer, synaesthetic experience is absolutely subjective and highly idiosyncratic. In fact, synaesthetes' reports appear ''alien'' or illogical to the majority of (non-synaesthetic) individuals (e.g., ''how can a letter have two colours simultaneously?''). In contrast, dreams or pain states, although private and idiosyncratic, can be framed in terms of everyone's common experience. Nevertheless, despite its elusiveness, recent research on synaesthesia has proved it to be a genuine phenomenon (e.g., Hubbard and Ramachandran, 2005; Robertson and Sagiv, 2005).

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Current research has revealed that synaesthetic 'photisms' can either assist or interfere with performance in visual tasks (Hubbard et al., 2005) and real and synaesthetic colours are able to interact perceptually (Kim et al., 2006). Interference effects arise when naming the ''objective'' colour of an object (e.g., a letter A) when at the same time this evokes a ''subjective'' or synaesthetic colour (Wollen and Ruggiero, 1983; Dixon et al., 2000; Mattingley et al., 2001; Nikolic et al., 2007). That is, when the ''objective'' and ''subjective'' colours are incongruent (e.g., the letter B is printed in red but evokes also the colour green) there is interference compared to when the colours are congruent (e.g., the B is in green). Most remarkably, synaesthetes can identify and localize a target object (e.g., one digit 5) among distracting objects (e.g., several digits 2) more efficiently than non-synaesthetes, if the target and distractors differ by a synaesthetic colour feature (e.g., Palmeri et al., 2002; Laeng et al., 2004; Laeng, 2009). For some of these subjects and in some situations, the synaesthetic colours can ''pop out'' or, more precisely, cause an accelerated narrowing of attention onto a purely synaesthetically defined odd-man-out element of a scene.

Neuroimaging seems a particularly appropriate tool for revealing whether a sensory experience is actually occurring when there are no ways for other observers to obtain the same experience and verify it. Studies in neuroscience indicate that colour is represented in a network of cortical areas of the human brain, located medially and inferior in the occipital and temporal lobes (Gulyas et al., 1994; Hadjikhani et al., 1998; McKeefry and Zeki, 1997a, 1997b; Tootell and Hadjikhani, 2001; Wade et al., 2002; Zeki and Moutoussis, 1997). Cortical areas responsive to colour include portions of the lingual and fusiform gyrus (Bartels and Zeki, 2000; Corbetta et al., 1991; Lueck et al., 1989). Most interestingly, the colour-processing areas V4 and V8 are active in normal individuals when they experience 'illusory' colours in the absence of chromatic stimuli, e.g., when seeing colour afterimages (Barnes et al., 1999; Hadjikhani et al., 1998; Morita et al., 2004; Sakai et al., 1995). Remarkably, it has been reported that these same areas can also be active when synaesthetes report experiencing their illusory colours (e.g., Nunn et al., 2002; Hubbard et al., 2005; Rich et al., 2006; Sperling et al., 2006; Steven et al., 2006).

The goal of the present study was to investigate what is perhaps the most puzzling phenomenon regarding the synaesthetic reports of some grapheme-colour synaesthetes who can apparently ''project'' the illusory colour in their visual field (e.g., Dixon et al., 2004; Rouw and Scholte, 2007): That is, a single visual stimulus (i.e., the shape of an alpha-numeric symbol) is perceived as having two colours at the same time.

In neural terms, ensembles of colour-opponent neurons in the colour-processing areas V4 and V8 (Hadjikhani et al., 1998; Tootell and Hadjikhani, 2001) might simultaneously code (for unknown reasons) both colours in the synaesthete's brain, so that two colour attributes can be bound to the same stimulus and, for some synaesthetes (as the ones investigated in the present study), to the stimulus's spatial position. Normally, one would expect than in such a case of neural competition, a winner-take-all mechanism (Desimone, 1996; Lee et al., 1999; Reynolds and Desimone, 1999) would settle for a single perceptual interpretation of the stimulus (e.g., the illusory colour). Yet, synaesthetes can report seeing both colours at once; in other words, ''a single feature gives rise to two different qualia'' (Treisman, 2005, p. 248). If one accepts this phenomenological report at face value, it follows that there is no winner between the illusory colour and the ''real'' colour and that both can become bound to the same shape. One possibility is that ''increased connectivity'' between neural networks of the synaesthete's brain (Rouw and Scholte, 2007; Hänggi et al., 2008) might make possible such a dual perceptual experience. One can speculate that, at least for the synaesthetes, the multiple colour areas of the human brain may support in parallel different colour conscious experiences (cf. Zeki et al., 1999).

Specifically, we hypothesized that an increased distance in colour space between real and illusory colours will influence the degree of activity in colour-processing areas. That is, increased colour distance (CD) should result in increased processing of colour features, thus resulting in greater recruitment of neural units in V4/V8. Such a modulatory activity of the colours' similarity could also be interpreted as evidence that multiple colours are simultaneously supported by the activity of colour-opponent neural cells within these visual areas (cf. Nikolic et al., 2007), so as to engender the simultaneous conscious experiences of more than one colour. In addition, based on previous neuroimaging studies of the Stroop task (e.g., Pardo et al., 1990; MacDonald et al., 2000; Gruber et al., 2002; Herd et al., 2006), one would expect that activity could be modulated by CD also in those areas that monitor the level of Stroop conflict.

In order to study the neural correlates of the simultaneous representations of two colours bound to the same stimulus or spatial position, we measured brain activity during the colour-word Stroop task (Stroop, 1935/2004) as well as single-letter variants of Stroop, with two grapheme-colour synaesthetes. Stroop tasks were chosen because in such tasks, both the relevant information (the target; e.g., the ink's colour) in a task and the irrelevant information (the distractor; e.g., the meaning of the word or the synaesthetic colour) are parts of the same stimulus. Research has shown that it is extremely difficult to ignore the irrelevant information (MacLeod, 1991). The classic ''Stroop effect'' is characterized by naming errors and slowing of responses when words indicate different colours than the one in which they are printed (e.g., the word 'blue' is printed with red ink), compared to when they match. In such a task, it seems impossible to ignore the word, which automatically calls attention to another (conflicting) meaning and elicits the tendency to simply read out the (wrong) colour name.

Remarkably, synaesthetes can show Stroop interference with just single coloured letters (e.g., Mattingley et al., 2001; Paulsen and Laeng, 2006). This may happen because the name of the illusory colour of a letter may be automatically activated and this would compete with the name of the physical colour. Indeed, the illusory colour's name should be for synaesthetes the first colour label to come to mind and especially so for ''projector'' than for ''associator'' synaesthetes (i.e., respectively, those synaesthetes who report perceptual-like colour sensations that are localized in external space *vs* those who experience the colours within an ''inner space'' or with the ''mind's eye''; Dixon et al., 2004).

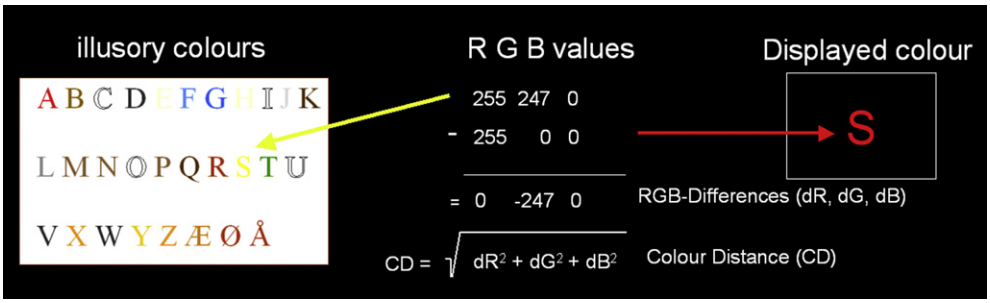


**Fig. 1 – Illustration of the computational method used for obtaining CDs. Each symbol has one ink colour but each letter simultaneously elicits one illusory colour.**

In contrast, for any other colour arbitrarily paired to the same symbol, the synaesthete should make an effort in inhibiting the name of the illusory colour so as to report the ink colour. Non-synaesthetic participants are not expected to show any remarkable effects due to the symbol's identity when naming its ink colour.

Different colours occupy different positions in colour space and the Euclidean distances between colours can be easily computed by using the triplets of RGB colour coordinates obtained from each synaesthete's selections from the colour palette of Microsoft Word and then applying the Euclidean distance formula for three dimensions (see Fig. 1). Although red, green, and blue (RGB) pixels' colour coordinates specify with precision the pixels' colours on a monitor, they bear no systematic relation to psychophysical/neurobiological colour space (e.g., colour-opponency). For example, in RGB space a pure red is just as close to pure blue as it is to green and a pure yellow is further away from its opponent colour than red and green are to each other. However, RGB colour coordinates can be easily converted to CIExyY coordinates (as defined by the International Commission on Illumination), which are instead linearly related to distances in a psychophysical colour space. Thus, for completeness, we shall present results using both coordinate systems.

Based on the above considerations, we expected to observe the following phenomena in our synaesthetes' brains: 1) the distance in colour space between real and illusory colours should influence the degree of activity in colour-processing areas (which we tested with the modified Stroop tasks where synaesthetes named one colour of single-letters while ignoring the other colour); 2) brain activations in the classic Stroop task (with coloured words) and single-letter synaesthetic Stroop tasks should overlap in the synaesthetes (but not in the non-synaesthete control participants).

## 1. Methods

### 1.1. *Participants*

PM is a 62 years old, female, musician and music teacher and TH is a 58 years old, female, psychologist. They both report grapheme-colour synaesthesia such that letters of the alphabet and the 10 digits have various positions within colour space (see Fig. 2). Both synaesthetes also report the synaesthetic colours as localized in external space and that the colour looks like it is on the page; hence, their phenomenology is consistent with the current classification into "projector" synaesthesia (Dixon et al., 2004). Both synaesthetes report no synaesthesia for any other stimuli.

Both PM and TH have normal vision and colour sensitivity. The latter was assessed with the Farnsworth–Munsell 100 Hues Test (PM's score = 26; TH's score = 68) and the Ishihara Pseudoisochromatic Plates (PM's score = 0; TH's error score = 1). PM and TH show high consistency in pairing colours to symbols, as revealed by selecting the same colours from the pantone palette (of Microsoft Word 2000) in two sessions, several months apart, and then correlating each session's values for each symbol and for each of three dimensions of colour: Hue, Saturation, and Luminance ($.83 < R < .99$). PM and TH were tested in sessions half a year apart from each other. Control subjects ($N = 10$) were matched to the synaesthetes by age (mean = 53.8; SD = 14) and sex.

### 1.2. *Methods*

The experimental design was a mixed event-related and block design with parametrically-varied probability of occurrence of congruent among incongruent colours (i.e., 20, 40, 60, 80, 100%). The colour-word Stroop or single-letters tasks had their own control conditions, which consisted of either a string of asterisks or a single asterisk, respectively. The asterisks appeared in the same colours used with words/letters. Finally, there was included also a rest condition.


**Fig. 2 – Alphanumeric symbols as coloured in Microsoft Word 2000 by PM (top two rows) and TH (bottom two rows).**

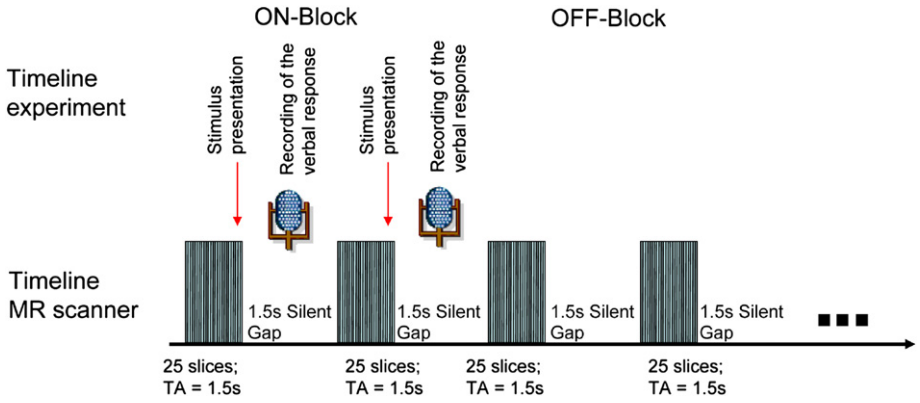


**Fig. 3 – Paradigm used in the fMRI experiments.**

There were 10 blocks with experimental stimuli (i.e., Stroop or single-letter trials), 10 blocks with control trials, and 5 rest conditions. Each block consisted of 10 trials, each with a different colour, and lasted 30 sec. The set of colours was constant across the blocks and the same for the experimental trials as well as the control trials. Subjects were requested to report aloud the colour in which the word, letter or asterisks were written.

The word Stroop task and the single-letter Stroop task were performed in separated runs, with a short break of a couple of minutes. The order of the tasks was randomized across the subjects. In the word Stroop task, we used the same colour words for all subjects (black, blue, brown, green, orange, pink, purple, red, white, and yellow). Instead, the single-letter task was custom-made for each synaesthete, since congruency is in this case entirely based on their

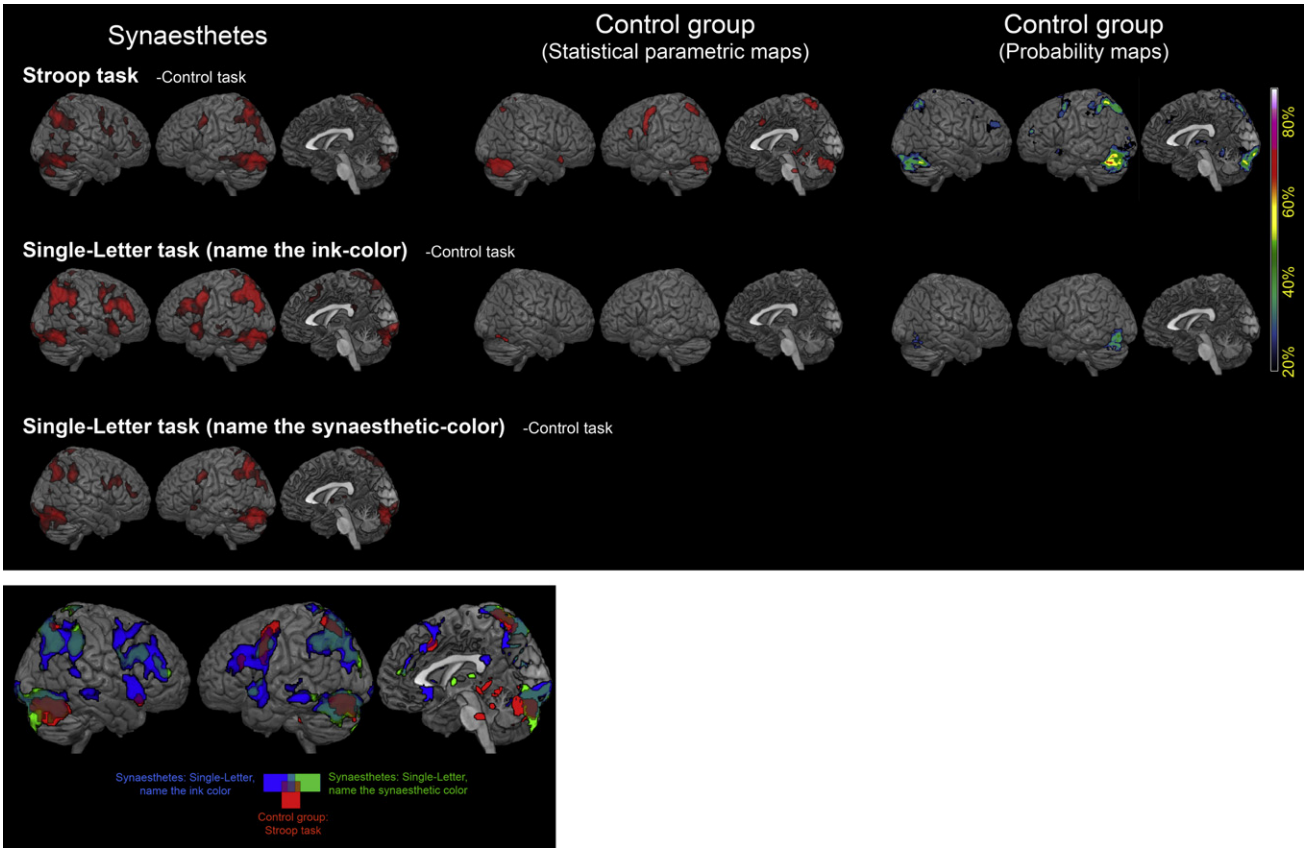


**Fig. 4 – Activations in the Stroop task and single-letter tasks for the synaesthetes (left panel) and the control group (middle panel). Probability maps based on the 10 single subjects analyses (right panel): Maps show for each voxel the probability of being found activated. Overlaps between the Stroop task in the non-synaesthetes with the two single-letter tasks in the synaesthetes (bottom panel).**

**Table 1 – Areas activated in the control group when performing the colour-word Stroop task and the single-letter task [peak-thresholds: *p*(FDR) < .05, extend threshold: 30 voxels].**

| Cluster size | *p*(FDR-cor) | *t*-value | x | y | z | Side | Anatomical description | Brodmann area |
|---|---|---|---|---|---|---|---|---|
| *Control group: Stroop task–control task* | | | | | | | | |
| 3032 | .001 | 8.75 | 22 | −72 | −24 | Right | Cerebellum/Declive | |
| | .001 | 8.74 | 48 | −56 | −24 | Right | Fusiform gyrus | 37 |
| | .001 | 8.43 | −4 | −80 | −20 | Left | Cerebellum/Declive | |
| | .001 | 6.63 | −44 | −76 | −18 | Left | Fusiform gyrus | 37 |
| 482 | .001 | 7.78 | 0 | −34 | −2 | Left | Cerebellum/Culmen | |
| 448 | .002 | 6.91 | −44 | −2 | 58 | Left | Precentral gyrus | 6 |
| | .002 | 6.62 | −44 | 6 | 28 | Left | Inferior frontal gyrus | 44 |
| 243 | .002 | 6.64 | 0 | −58 | 68 | L & R | Precuneus | 5, 7 |
| 348 | .004 | 5.61 | −28 | −62 | 58 | Left | Superior parietal lobule | 7 |
| | .005 | 5.41 | −32 | −54 | 66 | Left | Superior parietal lobule | 7 |
| | .008 | 4.94 | −22 | −68 | 40 | Left | Superior parietal lobule | 7 |
| 56 | .004 | 5.59 | 40 | 22 | −16 | Right | Inferior frontal gyrus | 47 |
| 142 | .006 | 5.23 | 4 | −32 | −30 | Right | Brainstem | |
| 69 | .009 | 4.84 | 0 | 20 | 40 | Left | Cingulate gyrus | 24 |
| 58 | .010 | 4.80 | −44 | 30 | 28 | Left | Inferior frontal gyrus | 45 |
| 60 | .011 | 4.68 | 24 | −62 | 56 | Right | Superior parietal lobule | 7 |
| 31 | .024 | 4.07 | −32 | −68 | −34 | Left | Cerebellum/Uvula | |
| *Control group: single-letter task–control task* | | | | | | | | |
| 44 | .035 | 7.34 | 48 | −70 | −18 | Right | Fusiform gyrus | 19 |
| | .042 | 6.15 | 48 | −60 | −22 | Right | Fusiform gyrus | 37 |

self-reported illusory colour experiences. For these experiments, 8 letters were selected which clearly differed in their synaesthetic colours and which could be easily distinguished with different verbal labels. For TH, we used the single-letters A, B, G, O S, T, V, Z, whereas for PM the letters A, B, C, H, I, K, N, S were used.

### 1.3. *Scanning procedure and data analysis*

The visual stimuli were presented through high-resolution Liquid Crystal Display (LCD) goggles (produced by *Nordic Neuro Lab Inc.*) that were connected to a PC located outside of the MR scanner chamber. Each letter was presented in central vision at a size of approximately 4 degrees of visual angle. Stimulus parameters (duration, number of presentations, order of presentations etc) were controlled from software written in the E-prime programming platform (Psychology Software Tools, Inc.). Silent gaps were inserted between successive Echo-Planar Imaging (EPI) volume acquisitions in order to record the response and not to confound the EPI images with movement artifacts associated with the brief verbal response on each trial. Fig. 3 gives an illustration of the paradigm used.

The data were spatially preprocessed and analyzed using Statistical Parametric Mapping (SPM); that is, Statistical Parametric Mapping software; that is, with SPM5-software package (latest release of SPM5, www.fil.ion.ucal.ac.uk) running on Matlab 2007b (produced by *The MathWorks Inc*, Natieck, MA, USA). The pre-processing of the data included a correction of the head movements ('realignment') and movement related images distortions ('unwarp procedure'). The data from each individual were then normalized to the Montreal Neurological Institute (MNI) anatomical reference space, defined by an EPI template. A transformation into the reference space was obtained by normalizing an averaged image of the respective participant, which was obtained by averaging all realigned and unwarped images across all sessions, into the MNI reference space. The thereby estimated transformation was also applied to all realigned and unwarped images of the respective participant. The normalized images were resampled with a voxel size of $2 \times 2 \times 2$ mm and finally smoothed with a Gaussian kernel of 8 mm.

For the statistical analyses, we followed two different approaches in order to reduce the influence of single outliers. The participants from the control group were first analyzed with individual fixed-effects models, and individual contrasts for the Stroop as well as single-letter task were specified as contrasts against the respective control condition. These individual contrast images were then subjected to a second-level analysis, for analyzing the group effects. The results were explored with a False Discovery Rate (FDR) corrected threshold (Genovese et al., 2004) of *p*(FDR) <.05 and at least 30 voxels per cluster. In order to assess the between subject variability, we estimated, based on the single subject analysis, probability maps (Wilms et al., 2005; Wohlschläger et al., 2005) that show for each voxel the probability of being found as activated above an individual threshold of *p*(FDR) <.05.

The two synaesthetes' were analyzed in a common fixed-effects model and results were explored, using a conjunction across subjects approach (global Null-hypothesis, Nichols et al., 2005), and the same thresholds as for the control group were applied.

To analyze the correlated neural effects of the CDs for the synaesthetic versus real colours, each condition was modelled as train of single events, even though the design was formally a block design. Thereby, the single-letter tasks were split into

**Table 2 – Areas activated in synaesthetes when performing the colour-word Stroop task and the two single-letter tasks ('name the synaesthetic colour' and 'name the ink colour'). Table provides an overview across all condition by displaying *t*-values and coordinates for the reported brain areas. *t*-values and coordinates are representing either global or local maxima of significance in the respective cluster [peak-thresholds: *p*(FDR) < .05, extend threshold: 30 voxels].**

| Side | Anatomical description | Brodmann area | *t*-value | x | y | z | *t*-value | x | y | z | *t*-value | x | y | z |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Synaesthetes: Stroop task–control task | | | | Synaesthetes: single-letter task (name the ink colour)–control task | | | | Synaesthetes: single-letter task (name the synaesthetic colour)–control task | | | |
| Left | Precentral gyrus | 6 | 4.28 | −52 | 0 | 44 | 7.13 | −48 | 0 | 40 | | | | |
| Left | Precentral gyrus | 6 | | | | | 6.81 | −54 | 8 | 42 | 4.31 | −56 | 6 | 40 |
| Left | Angular gyrus | 7 | | | | | | | | | 5.22 | −36 | −62 | 40 |
| Left | Inferior parietal lobule | 7 | 5.24 | −24 | −68 | 32 | 9.64 | −26 | −74 | 32 | 4.51 | −26 | −76 | 30 |
| Left | Superior parietal lobule | 7 | 5.52 | −30 | −64 | 54 | 10.37 | −30 | −70 | 52 | 6.75 | −28 | −68 | 54 |
| Left | Lingual gyrus | 17 | 1.86 | −2 | −74 | −2 | 1.90 | −4 | −72 | 0 | | | | |
| Left | Fusiform gyrus | 19 | 6.32 | −40 | −68 | −14 | 6.58 | −38 | −66 | −16 | | | | |
| Left | Inferior occipital gyrus | 19 | 6.11 | −46 | −74 | −12 | 7.11 | −48 | −74 | −12 | 5.12 | −50 | −72 | −12 |
| Left | Lingual/fusiform gyrus | 19 | 6.11 | −38 | −82 | −14 | 6.70 | −36 | −84 | −16 | 5.95 | −36 | −82 | −18 |
| Left | Middle temporal gyrus | 20 | | | | | 3.59 | −62 | −30 | −14 | | | | |
| Left | Middle temporal gyrus | 21 | | | | | 2.01 | −56 | −18 | −2 | | | | |
| Left | Cingulate gyrus | 23 | | | | | 2.55 | −2 | −38 | 26 | | | | |
| Left | Cingulate gyrus | 32 | | | | | 2.23 | −4 | 28 | 40 | | | | |
| Left | Inferior frontal gyrus | 44 | 2.68 | −42 | 2 | 22 | 7.77 | −38 | 4 | 30 | 3.40 | −40 | 4 | 26 |
| Left | Inferior frontal gyrus | 47 | | | | | 5.93 | −44 | 14 | −6 | 2.93 | −46 | 16 | −6 |
| Left | Rolandic Operculum | 48 | | | | | 4.05 | −54 | 10 | 2 | 2.48 | −60 | 10 | 2 |
| Left | Cerebellum/Declive | | | | | | 4.56 | −44 | −70 | −30 | 5.57 | −42 | −70 | −24 |
| Left | Cerebellum/Declive | | 3.93 | −12 | −84 | −26 | 4.06 | 0 | −82 | −26 | 5.52 | −4 | −82 | −28 |
| Left | Medial Globus Pallidus | | | | | | | | | | 2.02 | −12 | 2 | 0 |
| Right | Middle frontal gyrus | 6 | 3.20 | 40 | 2 | 60 | 3.11 | 40 | 4 | 58 | | | | |
| Right | Precentral gyrus | 6 | 3.23 | 44 | 4 | 28 | 5.02 | 48 | 4 | 46 | 3.40 | 46 | 2 | 30 |
| Right | Supplementary motor area | 6 | | | | | 3.11 | 8 | 12 | 50 | | | | |
| Right | Angular gyrus | 7 | | | | | 9.13 | 36 | −64 | 44 | 4.45 | 36 | −66 | 44 |
| Right | Superior parietal lobule | 7 | 5.45 | 32 | −64 | 46 | 9.13 | 36 | −64 | 44 | 4.29 | 30 | −72 | 56 |
| Right | Middle frontal gyrus | 9 | 2.63 | 36 | 38 | 48 | 3.10 | 40 | 36 | 44 | | | | |
| Right | Middle frontal gyrus | 10 | 2.50 | 32 | 54 | 8 | | | | | | | | |
| Right | Cuneus | 18 | | | | | 2.17 | 10 | −78 | 26 | | | | |
| Right | Fusiform gyrus | 19 | | | | | 7.29 | 46 | −60 | −18 | 5.30 | 46 | −60 | −18 |
| Right | Fusiform gyrus | 19 | 4.80 | 46 | −70 | −18 | 6.32 | 46 | −70 | −16 | 5.05 | 46 | −70 | −14 |
| Right | Inferior occipital gyrus | 19 | 5.45 | 48 | −60 | −20 | 7.31 | 48 | −58 | −20 | 5.30 | 46 | −60 | −18 |
| Right | Middle temporal gyrus | 20 | | | | | 2.79 | 52 | −24 | −12 | | | | |
| Right | Middle temporal gyrus | 21 | | | | | 2.75 | 66 | −28 | −6 | | | | |
| Right | Cingulate gyrus | 32 | | | | | 3.53 | 6 | 26 | 40 | | | | |
| Right | Inferior parietal lobule | 40 | | | | | | | | | 2.66 | 50 | −44 | 54 |
| Right | Supramarginal gyrus | 40 | 2.97 | 50 | −46 | 40 | 6.50 | 50 | −44 | 36 | 4.35 | 50 | −44 | 40 |
| Right | Inferior frontal gyrus | 44 | 3.17 | 44 | 14 | 28 | 7.40 | 44 | 10 | 24 | 3.60 | 44 | 14 | 28 |
| Right | Inferior frontal gyrus | 45 | | | | | | | | | 3.57 | 46 | 28 | 30 |
| Right | Middle frontal gyrus | 46 | 2.32 | 40 | 46 | 24 | 7.54 | 44 | 38 | 26 | 2.89 | 38 | 40 | 24 |
| Right | Middle frontal gyrus | 46 | 2.37 | 36 | 48 | 10 | 4.35 | 42 | 44 | 10 | 3.36 | 36 | 46 | 12 |
| Right | Inferior frontal gyrus | 47 | 2.09 | 46 | 22 | −8 | 5.65 | 36 | 24 | −2 | | | | |
| Right | Cerebellum/Declive | | 3.79 | 36 | −78 | −32 | | | | | | | | |
| Right | Putamen | | | | | | | | | | 2.38 | 2 | −4 | 2 |
| Right | Thalamus | | | | | | | | | | 2.33 | 2 | −22 | 10 |

congruent and incongruent trials. For the incongruent trails (i.e., all possible parings of one letter with the pixel colours that were equal to those indicated for the synaesthetic colours of the other letters in the set), we introduced four additional parameters, which modelled trial-by-trial the CD. We performed this analysis for two colour spaces; one based on the RGB that were obtained from the monitor's colour values and one based on the converted values in psychophysical CIExyY colour space. For both colour spaces, the CD was estimated as difference of the RGB values or CIExyY values, respectively, between the presented colour and the synaesthetically experienced colour. The four parameter represented the differences for red (dR), green (dG), and blue (dB), as well as the total (Euclidian) CD in three-dimensional colour space [$CD(RGB) = sqrt(dR^2+dG^2+dB^2)$], as described earlier (see also Fig. 1). In a second analysis, we specified the same design but used the CIExyY CD instead, i.e., dx, dy, dY, and CD (CIExyY), respectively.

Since we had an expectation for a CD effect, the results were explored with an *F*-contrast at an uncorrected threshold

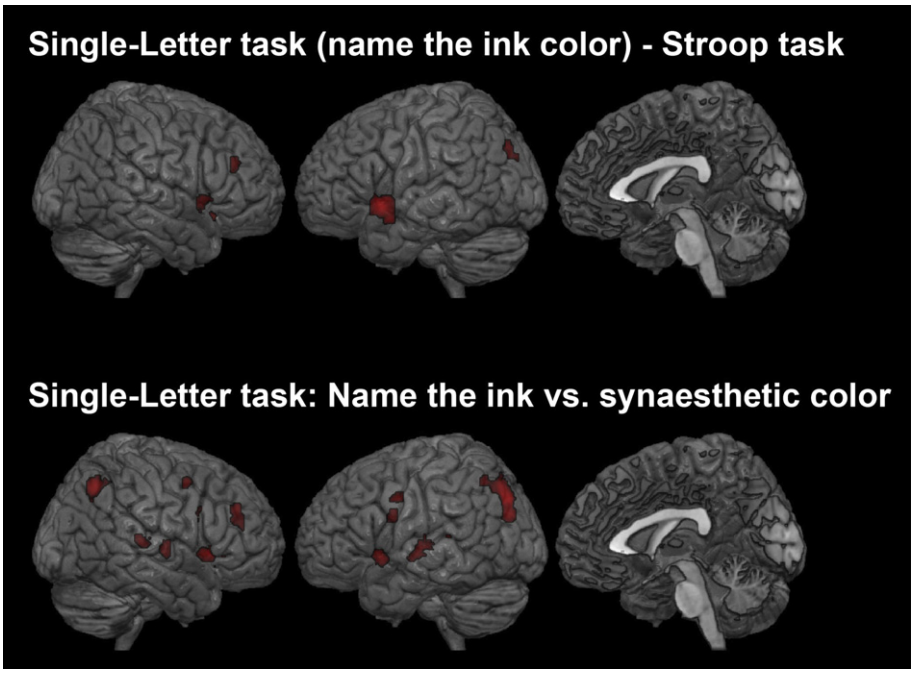


**Fig. 5 – Contrasts between the single-letter task 'name the ink colour' and the other two Stroop tasks in the synaesthetes.**

of $p < .001$ and, again, a cluster threshold of at least 30 voxels per cluster was applied.

## 2. Results

### 2.1. *Control participants*

The Stroop task revealed a network that comprised the occipital and frontal lobes and, in addition, the parietal lobe and the right ventro-lateral prefrontal cortex. By contrast, the single-letter task did not activate more areas than the control condition, except for a small spot in the right occipital lobe (see Fig. 4 and Table 1), possibly reflecting the fact that, on average, the coloured letters were larger in size than the asterisks. The probability maps reflect a very similar result by showing that the network, activated during the Stroop task (when compared to the control condition), was consistently activated also in more than 50% of the control subjects. By contrast, the single-letter task (when compared to the control condition) activated only the occipital areas with a reasonable high consistency, i.e., in more than 50% of the subjects.

### 2.2. *Synaesthetes*

The three main effects for the synaesthetes reflected a similar network as for the Stroop task in the control subjects, although more extended into the prefrontal cortex. While the detected networks for the three conditions were very comparable, the strength of the activations varied such that the condition under which the synaesthetes were asked to name the ink-colour caused the strongest activations (see Fig. 4 and Table 2).

The later notion was further validated by directly comparing the ''name the ink-colour'' condition to the two others, which revealed a fronto-parietal network, which was more active under the 'name the ink' condition than under the Stroop or 'name the synaesthetic colour' condition (see Fig. 5 and Table 3). The Stroop task showed only in medial frontal and sub-cortical areas significant differences when compared to the ''name the ink colour'' task.

Finally, the analysis of the CDs, for both colour spaces, revealed a mainly mainly bilateral parieto-occipital network that was more active when the CD became larger. Results for both colour spaces overlapped in the left inferior parietal lobe as well as bilaterally within the sulcus collateralis, which is the border between the fusiform gyrus and the inferior occipital gyrus (see Figs. 6 and 7 and Table 4). Comparing this with other studies on synaesthesia and colour vision, this area was close to the area, reported as anterior V4, human V4 (hV4), or V8 (see Fig. 7). Performing the same analysis for the condition, where the synaesthetes named the ink colour, only a small spot in the left superior parietal lobe was consistently detected, but no significant contribution of the colour difference was detected in the occipital lobe (see Table 4).

## 3. Discussion

We measured brain activations while two synaesthetes performed the classic Stroop task as well as modified single-letter Stroop tasks. The brain activations for the latter ''synaesthetic'' Stroop tasks and the classic Stroop task (with coloured

**Table 3 – Areas differentially activated in synaesthetes when comparing the three tasks [peak-thresholds: *p*(FDR) < .05, extend threshold: 30 voxel].**

| Cluster size | *p*(FDR-cor) | *t*-value | x | y | z | Side | Anatomical description | Brodmann area |
|---|---|---|---|---|---|---|---|---|
| *Synaesthetes: Stroop task–single-letters task (name the ink)* | | | | | | | | |
| 54 | .040 | 3.11 | 10 | 62 | 16 | Right | Medial frontal gyrus | 10 |
| 31 | .040 | 3.10 | −16 | 52 | 14 | Left | Superior frontal gyrus | 10 |
| 39 | .040 | 2.97 | 6 | 54 | −2 | Right | Medial frontal gyrus | 10 |
| 76 | .040 | 2.90 | 48 | −56 | 8 | Right | Middle temporal gyrus | 37 |
| 44 | .040 | 2.71 | −18 | 4 | 18 | Left | Caudate Nucleus | |
| 39 | .040 | 2.61 | −18 | 28 | 0 | Left | Caudate Nucleus | |
| *Synaesthetes: single-letters task (name the ink)–Stroop task* | | | | | | | | |
| 474 | .000 | 4.00 | −42 | 12 | −4 | Left | Insular | 48 |
| | .000 | 3.50 | −50 | 10 | 0 | Left | Temporal Pole | 38 |
| 110 | .001 | 3.31 | −26 | −76 | 36 | Left | Middle occipital gyrus | 19 |
| | .026 | 2.40 | −30 | −66 | 42 | Left | Inferior parietal lobe | 7 |
| 185 | .009 | 2.73 | 34 | 20 | 2 | Right | Insular | 48 |
| | .011 | 2.67 | 36 | 22 | −12 | Right | Inferior frontal gyrus | 47 |
| 50 | .010 | 2.70 | 46 | 38 | 26 | Right | Inferior frontal gyrus | 45 |
| *Synaesthetes: single-letters task: name the ink colour–name the synaesthetic colour* | | | | | | | | |
| 519 | .001 | 3.76 | −28 | −74 | 34 | Left | Middle occipital gyrus | 19 |
| | .001 | 3.35 | −28 | −70 | 44 | Left | Inferior parietal lobe | 7 |
| 283 | .001 | 3.44 | 36 | 24 | 0 | Right | Insular | 48 |
| 298 | .001 | 3.36 | 36 | −62 | 44 | Right | Angular gyrus | 7 |
| | .002 | 3.07 | 32 | −64 | 32 | Right | Middle occipital gyrus | 19 |
| 232 | .002 | 3.17 | −40 | 4 | 34 | Left | Precentral gyrus | 6 |
| 235 | .003 | 2.97 | −40 | 14 | −4 | Left | Insular | 48 |
| 98 | .006 | 2.72 | −52 | −16 | 2 | Left | Superior temporal gyrus | 22 |
| 122 | .006 | 2.70 | 46 | 40 | 32 | Right | Middle frontal gyrus | 46 |
| 45 | .007 | 2.66 | 52 | 4 | 50 | Right | Precentral gyrus | 6 |
| 30 | .009 | 2.59 | −46 | −34 | 10 | Left | Superior temporal gyrus | 41 |
| 55 | .009 | 2.59 | 66 | −28 | 8 | Right | Superior temporal gyrus | 21 |
| 66 | .010 | 2.54 | 4 | 10 | 58 | Right | Superior temporal gyrus | 22 |
| 36 | .020 | 2.33 | 44 | 10 | 28 | Right | Inferior frontal gyrus | 44 |

words) greatly overlapped for the two synaesthetes but they did not for the non-synaesthetes. This finding with synaesthetes supports the conclusion that illusory colours can automatically interfere with the naming of the ''real'' colours.

When a single coloured letter was shown at a time and the synaesthetic colour was to be named while ignoring the letter's ink colour, we found that the distance in colour space between ''real'' and illusory colours influenced the degree of activity in the visual cortical areas. These findings indicate that the ''real'' and synaesthetic colours can be represented together in areas of the brain known to support the conscious visual experience of colours. Interestingly, the cortical areas that were correlated with the CD between physical colours and synaesthetic colours (see Fig. 7) largely overlap with those of a previous study by Morita et al. (2004), who reported neural activations that were directly correlated with the awareness of the illusory colours of the McCollough aftereffect.

The above findings also indicate that increases in activity in the synaesthetes' cortical areas reflect the level of Stroop interference generated by the dual perception of both the real and illusory colour. Interestingly, the CD effect would seem rather robust since it was revealed by using either coordinate system (i.e., RGB or CIExyY) when computing CDs. Note however, that both synaesthetes failed to show CD effects in the 'name the ink colour' task and that it was only when they were allowed to fully focus attention on the synaesthetic colour (i.e., the 'name the synaesthetic colour' task) that the sensory effect of the physically present ink colour resulted in a modulation of activity within the colour areas. Thus, it would seem that attentional modulation may be necessary to reveal the neural correlate of dual (real and illusory) colour perception (cf. Mattingley et al., 2006; Sagiv et al., 2006). We also surmise that there is an asymmetry in how automatic it is to name a physical colour versus an illusory colour (Dixon et al., 2004), with automaticity favouring the naming of colours that are physically present and can be shared with other interlocutors (note also that this asymmetry is supported by the smaller Stroop interference shown by the synaesthetes in the 'name the ink colour' task *vs* the 'name the synaesthetic colour' task; see Table 5). Hence, we would expect that greater attentional modulation is needed when naming synaesthetic colours than when naming physical colours.

Interestingly, Nikolic et al. (2007) showed that increased CD (i.e., opponency) in a single-letter Stroop between the synaesthetic colour of the letter and its physical colour resulted in slower naming of the physical colour. It remains unclear whether longer processing, as reflected by longer response times (RTs), could also linearly influence activity in V4/V8. To evaluate this possibility in a future study, one would need to compare the effect of CD on RTs and the correlated activity levels in V4/V8.

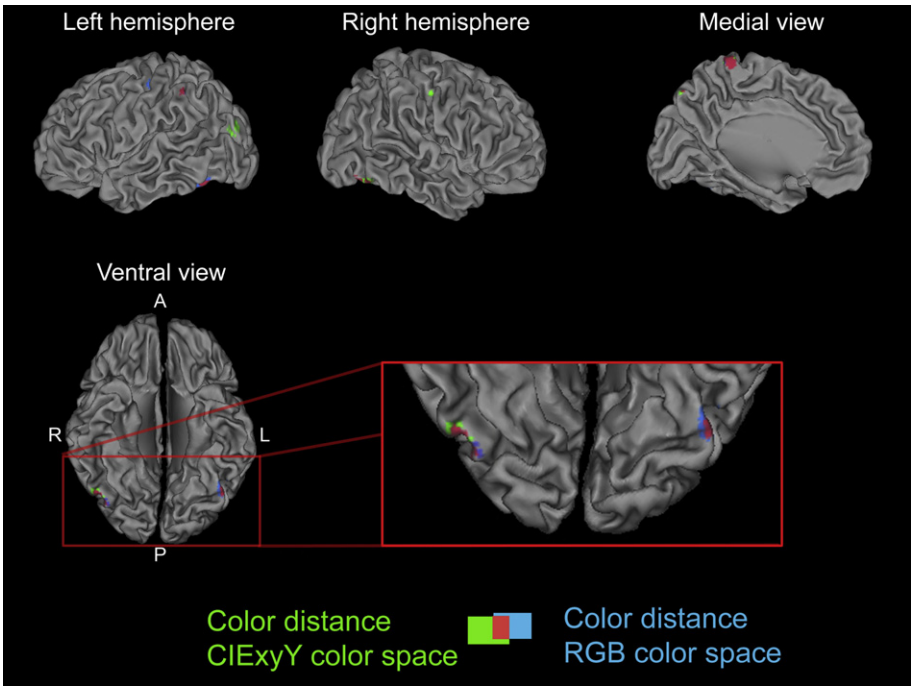


**Fig. 6 – Correlated activity with overall CD during the single-letter tasks 'name the synaesthetic colour' in the synaesthetes.**

Another conspicuous findings in the neuroimaging data was that the frontal network, which is typically activated by Stroop interference (e.g., MacDonald et al., 2000), as well as the cingulate cortex (e.g., Pardo et al., 1990), were highly activated by the synaesthetic Stroop tasks (although such activity was not modulated by CD). In particular, the frontal and parietal regions were significantly more active during the 'name the ink' synaesthetic Stroop task than the 'name the synaesthetic colour'.

As Table 5 shows, at the behavioural level, switching from the 'name the ink colour' to the 'name the synaesthetic colour' caused a lengthening (up to an average of 131 msec) in RT for PM. In other words, in the condition in which the activity in the frontal network was highest, Stroop interference (as measured by RT) was the lowest; in contrast, in the 'name the synaesthetic colour' condition for which activity in the frontal network was low, Stroop interference on RTs was highest. This pattern of results is interesting in the light of a neuroimaging study by MacDonald et al. (2000) on normal subjects performing a Stroop task, which showed that the individuals with highest activation in the frontal region also showed the smallest Stroop interference effect on RTs. Similarly, for our synaesthetic subjects, more activation in the frontal network was associated with smaller Stroop interference effects on RTs.

Finally, in all Stroop tasks, both PM and TH showed activations within the parietal lobes (see Fig. 4). Parietal lobe activity has been observed before in neuroimaging studies of synaesthesia (e.g., Rich et al., 2006). Most importantly, it has often been observed in neuroimaging studies of the classic colour-word Stroop task (e.g., Banich et al., 2000) and was absent in the control group, when they performed the simple

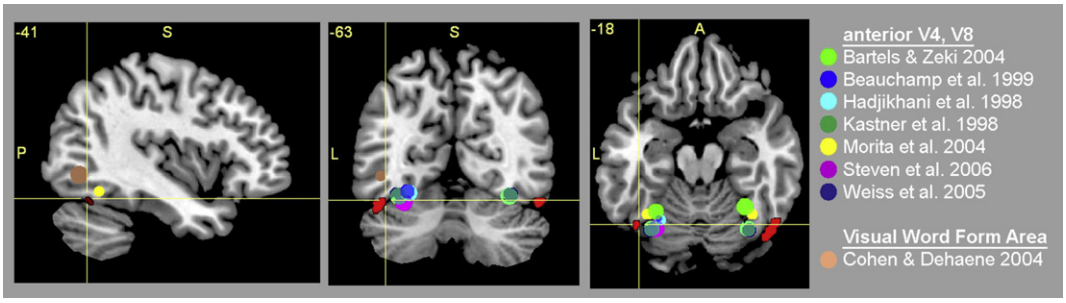


**Fig. 7 – Comparison between areas of the present study that showed activity correlated to CD between the physical and synaesthetic colours (red squares) to activations caused by experiencing either physical or illusory colours in a representative sample of previous studies (coloured circles). Where different coordinate frames were used, all coordinates were accordingly transformed into MNI coordinates (Brett et al., 2002).**

**Table 4 – Areas with activity correlated to the CD between the synaesthetic and physical colour using the RGB as well as the CIExyY colour space (peak-thresholds: $p < .001$, extend threshold: 30 voxel).**

| Cluster size | t-value | x | y | z | Side | Anatomical description | Brodmann area |
|---|---|---|---|---|---|---|---|
| *CD (RGB) name the ink colour* | | | | | | | |
| 134 | 5.82 | −16 | −68 | 46 | Left | Superior parietal lobule | 7 |
| *CD (CIExyY) name the ink colour* | | | | | | | |
| 34 | 5.26 | 10 | −34 | 38 | Right | Cingulate gyrus | 23 |
| 90 | 4.59 | −30 | −68 | −32 | Left | Cerebellum/Uvula | |
| 30 | 4.44 | −18 | −66 | 44 | Left | Superior parietal lobule | 7 |
| 37 | 4.13 | −14 | −52 | −36 | Left | Cerebellum | |
| 37 | 3.98 | 28 | −44 | −50 | Right | Cerebellum | |
| *CD (RGB) name the synaesthetic colour* | | | | | | | |
| 43 | 5.09 | 4 | −76 | 52 | Right | Precuneus | 7 |
| 75 | 4.64 | −4 | −40 | 72 | Left | Precuneus | 7 |
| 98 | 4.34 | −48 | −60 | −24 | Left | Fusiform gyrus, inferior occipital gyrus | 19, 37 |
| 39 | 4.25 | 20 | 8 | 40 | Right | Middle frontal gyrus | 6 |
| 45 | 4.24 | −38 | −40 | 26 | Left | Supramarginal gyrus | 48 |
| 43 | 4.13 | −54 | −46 | 50 | Left | Inferior parietal lobule | 40 |
| 58 | 4.09 | 50 | −68 | −20 | Right | Fusiform gyrus, inferior occipital gyrus | 19, 37 |
| 40 | 4.08 | −36 | −20 | 54 | Left | Precentral gyrus | 4 |
| 31 | 4.07 | 26 | 18 | 24 | Right | Inferior frontal gyrus | 44 |
| *CD (CIExyY) name the synaesthetic colour* | | | | | | | |
| 52 | 5.40 | 4 | −76 | 52 | Right | Precuneus | 7 |
| 52 | 5.04 | −30 | −84 | 22 | Left | Middle occipital gyrus | 19 |
| 69 | 4.82 | −4 | −40 | 72 | Left | Precuneus | 7 |
| 77 | 4.33 | 54 | −60 | −22 | Right | Inferior temporal gyrus | 37 |
| | 4.30 | 50 | −68 | −20 | Right | Fusiform gyrus, inferior occipital gyrus | 19, 37 |
| 36 | 4.15 | −54 | −46 | 50 | Left | Inferior parietal lobule | 40 |
| 92 | 4.12 | 58 | −12 | 38 | Right | Postcentral gyrus | 3.4 |
| 52 | 3.93 | −48 | −62 | −24 | Left | Fusiform gyrus, inferior occipital gyrus | 19, 37 |

single-letter task. However, our control participants were not trained to establish systematic associations between the symbols and specific colours, as in the studies by Elias et al. (2003) and Meier and Rothen (2009); hence, we must be cautious and point out that some of the observed activations in the synaesthetes that were absent in our control participants may have reflected their systematic associations between symbols and colours and could be observable in non-synaesthetic subjects after extensive training.

Although parietal activity would seem consistent with the known role of this region in filtering irrelevant information (Friedman-Hill et al., 2003), it remains unclear its functional role in the Stroop task, since Stroop interference seems unaffected by damage to the parietal lobe (Berti et al., 1994; Robertson et al., 1997; Vivas et al., 2003) or by bilateral stimulations (Hayward et al., 2004). In contrast, damage to the frontal lobe clearly results in alterations in Stroop performance (Stuss et al., 2001). However, Esterman et al. (2006) have shown that inhibition of the right posterior parietal lobe with transcranial magnetic stimulation reduces interference in synaesthetes performing a single-letter 'name the ink' task. These authors interpret this apparently unique role of the

**Table 5 – Stroop interference expressed as the difference in RTs (in msec) of incongruent (target and distractor relate to different colours) and congruent trials (target and distractor relate to same colour). Data were collected off-scanner ($N = 128$ for each task) for both synaesthetes (PM and TH) and a new group of control participants from those who participated in the fMRI study ($N = 12$; matched to PM and TH by sex and age: mean = 57; SD = 4.6).**

| | Colour-word Stroop | | Single-letter Stroop 'name the ink colour' | | Single-letter Stroop 'name the synaesthetic colour' | |
|---|---|---|---|---|---|---|
| | Mean RT | SD | Mean RT | SD | Mean RT | SD |
| Control subjects | 61.8 | 51.2 | 8 | 7.4 | – | – |
| PM | 139.5 | 58.7 | 68.1 | 76 | 131.2 | 92 |
| TH | 134.3 | 59.2 | 117.7 | 71 | – | – |

parietal lobe in synaesthetic Stroop on the basis of the known role of this neural network in attention-based feature binding (Ashbridge et al., 1997; Friedman-Hill et al., 1995; Shafritz et al., 2002). Specifically, the integration of forms to their synaesthetic colours would depend on this multimodal association region, so that the parietal cortex may contribute to the perception of the illusory colours. Several authors have pointed out that it is necessary for attention to be focused on the triggering stimulus in order for the synaesthetic colour to be evoked (Laeng et al., 2004; Mattingley et al., 2001, 2006; Rich and Mattingley, 2005; Sagiv et al., 2005, 2006).

To conclude, although several other functional imaging studies have clearly established that there can be activations of the cortical colour areas (V4 & V8) as well as of a network of fronto-parietal regions (e.g., Nunn et al., 2002; Rouw and Scholte, 2007; Sperling et al., 2006; Steven et al., 2006), the novel finding of the present study lies in revealing that the strength of activity in the network depends on how similar the real and illusory colour are to each other. That is, the CD between the real colour (which they were supposed to ignore) and the illusory colour (on which they focussed attention) modulated the activity in the synaesthetes' visual cortical areas. This strongly supports the view that the colour synaesthesia phenomenon is perceptual in nature. The modulatory activity due to the colours' similarity could also be interpreted as evidence that multiple colours are simultaneously supported by the activity of colour-opponent neural cells within these visual areas (Nikolic et al., 2007), so as to engender the simultaneous conscious experiences of more than one colour. However, the latter conclusion would need to be specifically addressed in future studies by selecting stimuli with a large variety of colours within each individual's colour space so as to directly compare activity levels within the colour areas for real-illusory colour pairs that either fall within the same opponent channel or in different ones.

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