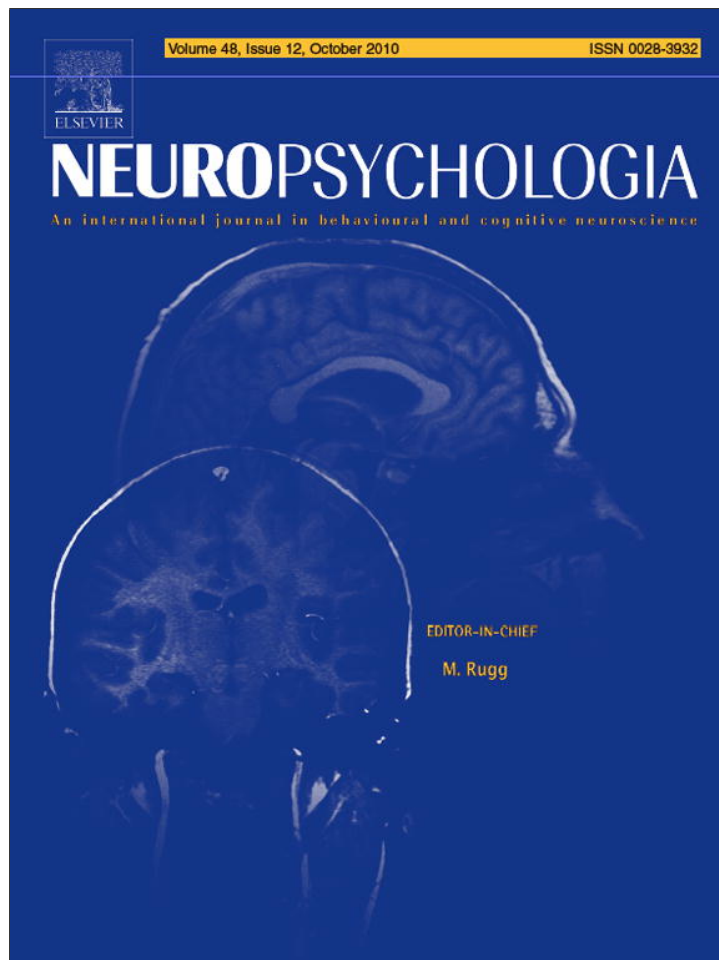


Provided for non-commercial research and education use.  
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



Contents lists available at ScienceDirect

## Neuropsychologia

journal homepage: [www.elsevier.com/locate/neuropsychologia](http://www.elsevier.com/locate/neuropsychologia)

## Parieto-occipital suppression eliminates implicit bidirectionality in grapheme-colour synaesthesia

Nicolas Rothen<sup>a</sup>, Thomas Nyffeler<sup>b</sup>, Roman von Wartburg<sup>b</sup>, René Müri<sup>b</sup>, Beat Meier<sup>a,\*</sup>

<sup>a</sup> University of Bern, Switzerland

<sup>b</sup> Perception and Eye Movement Laboratory, Department of Neurology, Department of Clinical Research, Bern University Hospital, University of Bern, Switzerland

## ARTICLE INFO

## Article history:

Received 15 December 2009

Received in revised form 23 June 2010

Accepted 26 July 2010

Available online 1 August 2010

## Keywords:

Synaesthesia

Bidirectionality

Transcranial magnetic stimulation

## ABSTRACT

Synaesthesia is a condition in which the input of one sensory modality triggers extraordinary additional experiences. On an explicit level, subjects affected by this condition normally report unidirectional experiences. In grapheme-colour synaesthesia for example, the letter A printed in black may trigger a red colour experience but not vice versa. However on an implicit level, at least for some types of synaesthesia, bidirectional activation is possible. In this study we tested whether bidirectional implicit activation is mediated by the same brain areas as explicit synaesthetic experiences. Specifically, we demonstrated suppression of implicit bidirectional activation with the application of transcranial magnetic stimulation over parieto-occipital brain areas. Our findings indicate that parieto-occipital regions are not only involved in explicit but also implicit synaesthetic binding.

© 2010 Elsevier Ltd. All rights reserved.

### 1. Introduction

Synaesthesia is a condition in which ordinary stimuli trigger extraordinary experiences (Dixon, Smilek, Cudahy, & Merikle, 2000). In grapheme-colour synaesthesia for example, the letter A printed in black may trigger a red colour experience. For a long time it was believed that synaesthesia is strictly unidirectional. However, recent findings show that at least in some types of synaesthesia bidirectional activations can occur. For example, a single case has been documented of a person experiencing colours when seeing numbers and also numbers when seeing colours, that is, explicit bidirectional activation (Cohen Kadosh, Cohen Kadosh, & Henik, 2007; Cohen Kadosh & Henik, 2006). More common, however, is the occurrence of implicit bidirectionality where no conscious experience of the link between colours and graphemes exists, but behaviour has been shown to be influenced by these associations nevertheless (Brang, Edwards, Ramachandran, & Coulson, 2008; Brugger, Knoch, Mohr, & Gianotti, 2004; Cohen Kadosh et al., 2005; Gebuis, Nijboer, & van der Smagt, 2009b; Knoch, Gianotti, Mohr, & Brugger, 2005; Meier & Rothen, 2007; Ward & Sagiv, 2007; Weiss, Kalckert, & Fink, 2009). The question remains as to whether these effects are mediated by the same brain areas as the more typical unidirectional effects of synaesthesia. In this study we demon-

strate that the application of a transcranial magnetic stimulation (TMS) protocol which has been used to suppress the unidirectional expression of synaesthesia (Esterman, Verstynen, Ivry, & Robertson, 2006; Muggleton, Tsakanikos, Walsh, & Ward, 2007) is also effective at suppressing implicit bidirectional effects.

There is converging evidence from functional (Nunn et al., 2002; Weiss, Zilles, & Fink, 2005) and structural (Rouw & Scholte, 2007; Weiss & Fink, 2009) MRI studies that temporal and parietal regions play an important role in synaesthesia (Hubbard & Ramachandran, 2005; Hubbard, 2007; Ramachandran & Hubbard, 2001). In addition, two TMS studies have provided further evidence for the involvement of parieto-occipital areas (Esterman et al., 2006; Muggleton et al., 2007). In one study (Esterman et al., 2006) two synaesthetes were engaged in a Stroop-like colour naming task during the application of repetitive TMS over the posterior parietal lobes. The results showed that the synaesthetic Stroop effect was suppressed when TMS was applied over the right hemisphere. In addition, in one subject, there was also a marginally significant effect for left-sided stimulation of the same area. However, suppression of the visual area V1 did not affect performance demonstrating the specificity of TMS effects. In another study with five synaesthetes TMS application over the right parieto-occipital cortex (RPO) disrupted synaesthetic Stroop interference (Muggleton et al., 2007). In addition, there was also a marginally significant effect for the left parieto-occipital site, while suppression of other parietal areas showed only minimal performance disruption. Even though the samples were small which potentially limits the generalization of these findings (Rothen & Meier, 2009), the results suggest that synaesthetic colour experiences

\* Corresponding author at: Department of Psychology, University of Bern, 3000 Bern 9, Switzerland. Tel.: +41 31 631 40 39; fax: +41 31 631 82 12.

E-mail address: [beat.meier@psy.unibe.ch](mailto:beat.meier@psy.unibe.ch) (B. Meier).

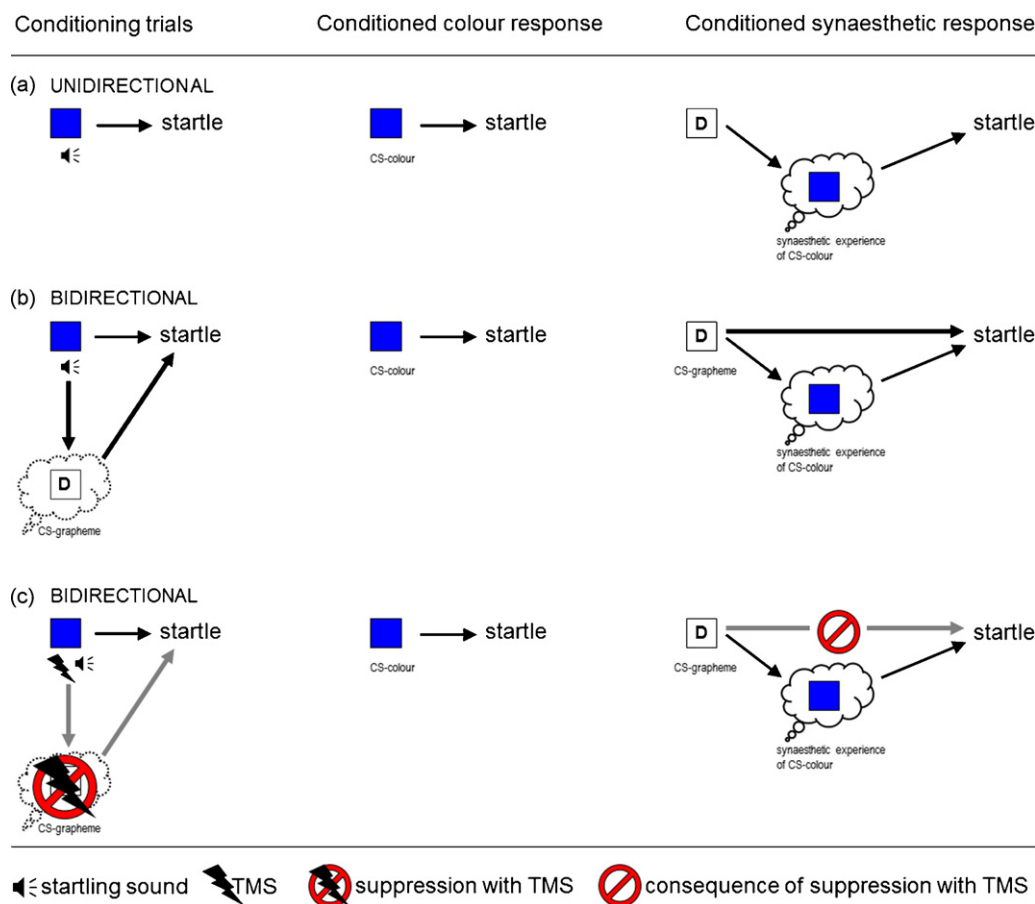
rely specifically on parieto-occipital pathways similar to normal colour perception (Esterman et al., 2006; Sagiv, Heer, & Robertson, 2006).

First evidence for bidirectional influences came from digit-colour synaesthesia. It was shown that synaesthetic colours can influence magnitude judgments and other characteristics of number processing implicitly (Brugger et al., 2004; Cohen Kadosh et al., 2005; Knoch et al., 2005). In a previous study, we have presented the first evidence that implicit bidirectionality may be a more general phenomenon that is not restricted to digit-colour synaesthesia (Meier & Rothen, 2007). Using a new method, a startle reaction was conditioned to a particular colour. The colour was chosen such that it corresponded to the colour that was elicited by a specific grapheme for each individual synaesthete. Although the grapheme was never coupled with the startling sound, it elicited a startle response after conditioning. According to a unidirectional account, this result may be due to a generalized conditioned colour response. That is, the grapheme evoked the colour which was coupled with the conditioned startle response (Fig. 1(a)). According to a bidirectional account an implicit activation of the grapheme representation occurred in the conditioning trials. The conditioned synaesthetic response was then supported by a direct association between the grapheme and the startle response (Fig. 1(b)).

If, in fact, there is an implicit activation of the grapheme representation in response to colour that contributes to the conditioned synaesthetic response, and if the source of this activation is

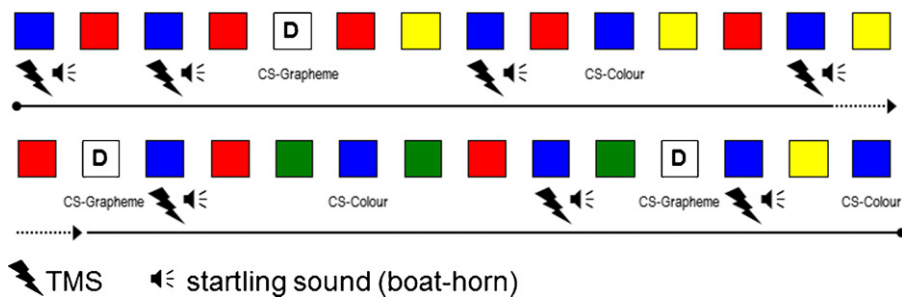
located in the same parieto-occipital regions that have been shown to be involved in unidirectional synaesthetic colour experiences, then the application of TMS over this area should substantially reduce the synaesthetic conditioning effect. Specifically, suppressing parieto-occipital areas in the conditioning trials should affect the expression of the conditioned response via the bidirectional route (Fig. 1(c)). A further goal was to test whether the effect of TMS would be limited to the right parieto-occipital cortex.

A sample of thirty-six grapheme-colour synaesthetes who reported explicit unidirectional synaesthetic experiences, but no explicit bidirectional synaesthetic experiences, were tested in one of three TMS conditions. In one condition, TMS was applied over the right parieto-occipital junction (RPO), in another condition TMS was applied over the left parieto-occipital junction (LPO), and in the control condition, sham stimulation was applied over the right parieto-occipital junction. The synaesthetic conditioning task consisted of three phases, habituation, conditioning and extinction during which skin conductance response (SCR) was measured continuously (Meier & Rothen, 2007; 2009). The critical TMS trials were administered online during the conditioning phase when colour was coupled with the unconditioned stimulus (US). TMS was never administered when the conditioned colour (CS-colour) was presented or when the CS-grapheme was presented. A conditioned response to the CS-colour, but not to the CS-grapheme would be convincing evidence for a bidirectional account of synaesthesia and would be a clear indication for the involvement of parieto-occipital regions for implicit bidirectionality.



**Fig. 1.** Schematic depiction of the two accounts of the synaesthetic conditioning effect. (a) According to a unidirectional account, the conditioned synaesthetic response is mediated by the conditioned colour response. (b) According to an implicit bidirectional account an implicit activation of the grapheme representation occurs during conditioning trials. (c) According to an implicit bidirectional account, TMS over parieto-occipital areas should suppress the implicit activation of the grapheme during the conditioning trials. As a consequence the conditioned synaesthetic response should be largely reduced.

## Conditioning Phase



**Fig. 2.** Depiction of an example of the conditioning phase. A startle response is conditioned to the blue colour (CS-colour). Graphemes (CS-grapheme) were selected such that they elicited the colour which was coupled with the startling sound during conditioning. For the synaesthete in this particular example the letter “D” would have elicited a blue colour experience.

## 2. Method

### 2.1. Subjects

Thirty-six synaesthetes (33 female and 3 male; age  $M=31.1$  years,  $SD=8.6$ ; years of education  $M=17.2$ ,  $SD=3.3$ ; 32 right-handed and 4 left-handed; ISEQ (Skelton, Ludwig, & Mohr, 2009)  $M=-1.57$ ,  $SD=2.26$ ) were pseudo-randomly assigned to one of three TMS conditions (sham, LPO, RPO). The same number of participants was assigned to each experimental condition such that age, gender, handedness, years of education and ISEQ-score were comparable. All synaesthetes reported strictly unidirectional explicit synaesthetic experiences. A test of consistency of grapheme-colour associations was conducted in the original test session and in a retest-session about half a year later ( $M=7.2$  months). Consistency was  $r=.77$  for hue,  $r=.85$  for saturation, and  $r=.77$  for value (brightness). All consistency values were significantly different from zero (all  $ps < .001$ ) and similar in size to a previous study with a different sample of synaesthetes (Meier & Rothen, 2007). The experimental procedure conformed to the Declaration of Helsinki and was approved by the local ethics committee. All subjects gave written consent prior to participation.

### 2.2. Stimuli

Five coloured squares (red, green, blue, yellow, and white) which covered a visual angle of approximately  $10.6^\circ$  were used as stimuli, on a black background. The white square included a specific grapheme which was selected separately for each individual synaesthete. Whenever possible, the grapheme was selected to elicit either a red or blue synaesthetic experience. The graphemes were presented in a standard Arial 320 point font and each covered a visual angle of about  $6.6^\circ$  in width and about  $8.1^\circ$  in height.

### 2.3. Apparatus

Presentation of stimuli and triggering of TMS pulses was controlled by E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA, USA) running on an IBM-compatible computer. Visual materials were presented against a black background at the centre of a 17 VGA-monitor. Auditory materials were presented with 100dB on two speakers by a stereo integrated amplifier. rTMS was applied using a MagPro R30 stimulator (Medtronic Functional Diagnostics, Skovlunde, Denmark), connected to a round coil with an outer radius of 60 mm (Magnetic Coil Transducer MC-125; Medtronic Functional Diagnostics) in the experimental condition and a sham coil (Magnetic Coil Transducer MC-P-B70; Medtronic Functional Diagnostics) in the sham condition. SCRs were measured with two shielded Ag/AgCl-electrodes (FMS Falk Minow Services,

Herrsching, Germany) with 8 mm in diameter filled with TD-246 (PAR Medizintechnik GmbH, Berlin, Germany), a neutral medium with 0.5% NaCl. SCR data were acquired with a skin conductance level meter (UFI, model 2701, Morro Bay, CA, USA). To digitalize SCR data an analogue to digital converter (MacLab/4s ML740, AD Instruments Ltd., Castle Hill, NSW, Australia) was used. SCR data were recorded with a Macintosh G4 computer (Apple Computer Inc., Cupertino, CA, USA) with Chart v4.2 software (AD Instruments Ltd., Castle Hill, NSW, Australia).

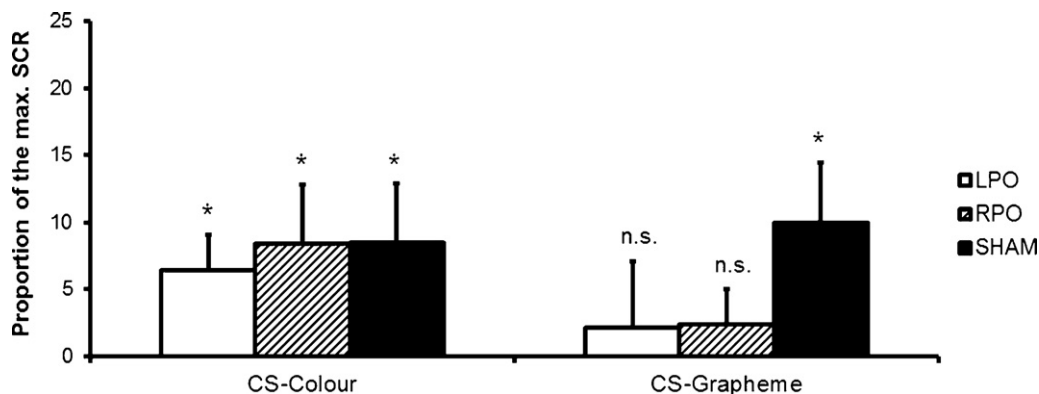
### 2.4. Procedure

SCR was sampled at 20 Hz with two electrodes, attached to the thenar and hypothenar eminences of the non-dominant hand. Subjects were seated in a comfortable chair, 60 cm in front of a computer screen. They were asked to relax, to remain silent, and to attend to the squares that would appear on the screen. Each square was shown for 500 ms and a new square was not presented until the SCR was stable. In the habituation phase stimuli were presented in a fixed pseudo-random order twelve times for a total of 60 trials. In parallel, TMS was applied in a different pseudo-random order online during the presentation of 12 squares with the restriction that each colour was coupled with TMS at least once. Importantly, the inter-stimulus interval was rather long (about 10 s) because, as mentioned above, a new trial was not initiated before the SCR was stable. Therefore, TMS was applied very infrequently and was nowhere near the 1-Hz range that typically leads to long-lasting TMS effects.

In the conditioning phase, a total of 28 trials were presented in a fixed pseudo-random order. TMS was applied during the conditioning trials in order to interfere with implicit bidirectionality. Three white squares including the grapheme were used as conditioned grapheme stimuli (CS-grapheme) and three coloured squares with the corresponding colour were used as the conditioned colour stimuli (CS-colour). None of the CS stimuli was followed by the US. An additional 15 squares of the remaining three colours which were never followed by the startling sound were used as filler stimuli. An example of the specific procedure for the condition with blue as the CS-colour and D as CS-grapheme is depicted in Fig. 2.

In the extinction phase, two CS-colour trials and two CS-grapheme trials were presented alternating twelve times for a total of 24 trials. These trials were included to extinguish the conditioned response and were not considered for the analysis. At the end of the experiment subjects were asked whether the grapheme elicited a colour experience at all.

Before the synaesthetic conditioning task, the motor threshold of the relaxed small hand muscles was determined by stimulating the right motor cortex with single pulses. Over the experimental procedure, rTMS was delivered at 115% of each individual's motor



**Fig. 3.** Mean differences (conditioning – habituation) for CS-grapheme and CS-colour trials and the three experimental conditions (sham, LPO, RPO). Larger differences indicate stronger conditioning. Error bars show standard errors.

rest threshold at a rate of 10 Hz during the presentation of the specific slides. The localization of the stimulation site was based on a previous study (Muggleton et al., 2007). The Talairach coordinates of the RPO site ( $x=22, y=-71, z=27$ ) were converted to the 10–20 electrode system. The left hemisphere site (LPO) was chosen to be homologous to the RPO location. The TMS-coil was handled tangentially, with the direction of the induced current from posterior to anterior. For the analysis of the SCRs, a data window of 10 s after each stimulus presentation was defined. The event-related SCR was calculated as the difference between the highest amplitude and its precedent minimum in the data window.

### 3. Results

In Fig. 3, SCR differences between habituation and conditioning are presented separately for CS-colour and CS-grapheme and for each of the three stimulation conditions. SCRs are expressed as the proportion of maximum SCR for the unconditioned responses. For all statistical analyses alpha level was set at .05.

In the first set of analyses, we tested whether a conditioned response occurred for the CS-colour. Directed comparisons showed that SCRs differed significantly from 0 for all conditions, with  $t(11)=1.98, \eta^2=.26$  for sham,  $t(11)=1.96, \eta^2=.26$  for RPO, and  $t(11)=2.40$  for LPO,  $\eta^2=.34$  (all  $ps < .05$ , one-tailed).

In the second and critical set of analyses, we tested whether a synaesthetic conditioning effect occurred. Directed comparisons showed that SCRs of CS-grapheme trials differed significantly from 0 for the sham condition  $t(11)=2.27, p < .05, \eta^2=.32$  but not for the two experimental conditions with  $t(11)=.90, p=.19, \eta^2=.07$  for RPO and  $t(11)=.43, p=.34, \eta^2=.02$  for LPO (all one-tailed). This indicates that a conditioning effect in response to the colour was evident in all conditions, while the synaesthetic conditioning effect was suppressed in both TMS conditions, but not in the sham condition.

We have asked the participants at the end of the experiment whether they had a colour experience in response to the graphemes during the experiment. In both TMS conditions, 50% of the participants were aware of a colour experience in response to graphemes. In contrast, however, in the sham condition only 17% reported that they were aware of a colour experience. Therefore, we can be sure that at least some of the participants had a colour experience (and were still aware of it at the end of the experiment). The number of “aware” participants was even higher in the TMS conditions. However, the rather low number in the sham condition indicates that these phenomenological reports should, eventually, be treated with caution. Nevertheless, as can be seen in Fig. 3, the SCRs for

graphemes (CS-Graphemes) are still above zero, which may be indicative for a potential, but weak, unidirectional activation.

### 4. Discussion

The present study demonstrates that parieto-occipital TMS suppresses implicit bidirectionality. It also demonstrates that implicit bidirectional cross-activation is involved in synaesthetic conditioning and that a simple unidirectional account is not sufficient to explain the synaesthetic conditioning effect. TMS during conditioning (i.e., the presentation of the CS-colour coupled with the US) prevented a synaesthetic conditioning effect during retrieval of the conditioned response (i.e., the presentation of the CS-grapheme) in the TMS conditions but not in the sham condition. As the synaesthetic inducer (CS-grapheme) never co-occurred with the US (startling sound), the results suggest that implicit activation of the grapheme representation during conditioning is necessary to establish an association with the startle response, which fires back when the grapheme is presented physically (Meier & Rothen, 2007). Whilst at the level of subjective report activation of the synaesthetic colour experience was unidirectional, at the level of performance a bidirectional relationship between synaesthetic inducers (CS-grapheme) and concurrents (CS-colour) existed in the sham condition, but not in the TMS conditions.

In other words, real colours consistently elicited a conditioned response, independent of the presence of parieto-occipital TMS. In contrast, synaesthetic colours were not sufficient to elicit a conditioned response. This would have been expected with a simple unidirectional account. With a bidirectional account, however, the occurrence of the conditioned synaesthetic response is not simply a generalized conditioned colour response. Rather, it emphasizes the importance of the coupling between the implicit activation of the grapheme with the startle response during conditioning trials. As a result the conditioned synaesthetic response is strongly boosted by a direct link between grapheme and startle response (cf. Fig. 1(b)). This explanation is supported by the fact that a small, but non-significant synaesthetic conditioning effect also occurred in the TMS conditions via a unidirectional route (grapheme  $\Rightarrow$  colour  $\Rightarrow$  startle).

However, it might be argued that the suppression of the conditioned synaesthetic response is the result of a lingering TMS effect. According to this explanation TMS effects would last for several seconds (or even minutes) and as a consequence the event-related application of TMS would become obsolete. However, and critically, the specific TMS protocol used in the present study (i.e., stimulation rate, stimulation strength, stimulation site etc.) and the long inter-trial-intervals argue against a summation- or carryover-effect

of TMS (cf. Göbel, Rushworth, & Walsh, 2006; Leff, Scott, Rothwell, & Wise, 2001; Rosenthal et al., 2006).

Our findings have important implications for understanding the neuronal correlates of binding colour and form in synaesthesia. They suggest that parieto-occipital regions are not only involved in explicit (Hubbard & Ramachandran, 2005; Ramachandran & Hubbard, 2001; Sagiv et al., 2006) but also in implicit synaesthetic binding. As parieto-occipital areas are also involved in normal binding, these findings reinforce the notion that synaesthesia can be viewed as a phenomenon of abnormal feature binding (Sagiv et al., 2006). Our results extend those of a recent EEG study in which implicit bidirectionality elicited activations at parietal electrodes (Gebuis, Nijboer, & van der Smagt, 2009a) and fMRI findings in a case of explicit bidirectionality in which the activation from grapheme to colour also activated parietal areas (Cohen Kadosh, Cohen Kadosh, & Henik, 2007). They go beyond previous reports of mainly right-sided effects of TMS suppression for unidirectional synaesthetic binding (Esterman et al., 2006; Muggleton et al., 2007). In the present study, suppression of both left and right parieto-occipital cortex affected synaesthetic conditioning, suggesting that both hemispheres are involved in implicit synaesthetic binding. In contrast, the conditioned colour response was not affected by TMS, which indicates that parieto-occipital areas are selectively involved in the synaesthetic conditioning effect.

Our results also extend previous reports of implicit bidirectionality in synaesthesia by showing that it is not restricted to numerical cognition (Meier & Rothen, 2007; Weiss et al., 2009). In addition, they suggest that bidirectionality is an intrinsic property of synaesthesia which may be the consequence of the lifetime of extensive associations between synaesthetic inducers and concurrents (cf. Berteletti, Hubbard, & Zorzi, 2010). At first glance, this notion seems to conflict with a model of synaesthesia put forward by Cohen Kadosh and Henik (2007) according to which different types of synaesthesia can be distinguished as a function of awareness of synaesthetic experiences, ranging from the complete absence of awareness (i.e., non-synaesthetes) to complete awareness of synaesthesia (including explicit bidirectionality). However, it is likely that the synaesthetes tested in the present study were all in the medium range of this hypothetical scale, and although there may be variations in the extent to which they are aware of their unidirectional synaesthesia, implicit bidirectionality also emerged on a physiological level.

While the consideration of implicit bidirectionality in synaesthesia research increases, so far there has not been much theorizing about why synaesthesia should be a unidirectional phenomenon at all. If numbers induce sensations of colours then why do colours not also induce synaesthetic sensations of numbers? It is possible that the dissociation between experience and behaviour due to explicit and implicit activations can be explained by the properties of the human knowledge representation system. Typically inducers are cultural artefacts, that is, stimuli such as numerals, letters and words which are comprehended only after extensive experience. In contrast, concurrents represent more natural categories which are “just there” in the outside world and which can be comprehended without cultural education. If cultural artefacts (i.e., inducers) are more symbolic and less concrete than natural categories (i.e., concurrents), then according to a spreading-activation theory of knowledge representation (Collins & Loftus, 1975) an inducer would activate fewer nodes compared to a concurrent. As a concept divides its activation among all the concepts connected to it, it would take longer to retrieve associations of concurrents compared to retrieving associations of inducers, resulting in a fan effect (Anderson, 1974). By this explanation, the association between inducer and concurrent is stronger and therefore the threshold for a conscious experience may be crossed more quickly. Reciprocally, the association between concurrent and inducer is weaker

and therefore the threshold for a conscious experience may not be crossed. Using appropriate measures, its existence can be demonstrated nevertheless as shown in the present study.

On a neuronal level, there is converging evidence that parietal regions contribute to the fan effect (Khader, Burke, Bien, Ranganath, & Röslér, 2005; Sohn et al., 2005). Thus, synaesthesia may be conceptualized as a binding phenomenon and synaesthetic feature binding may rely on similar processes as normal feature binding (Corbetta, Shulman, Miezin, & Petersen, 1995; Esterman et al., 2006; Muggleton et al., 2007; Robertson, 2003; Sagiv et al., 2006). Here we have demonstrated that this kind of binding can even occur implicitly.

## Acknowledgement

We would like to thank Josephine Cock for helpful comments on an earlier version of the manuscript.

## References

- Anderson, J. R. (1974). Retrieval of propositional information from long-term memory. *Cognitive Psychology*, 6(4), 451–474. doi:10.1016/0010-0285(74)90021-8
- Berteletti, I., Hubbard, E. M., & Zorzi, M. (2010). Implicit versus explicit interference effects in a number-color synesthete. *Cortex*, 46(2), 170–177. doi:10.1016/j.cortex.2008.12.009
- Brang, D., Edwards, L., Ramachandran, V. S., & Coulson, S. (2008). Is the sky 2? Contextual priming in grapheme-color synaesthesia. *Psychological Science*, 19(5), 421–428. doi:10.1111/j.1467-9280.2008.02103.x
- Brugger, P., Knoch, D., Mohr, C., & Gianotti, L. R. R. (2004). Is digit-color synaesthesia strictly unidirectional? Preliminary evidence for an implicitly colored number space in three synaesthetes. *Acta Neuropsychologica*, 2(3), 252–258.
- Cohen Kadosh, R., Cohen Kadosh, K., & Henik, A. (2007). The neuronal correlate of bidirectional synesthesia: A combined event-related potential and functional magnetic resonance imaging study. *Journal of Cognitive Neuroscience*, 19(12), 2050–2059. doi:10.1162/jocn.2007.19.12.2050
- Cohen Kadosh, R., & Henik, A. (2006). When a line is a number: Color yields magnitude information in a digit-color synesthete. *Neuroscience*, 137(1), 3–5. doi:10.1016/j.neuroscience.2005.08.057
- Cohen Kadosh, R., & Henik, A. (2007). Can synaesthesia research inform cognitive science? *Trends in Cognitive Sciences*, 11(4), 177–184. doi:10.1016/j.tics.2007.01.003
- Cohen Kadosh, R., Sagiv, N., Linden, D. E. J., Robertson, L. C., Elinger, G., & Henik, A. (2005). When blue is larger than red: Colors influence numerical cognition in synesthesia. *Journal of Cognitive Neuroscience*, 17(11), 1766–1773.
- Collins, A. M., & Loftus, E. F. (1975). A spreading-activation theory of semantic processing. *Psychological Review*, 82(6), 407–428.
- Corbetta, M., Shulman, G. L., Miezin, F. M., & Petersen, S. E. (1995). Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. *Science*, 270(5237), 802–805.
- Dixon, M. J., Smilek, D., Cudahy, C., & Merikle, P. M. (2000). Five plus two equals yellow. *Nature*, 406(6794), 365. doi:10.1038/35019148
- Esterman, M., Verstynen, T., Ivry, R. B., & Robertson, L. C. (2006). Coming unbound: Disrupting automatic integration of synesthetic color and graphemes by transcranial magnetic stimulation of the right parietal lobe. *Journal of Cognitive Neuroscience*, 18(9), 1570–1576. doi:10.1162/jocn.2006.18.9.1570
- Gebuis, T., Nijboer, T. C. W., & van der Smagt, M. J. (2009a). Multiple dimensions in bidirectional synesthesia. *European Journal of Neuroscience*, 29(8), 1703–1710. doi:10.1111/j.1460-9568.2009.06699.x
- Gebuis, T., Nijboer, T. C. W., & van der Smagt, M. J. (2009b). Of colored numbers and numbered colors. *Experimental Psychology*, 56(3), 180–187. doi:10.1027/1618-3169.56.3.180
- Göbel, S. M., Rushworth, M. F., & Walsh, V. (2006). Inferior parietal rTMS affects performance in an addition task. *Cortex*, 42(5), 70416–70417. doi:10.1016/S0010-9452(08)70416-7
- Hubbard, E. M. (2007). Neurophysiology of synesthesia. *Current Psychiatry Reports*, 9(3), 193–199. doi:10.1007/s11920-007-0018-6
- Hubbard, E. M., & Ramachandran, V. S. (2005). Neurocognitive mechanisms of synesthesia. *Neuron*, 48(3), 509–520. doi:10.1016/j.neuron.2005.10.012
- Khader, P., Burke, M., Bien, S., Ranganath, C., & Röslér, F. (2005). Content-specific activation during associative long-term memory retrieval. *NeuroImage*, 27(4), 805–816. doi:10.1016/j.neuroimage.2005.05.006
- Knoch, D., Gianotti, L. R., Mohr, C., & Brugger, P. (2005). Synesthesia: When colors count. *Cognitive Brain Research*, 25(1), 372–374. doi:10.1016/j.cogbrainres.2005.05.005
- Leff, A., Scott, S., Rothwell, J., & Wise, R. (2001). The planning and guiding of reading saccades: A repetitive transcranial magnetic stimulation study. *Cerebral Cortex*, 11(10), 918–923.
- Meier, B., & Rothen, N. (2007). When conditioned responses “fire back”: Bidirectional cross-activation creates learning opportunities in synesthesia. *Neuroscience*, 147(3), 569–572. doi:10.1016/j.neuroscience.2007.04.008

- Meier, B., & Rothen, N. (2009). Training grapheme-color associations produces a synaesthetic stroop effect, but not a conditioned synaesthetic response. *Neuropsychologia*, 47(4), 1208–1211. doi:10.1016/j.neuropsychologia.2009.01.009
- Muggleton, N., Tsakanikos, E., Walsh, V., & Ward, J. (2007). Disruption of synaesthesia following TMS of the right posterior parietal cortex. *Neuropsychologia*, 45(7), 1582–1585. doi:10.1016/j.neuropsychologia.2006.11.021
- Nunn, J. A., Gregory, L. J., Brammer, M., Williams, S. C. R., Parslow, D. M., Morgan, M. J., et al. (2002). Functional magnetic resonance imaging of synesthesia: Activation of V4/V8 by spoken words. *Nature Neuroscience*, 5(4), 371–375. doi:10.1038/nn818
- Ramachandran, V. S., & Hubbard, E. M. (2001). Synaesthesia: A window into perception, thought and language. *Journal of Consciousness Studies*, 8(12), 3–34.
- Robertson, L. C. (2003). Binding, spatial attention and perceptual awareness. *Nature Reviews Neuroscience*, 4(2), 93–102. doi:10.1038/nrn1030
- Rosenthal, C. R., Walsh, V., Mannan, S. K., Anderson, E. J., Hawken, M. B., & Kennard, C. (2006). Temporal dynamics of parietal cortex involvement in visual search. *Neuropsychologia*, 44(5), 731–743. doi:10.1016/j.neuropsychologia.2005.07.014
- Rothen, N., & Meier, B. (2009). Do synesthetes have a general advantage in visual search and episodic memory? A case for group studies. *PLoS ONE*, 4(4), e5037, 10.1371/journal.pone.0005037.
- Rouw, R., & Scholte, H. S. (2007). Increased structural connectivity in grapheme-color synesthesia. *Nature Neuroscience*, 10(6), 792–797. doi:10.1038/nn1906
- Sagiv, N., Heer, J., & Robertson, L. (2006). Does binding of synesthetic color to the evoking grapheme require attention? *Cortex*, 42(2), 232–242. doi:10.1016/S0010-9452(08)70348-4
- Skelton, R., Ludwig, C., & Mohr, C. (2009). A novel, illustrated questionnaire to distinguish projector and associator synaesthetes. *Cortex*, 45(6), 721–729. doi:10.1016/j.cortex.2008.02.006
- Sohn, M., Goode, A., Stenger, V. A., Jung, K., Carter, C. S., & Anderson, J. R. (2005). An information-processing model of three cortical regions: Evidence in episodic memory retrieval. *NeuroImage*, 25(1), 21–33. doi:10.1016/j.neuroimage.2004.11.001
- Ward, J., & Sagiv, N. (2007). Synaesthesia for finger counting and dice patterns: A case of higher synaesthesia? *Neurocase*, 13(2), 86–93. doi:10.1080/13554790701300518
- Weiss, P. H., Kalckert, A., & Fink, G. R. (2009). Priming letters by colors: Evidence for the bidirectionality of grapheme-color synesthesia. *Journal of Cognitive Neuroscience*, 21(10), 2019–2026. doi:10.1162/jocn.2008.21166
- Weiss, P. H., & Fink, G. R. (2009). Grapheme-color synaesthetes show increased grey matter volumes of parietal and fusiform cortex. *Brain*, 132(1), 65–70. doi:10.1093/brain/awn304
- Weiss, P. H., Zilles, K., & Fink, G. R. (2005). When visual perception causes feeling: Enhanced cross-modal processing in grapheme-color synesthesia. *NeuroImage*, 28(4), 859–868. doi:10.1016/j.neuroimage.2005.06.052