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Psychophysiological evidence for the genuineness of swimming-style colour synaesthesia

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ABSTRACT

Recently, swimming-style colour synaesthesia was introduced as a new form of synaesthesia. A synaesthetic Stroop test was used to establish its genuineness. Since Stroop interference can occur for any type of overlearned association, in the present study we used a modified Stroop test and psychophysiological synaesthetic conditioning to further establish the genuineness of this form of synaesthesia. We compared the performance of a swimming-style colour synaesthete and a control who was trained on swimming-style colour synaesthesia can be mimicked in a trained control. Importantly, however, our results showed a psychophysiological conditioning effect for the synaesthete only. We discuss the theoretical relevance of swimming-style colour synaesthesia according to different models of synaesthesia. We conclude that swimming-style colour synaesthesia is a genuine form of synaesthesia, can be mimicked behaviourally in non-synaesthetes, and is best explained by a re-entrant feedback model.

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1. Introduction

Synaesthesia is characterized by extraordinary experiences in response to ordinary stimuli. Several forms of this condition have been documented, such as 'colours' to graphemes (Grossenbacher & Lovelace, 2001; Simner et al., 2006), 'tastes' to words (Ward & Simner, 2003; Ward, Simner, & Auyeung, 2005), and 'shapes' to tastes (Cytowic, 1993). Many other forms exist and recently, we have provided evidence for a new form of synaesthesia, swimming-style colour synaesthesia, in which the conceptual representation of swimming in a particular style (i.e., breast, backstroke, crawl, butterfly) triggered highly specific colour photisms (Nikolić, Jürgens, Rothen, Meier, & Mroczko, 2011). Given the limitations of this previous study and the far-reaching theoretical implications for the nature of synaesthesia in general, the main goal of the present study was to seek further and stronger evidence for the genuineness of this new form of synaesthesia.

Over the last 15 years, evidence for a strong conceptual component to synaesthesia has accumulated. For instance, synaesthetes were faster at naming a colour patch when a preceding arithmetic problem (i.e., 5 + 2) lead to a solution for which synaesthetic colour was congruent rather than incongruent (Dixon, Smilek, Cudahy, & Merikle, 2000). Context dependent

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interpretation of ambiguous stimuli was also shown to play an important role in the specific synaesthetic experience (Dixon, Smilek, Duffy, Zanna, & Merikle, 2006; Ramachandran & Hubbard, 2001). Moreover, synaesthetic experiences can occur for imagined synaesthetic inducers (Frith & Paulesu, 1997; Grossenbacher, 1997; Ramachandran & Hubbard, 2001; Rich, Bradshaw, & Mattingley, 2005). Importantly, for all these experiences the format of the synaesthetic inducer (e.g., 5 + 2) was present at the same level (i.e., in the same task set) as the synaesthetic inducer is present typically (e.g., as numbers). Thus, a conceptual representation of a *grapheme* was activated by presenting, thinking about, or imagining *graphemes*, thereby probably still activating a perceptual representation of the inducer (e.g., Grossenbacher & Lovelace, 2001; cf. also, D'Esposito et al., 1997; Kosslyn, Thompson, Kim, & Alpert, 1995). In contrast, in a study by Nikolić et al. (2011), synaesthetic colour experiences for swimming-styles were elicited by a photograph of the inducer and thus presented in a completely different task set than that in which the inducer typically occurs (i.e., as proprioceptive input of swimming). Hence, perceptual representations were even less likely to be activated, suggesting that the constitutional property of an inducer is its semantics and not its sensory input (cf. also, Mroczko-Wąsowicz & Werning, 2012).

Specifically, in the study of Nikolić et al. (2011), during a test of consistency and a synaesthetic Stroop task, the synaesthetes and non-synaesthetic controls were presented with different photographs of a person swimming in one of the four main swimming-styles. The synaesthetes were more consistent than the controls in choosing a colour associated with the different swimming-styles in a test and retest several weeks later. In the Stroop task, the synaesthetes showed significantly shorter reaction times for photographs presented in the colours congruent with the depicted swimming-style in comparison to photographs in colours incongruent with the depicted swimming-style. Such interference effects were not present in the controls.

However, the test of consistency and the Stroop effect are not entirely conclusive regarding the genuine nature of swimming-style colour synaesthesia. Tests of consistency rely on synaesthetic colour matching. Crucially, there is evidence that the precision of synaesthetic colour matching resembles that of recollected colours rather than physical colours (Arnold, Wegener, Brown, & Mattingley, 2012). Hence, overlearned and recollected colour associations are sufficient to pass a test of consistency. This is not problematic for most forms of synaesthesia where the sets of inducer-concurrent associations are large enough to prevent pure recollection of these associations. Even so, since only four different swimming-styles exist, high consistency does not provide conclusive evidence for the genuine nature swimming-style colour synaesthesia. Similarly, Stroop effects can be detected for any type of overlearned associations (Nikolić, Lichti, & Singer, 2007) and hence, can never provide sufficient evidence that an association is synaesthetic. Notably, studies with sample sizes as large as 20 and 40 participants, respectively, provided evidence that even synaesthetic Stroop effects and inverse Stroop-like priming effects can be mimicked in non-synaesthetes after several days of training grapheme-colour associations (Meier & Rothen, 2009; Rothen, Wantz, & Meier, 2011). However, trained participants did not report colour experiences in response to associated graphemes in follow-up questioning (for similar findings cf. also, Elias, Saucier, Hardie, & Sarty, 2003; Hancock, 2006). Critically for the purpose of the present study, Meier and Rothen (2009) also demonstrated that grapheme-colour pairings, simply associated through training, are not sufficient for a synaesthetic conditioning effect, as is the case for genuine synaesthetes (Meier & Rothen, 2007; Rothen, Nyffeler, von Wartburg, Müri, & Meier, 2010). That is, a startle reaction to a loud sound repeatedly coupled with a colour does not generalize to the associated grapheme in the case of trained non-synaesthetes, where the grapheme does not elicit a synaesthetic colour experience. Hence, in contrast to synaesthetic inducers, synaesthetic concurrents seem to be more than a mere semantic representation of colour information in real synaesthetes.

The present study was conducted with several aims. The first was to demonstrate strong evidence for the genuine nature of swimming-style colour synaesthesia. The second was to provide further evidence that Stroop-like synaesthetic priming effects can occur simply due to trained synaesthetic associations and without genuine synaesthetic *experiences*, even for swimming-style colour synaesthesia Therefore, we presented a swimming-style colour synaesthete and a non-synaesthete who was trained on swimming-style colour associations, with the synaesthetic conditioning paradigm (Meier & Rothen, 2007, 2009) and a synaesthetic priming paradigm (Gebuis, Nijboer, & van der Smagt, 2009; Rothen et al., 2011). In both tasks, we used pictograms of swimming-styles to trigger synaesthetic colour experiences. Note, pictograms are likely to act at a higher level of abstract conceptual representation than photographs as used in the previous study (Nikolić et al., 2011) and thus, they are even less likely to trigger brain activation representing perceptual aspects of swimming (i.e., proprioceptive input). We hypothesized that the swimming-style colour synaesthete would show a synaesthetic conditioning effect. The third aim was to elaborate on the theoretical relevance of swimming-style colour synaesthesia with respect to three basic models of the genesis of synaesthetic experiences (i.e., cross-activation model, disinhibited feedback model, re-entrant feedback model).

2. Methods

2.1. Participants

H.T. (25 years, right-handed, male) already participated in our previous study (Nikolić et al., 2011). He has colour experiences for digits, but not for letters. More interestingly, H.T. involuntarily experiences vivid and highly specific colours for swimming-styles (i.e., butterfly, breaststroke, backstroke, and crawl). He started swimming early in childhood and began competing at the age of six. He won his first championship in butterfly-style at the age of eight years and was national champion for several years until he stopped competing at the age of 16 years. Today, he still actively swims on a regular basis. As a matched control, we tested a 23 year old, right-handed, male non-synaesthete. The control did not receive any monetary or material reinforcement for participation in this study, but showed high intrinsic motivation to participate in the training.

Informed consent was obtained from both participants before testing. All experimental procedures were carried out according to the Declaration of Helsinki and were approved by the ethics committee of the Human Sciences Faculty of the University of Bern.

2.2. Test of consistency

On a computer screen, H.T. was presented with a pictogram for each of the four different swimming-styles (butterfly, breaststroke, backstroke, and crawl) and a colour palette with 144 different colours from which he had to choose his appropriate colour for each particular style. More than 2 months later, without warning, the colour experiences were retested with the same procedure. H.T.'s scores for hue, saturation, and value (brightness) were assessed (from 0 to 255 for each scale). The same test was conducted with the control participant. He was asked to select colours, according to personal choice, for the different swimming-styles in the first session (before training) and again in the last session (after training). Table 1 provides an overview for the different testing sessions of the control. The ordering of activities in the test session of the synaesthete was identical with the post-test session of the control (cf. Table 1).

2.3. Training

The training method was adopted from our previous studies (Meier & Rothen, 2009; Rothen et al., 2011). It was intended to build up highly automatic associations between colours and swimming-styles in the control person.

2.3.1. Apparatus

Presentation of stimuli and response collection were controlled by E-Prime 1.2 software (Psychology Software Tools, Pittsburgh, PA, USA) running on an IBM-compatible laptop. Visual materials were presented against a grey background at the centre of an LCD screen.

2.3.2. Material

Pictograms of the four main swimming-styles (butterfly, breaststroke, backstroke, and crawl) were used as stimuli (Fig. 1). They were presented at a visual angle of approximately 4.6° width and maximally 1.7° height, on a grey background.

2.3.3. Procedure

After the first session, the control was trained on swimming-style colour associations, during which time he learned to associate the different swimming-styles with the colours corresponding to H.T.'s synaesthetic experiences. At a viewing distance of approximately 60 cm, he was presented with a series of single pictograms of the four swimming-styles on the computer screen. He was instructed to press as quickly and accurately as possible one key if the swimming-style and the colour matched H.T.'s colours and another if they did not. The training was administered 10 minutes per day on 20 consecutive days. In each training session, 480 trials, 240 requiring a "match"-response and 240 requiring a "no-match"-response, were presented in random order. For "match"-responses each of the four swimming-styles was presented equally often in one of the other three colours. Each pictogram remained on screen until a key press was made and the next pictogram followed immediately. Feedback about proportion of correct responses and mean reaction time was given after blocks of 48 trials.

2.4. Behavioural testing: priming (Stroop test)

The procedure for the priming task was adopted from previous studies (Gebuis et al., 2009; Rothen et al., 2011). It is based on the logic of the synaesthetic Stroop effect (Mattingley, Rich, Yelland, & Bradshaw, 2001; Stroop, 1935): Naming

Table 1

Testing and training sessions. Overview of the tasks conducted with the control on the specified testing and training days. The synaesthete was tested according to ordering of activities on Day 22, with the consistency retest (trial 2) more than 2 months later.

Session	Day	Ordering of activities
Pre-training test	1	Test of consistency (trial 1) Behavioural priming (Stroop) test
Training Post-training test	2-21 22	Swimming-style colour association task Test of consistency (trial 2) Behavioural priming (Stroop) test Psychophysiological conditioning test

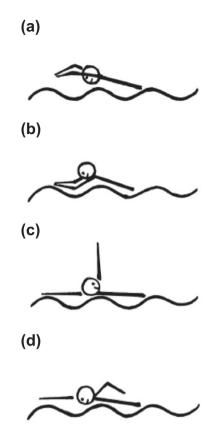


Fig. 1. Pictograms of the swimming-styles: (a) butterfly, (b) breaststroke, (c) backstroke, and (d) crawl.

synaesthetic inducers is slower when primed with concurrents which are incongruent with the specific synaesthetic experience as compared to when they primed with concurrents which are congruent with the specific synaesthetic experience. This slowing reflects interference between the involuntary and automatic synaesthetic association of the prime and the target stimulus. The paradigm consisted of two tasks (i.e, inducer-concurrent priming and concurrent-inducer priming).

2.4.1. Apparatus

Presentation of stimuli and response collection were controlled by E-Prime 1.2 software (Psychology Software Tools, Pittsburgh, PA, USA) running on an IBM-compatible computer. Visual materials were presented against a grey background at the centre of a 17" VGA monitor.

2.4.2. Analysis

Only reaction times of correct trials were analysed. Reaction times above and below two standard deviations of the mean reaction time of each condition were excluded as outliers. Hence, there were different numbers of trials in each task for each condition. Therefore and because our main interest was only in the presence/absence of a synaesthetic Stroop effect, the data were analysed using an independent samples *t*-test treating different trials of one condition as different subjects. We acknowledge that, strictly speaking, our design is in violation of the assumption of independence of data points because trials were not independent of one another. However, it is important to note that our approach is more conservative than using a paired samples *t*-test. Furthermore, we calculated effect sizes (Cohen's *d*) to provide additional evidence for the presence/ absence of synaesthetic Stroop effects. Cohen's *d* was calculated according to Thalheimer and Cook (2002) taking different numbers of trials into account.

2.4.3. Material

Black on white line drawings of the four main swimming-styles (butterfly, breaststroke, backstroke, and crawl) and four coloured rectangles (red, blue, white, and pale yellow) were used as stimuli, on a grey background. All stimuli subtended a visual angle of approximately 5.7° in width and maximally 2.4° in height.

2.4.4. Procedure

To assess inducer-concurrent priming, black on white line-drawings of the four swimming-styles and corresponding colour-patches were used as stimuli. Each trial consisted of five slides: Fixation, prime, inter-stimulus interval, target, and inter-trial interval. Each was presented for 500 ms except the target, which was presented until a key press was made. The task consisted of congruent and incongruent trials (192 trials each) which were presented in random order. Participants were instructed to respond with the middle and index fingers of both hands. Each of the colours was mapped to one specific finger-response.

To assess concurrent-inducer priming, the procedure was identical to inducer-concurrent priming except that the colours were used as primes and the pictograms as targets. Participants were instructed to make swimming-style decisions. Before each of these tasks, they performed a practice block to become familiar with the finger-response mappings. Practice blocks consisted of 40 trials and were identical to the priming tasks but omitting the prime and inter-stimulus intervals.

2.5. Physiological testing: synaesthetic conditioning

The procedure for the synaesthetic condition task was adopted from our previous studies (Meier & Rothen, 2007, 2009; Rothen et al., 2010). There, we demonstrated synaesthetic conditioning effects for grapheme–colour synaesthetes but not for controls, and we showed that the effect relies on implicit bidirectional activation.

2.5.1. Apparatus

Presentation of stimuli was controlled by E-Prime 1.2 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 100 dB on two speakers by a stereo integrated amplifier. SC (Skin Conductance) was 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. SC data were acquired with a skin conductance level metre (UFI, model 2701, Morro Bay, CA, USA). To digitize SC data, an analogue to digital converter (MacLab/4 s ML740, AD Instruments Ltd., Castle Hill, NSW, Australia) was used. SC 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).

2.5.2. Analysis

Using Ledalab (version 3.2.6) for continuous decomposition, SC data were separated into phasic and tonic activity (Benedek & Kaernbach, 2010). For the analysis of SCRs (Skin Conductance Response; phasic activity), a data window of 3 s was used. The starting point was defined as the virtual offset of the UCS (Unconditioned Stimulus; i.e., startling sound). SCRs were defined as the mean phasic amplitude in the response window with higher SCR indicating higher autonomic arousal.

2.5.3. Material

Five coloured squares (red, green, blue, yellow, and white) which covered a visual angle of approximately 10.6° were used as stimuli on a black background. The white square included the pictogram of the butterfly swimming-style which was associated with red for H.T. and for the trained control. The pictogram was presented in a visual angle of about 5.7° in width and about 2.5° in height.

2.5.4. Procedure

SCR (skin conductance response) was continuously measured to assess autonomic arousal. It was sampled at 20 Hz with two electrodes, attached to the thenar and hypothenar eminences of the non-dominant hand. Participants were seated comfortably, 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. No motor or verbal response was required. Each square was shown for 2 s and the inter-trial-interval (ITI) was about 10 s. In the habituation phase, stimuli were presented in a random order twelve times for a total of 60 trials.

In the conditioning phase, a total of 28 trials were presented in a fixed pseudo-random order. Seven red squares were followed by a loud startling sound (UCS). Six white squares including the butterfly-style pictogram were used as conditioned stimuli (CS). None of the CS stimuli was followed by the UCS. An additional 15 squares showing the other three colours which were never followed by the startling sound were used as neutral filler stimuli. Neutral stimuli were only considered for the analysis if the previous trial was not an UCS or CS trial, respectively. The specific conditioning procedure is depicted in Fig. 2.

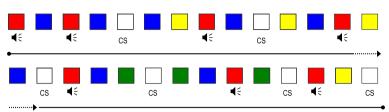
In the extinction phase, two white squares and two red squares were presented in alternating order for a total of 24 trials. These trials were included to extinguish the conditioned response and were not considered for the analysis.

3. Results

3.1. Test of consistency

For the swimming-style colour synaesthete, the specific colours for butterfly (red), breaststroke (blue), and crawl (white) were 100% identical in both sessions. For backstroke (pale yellow) the colour was identical in terms of hue and saturation, and for brightness there was only a minimal difference of eight points on the V-scale of the HSV spectrum. These findings show that H.T.'s synaesthetic experiences are reliable and stable over time.





I STARTLING SOUND (boat-horn)

Fig. 2. Schematic depiction of the conditioning phase. For reasons of simplicity, the pictogram of butterfly swimming-style, which was presented in the white slides, is not included in the figure.

In the first session, the control participant made decisions on a semantic basis: For him, butterfly (in German Delfin, meaning dolphin) was grey-bluish "like the colour of a dolphin's skin". Breaststroke was green like a frog "because the movements of this particular style resemble a frog swimming". Backstroke was yellow because "you see the lights of the indoor swimming pool's ceiling when swimming on your back". Crawl was blue "because you see down into the deep blue ocean when swimming in that style". In the re-test, 1 day after the last session of the swimming-style colour association training, the control perfectly remembered the colours he associated with the different swimming-styles before training. However, he stated that "somehow these colours do not fit the specific swimming-styles anymore". Even so, when asked to identify a colour for each particular swimming-style, he still selected the colours on which he was trained. After training, the HSV-values for butterfly, breaststroke, and crawl were 100% consistent with the trained colours. For backstroke, they were identical for hue and saturation, and for brightness, there was a difference of sixty points on the V-scale of the HSV spectrum between the associations of the control participant and the trained colour.

3.2. Training

Accuracy of the swimming-style colour associations was high from the beginning; across all sessions mean accuracy was M = .95 (SD = .02). Median response times for the swimming-style colour associations were 762 ms on Day 1 and dropped to 422 ms on Day 20. The response time data were modelled using a power function which explained 93.6% of the variance (Fig. 3).

3.3. Behavioural facets of synaesthesia

Mean reaction times and error rates are shown in Fig. 4. For each of the conditions, the proportion of reaction time outliers was always ≤ 0.07 of correct trials. H.T. was significantly slower for colours which were primed with incongruent swimming-styles compared to colours primed with congruent swimming-styles (t(362) = 29.46, p < .001; Cohen's d = 3.10; Fig. 4a). Consistently, H.T. was significantly slower for swimming-styles primed with incongruent colours compared to those

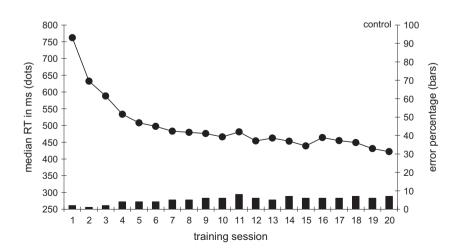


Fig. 3. Swimming-style colour association training: Median response times in ms and error percentage for 10 min of training on 20 consecutive days.

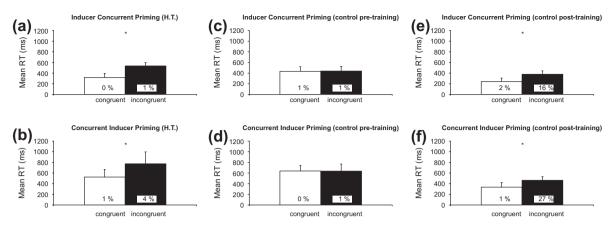


Fig. 4. Synaesthetic Stroop: Mean response times in ms and error percentage for congruent and incongruent trials, respectively. Error bars represent standard deviations.

primed with congruent colours (t(360) = 12.75, p < .001; Cohen's d = 1.34; Fig. 4b). The trained control was tested twice, before and after training. Before training, he did not show any response time differences between congruent and incongruent trials (t(369) = .61, p = .541; Cohen's d = 0.06 for colours primed with swimming-styles; Fig. 4c and t(361) = .17, p = .867; Cohen's d = 0.02 for swimming-styles primed with colours; Fig. 4d). In contrast, after training, his pattern of response times was similar to H.T.'s. The control was significantly slower for colours primed with incongruent swimming-styles compared to colours primed with congruent swimming-styles (t(328) = 19.24, p < .001; Cohen's d = 2.13; Fig. 4e), and also vice versa, for swimming-styles primed with incongruent colours compared to swimming-styles primed with congruent colours (t(317) = 14.26, p < .001; Cohen's d = 1.62; Fig. 4f).

3.4. Physiological facets of synaesthesia

A two-factorial ANOVA (analysis of variance) with participant (synaesthete vs. control) as between subjects factor and phase (habituation vs. conditioning) as within subjects factor was conducted to show that both, H.T. and the control, exhibited an SCRs following the red slides coupled with the UCS (i.e., boat horn) in the conditioning phase. The ANOVA revealed a main effect phase F(1,12) = 63.37, p < .001, indicating higher autonomic arousal for the conditioning phase (mean SCR in μ S

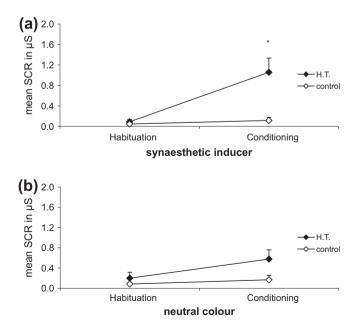


Fig. 5. Synaesthetic conditioning: Mean SCRs in µ-Siemens for habituation and conditioning of synaesthetic inducer trials and neutral colour trials, respectively. Error bars represent standard errors.

for H.T. = 2.75, *SE* = 0.50 and for the control = 1.73, *SE* = 0.27) as compared to the habituation phase (mean SCR in μ S for H.T. = 0.19, *SE* = 0.05 and for the control = 0.16 *SE* = 0.11). The main effect participant and the interaction participant × phase were both not significant, *Fs* < 3.67 *ps* > .05.

Crucially, the same two-factorial ANOVA revealed a significant increase in SCRs for white slides after conditioning for H.T., but not for the control (participant \times phase, F(1,10) = 8.17, p < .05). Post hoc *t*-tests indicated a significant difference between SCRs of the synaesthete and the control in the conditioning phase (t(10) = 3.33, p < .01; Fig. 5a). This indicates higher autonomic arousal and thus a conditioned startle reaction for the synaesthete but not for the control. Again, the same two-factorial ANOVA was conducted for the neutral colour slides to control for unspecific SCR effects. Neither H.T. nor the control showed a significant increase in SCRs after conditioning (participant \times phase F(1,7) = .87, p > .05; Fig. 5b).

4. Discussion

In summary, the swimming-style colour synaesthete showed high consistency for swimming-style colour associations. After training, the control participant selected colours which were highly consistent with the colours he was trained on from memory, but *without experiencing colours* for the different swimming-styles. Moreover, the control participant showed a synaesthetic priming effect after the training, but not before. This effect was also present for the swimming-style colour synaesthete. However, only the synaesthete and not the trained control showed a synaesthetic conditioning effect.

The findings are consistent with the conclusions of the original study on swimming-style colour synaesthesia (Nikolić et al., 2011) and with previous studies on grapheme-colour synaesthesia (Meier & Rothen, 2007, 2009; Rothen et al., 2010, 2011): Swimming-style synaesthesia goes beyond "simply" learned associations between swimming-styles and colours. That is, only on a behavioural level – but not on a psychophysiological level – can swimming-style colour synaesthesia be mimicked in a trained control. Hence, swimming-style colour synaesthesia is no less a genuine form of synaesthesia than, for example, grapheme-colour synaesthesia.

Several reasons can be put forward to support this conclusion. Unlike self-reports, SCRs reflect autonomic nervous system arousal and thus cannot be 'faked' easily (hence the technique is often used as part of 'lie detecting'; for a similar argumentation see, Armel & Ramachandran, 2003; Ramachandran & Brang, 2008). Previous studies with sample sizes of 13 and 36 grapheme–colour synaesthetes, respectively, have demonstrated that this effect occurs only in real synaesthetes (Meier & Rothen, 2007; Rothen et al., 2010). A study with a sample size of 20 non-synaesthetes has shown that the effect does not occur in non-synaesthetes even after training grapheme–colour associations (Meier & Rothen, 2009).

Moreover, training grapheme–colour associations did not result in colour experiences. However, a synaesthetic Stroop effect in the absence of phenomenological reports of colour experiences has been documented repeatedly (Elias et al., 2003; Meier & Rothen, 2009; Rothen et al., 2011). A recent study provided further evidence for the non-trainability of synaesthetic experiences with a very extensive coloured-letter reading training (Colizoli, Murre, & Rouw, 2012). That is, a Stroop effect was found but no synaesthetic crowding effect (i.e., no perceptual effect). This is entirely in line with the current results and the subjective reports of our participants. The synaesthetic priming effects fit well with H.T.'s report of the involuntary nature of his experiences and are also consistent with the control's report of automatic and involuntary associations between the trained swimming-styles and colours after the training. Also, the differential psychophysiological effects in the synaesthetic conditioning paradigm match the subjective reports of H.T., who *experiences* colours for swimming-styles, whereas the control did not report any colour *experiences* for the swimming-styles.

Furthermore, the fact that H.T. reports digit-colour synaesthesia, a well-accepted form of synaesthesia, strengthens the interpretation of the current findings that swimming-style colour synaesthesia is a genuine form of synaesthesia. That is, having one form of synaesthesia increases the chance of also experiencing another form of synaesthesia (cf., Barnett et al., 2008).

Importantly, our control was highly motivated to participate in this study and did not receive monetary reinforcement. Thus, the absence of the synaesthetic conditioning effect cannot be explained by lack of motivation/attention to the stimuli. This is consistent with the presence of a synaesthetic Stroop effect in the last session of the study and the duration of the reaction times in this task (and the training) which were no longer than those of H.T.

Given the evidence of previous studies with these tasks and trained controls and synaesthetes respectively, we would like to point out that matching and motivation are more important for the current results than a larger sample of insufficiently matched and unmotivated controls. That is, our current approach is a more conservative approach compared to cumulate control participants from an arbitrary (student) population. More generally, matching synaesthetes to a control (group) is an important issue in synaesthesia research. Specifically, careful (yoked) matching allows us to exclude the alternative interpretation that the results may be caused by individual differences which are independent of synaesthesia (Rothen & Meier, 2009). Hence, careful matching provides for a more sensitive test than simply boosting the size of the control group.

Our findings go beyond previous studies of conceptually induced synaesthesia (e.g., Dixon et al., 2000, 2006; Frith & Paulesu, 1997; Grossenbacher, 1997; Ramachandran & Hubbard, 2001; Rich et al., 2005) and question the predominant view of synaesthetic concurrents being elicited through sensory input. To the best of our knowledge, so far synaesthetic experiences – when triggered conceptually – were always induced via stimuli of some instance of the same task-set (e.g., thinking of graphemes, calculating with digits, etc.) as the primary inducer (e.g., graphemes). Activating an entirely *different task set* than the usual inducer, the pictograms used in our study seem therefore less likely to activate inducer-related early sensory

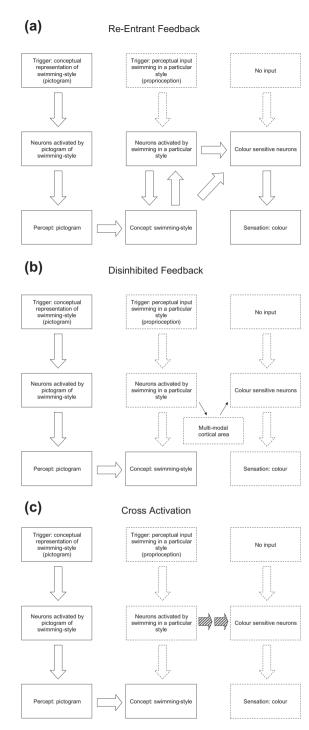


Fig. 6. The three main neurophysiological models to explain the genesis of synaesthetic experiences. Note, the models are adapted to implement synaesthetic concurrents being triggered due to conceptual representation of the according inducer in swimming-style colour synaesthesia. Solid lines represent active brain regions and pathways and dashed lines indicate inactive regions and pathways. (a) The re-entrant feedback model. Perception of the pictogram leads to a conceptual representation of the swimming-style which activates colour sensitive neurons via top-down processes due to direct and indirect re-entrant pathways which leads finally to the synaesthetic colour experience. (b) The disinhibited feedback model. A multimodal area providing feedback from lower level proprioceptive areas to colour sensitive areas is the hypothesized key for synaesthetic experiences to occur. Due to missing feedback connections from higher order conceptual areas, the model cannot explain synaesthetic experiences triggered by conceptual representations of the inducer. (c) The cross-activation model. Proprioceptive areas, the model is not able to explain synaesthetic experiences without direct sensory input of its actual inducer. Adapted from Mulvenna and Walsh (2006) and Hubbard et al. (2011).

areas than stimuli used in previous studies of conceptually induced synaesthesia. Therefore, we regard it as necessary to link and discuss our findings in terms of the three basic models assumed to underlie the genesis of synaesthetic experiences (i.e., re-entrant feedback model, disinhibited feedback model, cross-activation model). Although these models were initially formulated to elucidate grapheme–colour synaesthesia, we will focus predominantly on their general nature as the same mechanisms are expected to account for other forms of synaesthesia.

The re-entrant feedback model was first proposed by Smilek, Dixon, Cudahy, and Merikle (2001). It was suggested that, in grapheme-colour synaesthesia, colour experiences are modulated in V4 via feedback connections from anterior fusiform and posterior inferotemporal activation of the meaning of a grapheme (i.e., inducer). Critically, top-down categorization of a synaesthetic inducer (i.e., its conceptual representation) seems to play an important role in the generation of the synaesthetic concurrent. This is entirely consistent with our results. Despite the absence of any proprioceptive input of swimming, H.T. showed typical synaesthetic effects in a Stroop type task and the synaesthetic conditioning paradigm. That is, colour experiences were presumably modulated in V4 via feedback connections from activation of the meaning of the swimming-style pictogram (i.e., inducer). Accordingly, top-down categorization of the synaesthetic inducer (i.e., its conceptual representation) played an important role in the genesis of the synaesthetic concurrent. Moreover, the re-entrant feedback model suggests synaesthetic colours are modulated in V4 and thus are more than a semantic or conceptual representation of colour information. This is also supported by our findings that H.T. reported colour experiences when presented with pictograms of swimming-styles and that he also showed a synaesthetic conditioning effect while the trained control – who did not report colour experiences - did not show a conditioned synaesthetic response. More indirect support for the re-entrant feedback model comes from various studies which found V4 activation to play a critical role in grapheme-colour synaesthesia (e.g., Hubbard, Arman, Ramachandran, & Boynton, 2005; Nunn et al., 2002; for a discussion about V4 activation for synaesthetic colour experiences see Rouw, Scholte, & Colizoli, 2011). A schematic depiction of the re-entrant feedback model for swimming-style colour synaesthesia can be found in Fig. 6a.

The disinhibited feedback model (Grossenbacher, 1997; Grossenbacher & Lovelace, 2001) is very similar to the re-entrant feedback model. Instead of direct re-entrant feedback, it was suggested that disinhibited feedback from a "multisensory nexus" comprising higher visual areas, as for instance the temporo-parieto-occipital junction, gives rise to synaesthetic experiences. It was also suggested that the identity of a stimulus determines a synaesthetic concurrent, and that neural representation of an inducer is required to represent its identity to mediate a particular form of synaesthesia. Although it was recognized that voluntary imagery of an inducer can give rise to the experience of a synaesthetic concurrent, this was not regarded as exclusively conceptual: "Imagery involves many parts of the brain that are also active during perception." (Grossenbacher & Lovelace, 2001, p. 37). Hence, according to this model, perceptual components are involved in the generation of a synaesthetic concurrent. Correspondingly, the model does not implement the possibility of a synaesthetic concurrent being triggered solely by the concept of its inducer and therefore, the model is questioned by our findings. Fig. 6b represents a schematic depiction of the disinhibited feedback model for swimming-style colour synaesthesia.

According to the cross-activation model, neural representation of synaesthetic inducer and concurrent are often adjacent to each other and lie in densely interconnected brain areas (Ramachandran & Hubbard, 2001). The basic assumption of the model is that, due to a failure of pruning in infancy and consequential anatomical differences, activation in the inducer related brain region "cross-activates" the concurrent related brain region leading to a concurrent synaesthetic experience. The model was recently modified to account for parietal activations which were often found in grapheme–colour synaesthesia (Hubbard, Brang, & Ramachandran, 2011). According to the model, parietal activation reflects binding processes between inducer and concurrent, but these processes are not the cause for synaesthesia. The cross-activation model does not rule out top-down influences on synaesthetic experiences (e.g., in ambiguous contexts). However, top-down processes are not regarded as crucial for the genesis of synaesthetic experiences (cf., Hubbard et al., 2011). In this respect, synaesthetic experiences triggered by the mere conceptual representation of its inducer are ineligible. Consequentially, the cross-activation model for swimming-style colour synaesthesia is shown. Despite the clear support for the re-entrant feedback model in the current case of swimming-style colour synaesthesia, it is to be noted that some forms of synaesthesia or discrete subtypes of synaesthesia may be explained by other mechanisms (Specht, 2012; van Leeuwen, den Ouden, & Hagoort, 2011).

On a more general level, our results suggest that two conditions must be met for synaesthesia to occur. First, as suggested by many others, the organism must be prepared for synaesthesia, probably by a genetic predisposition (Asher et al., 2009; Barnett et al., 2008; Baron-Cohen, Burt, Smith-Laittan, Harrison, & Bolton, 1996; Ward & Simner, 2005). For instance, this may then lead to enhanced colour processing in different forms of colour synaesthesia (cf., Banissy, Walsh, & Ward, 2009; Rothen, Meier, & Ward, 2012; Yaro & Ward, 2007). Second, as humans are not born with an inherent knowledge of swimming-style classifications, a learning component must also be involved in the development of synaesthesia (Marks & Odgaard, 2005; Rothen et al., 2010). Thus, a threshold-model, in which a predisposition determines the preparedness of the organism and a learning component that is triggered during a critical period, may be preconditions for synaesthesia. Genuine synaesthetic *experiences* which seems to be a precondition for the synaesthetic conditioning effect may evolve only when the specific associations are built up early in life (Simner, Harrold, Creed, Monro, & Foulkes, 2009).

To summarize, this study provides strong support for the genuineness of swimming-style colour synaesthesia and suggests that behavioural facets of it – but not psychophysiological facets – can be mimicked in trained non-synaesthete controls. Moreover, we demonstrate that synaesthetic inducers can act at a semantic level rather than on a perceptual. We think

that swimming-style colour synaesthesia can be best explained by the re-entrant feedback model suggesting that this model is most promising for explaining different forms of conceptually induced synaesthesia.

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