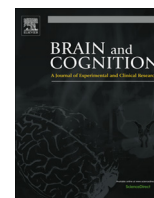


Contents lists available at [ScienceDirect](http://ScienceDirect.com)

Brain and Cognition

journal homepage: www.elsevier.com/locate/b&c

What spatial coordinate defines color-space synesthesia?



Isabel Arend*, Shiran Ofir, Avishai Henik

Department of Psychology and Zlotowski Center for Neuroscience, Ben-Gurion University of the Negev, Beer-Sheva, Israel

ARTICLE INFO

Article history:

Received 27 November 2015

Revised 9 April 2016

Accepted 11 April 2016

Available online 21 April 2016

Keywords:

Synesthesia

Automaticity

Space-color

Frames of reference

Spatial representation

ABSTRACT

Synesthesia is characterized by the association between different stimuli modalities. For example, in sequence-space synesthesia, numbers, weekdays, months, and musical tones are visualized in specific spatial locations. Although sequence-space synesthesia tends to co-occur with other types of synesthesia (e.g., grapheme-color), our knowledge about how these individuals represent space is still limited. A central issue for understanding spatial processing refers to the coordinate system used to represent spatial locations. We report on a space-color synesthete (N.W.) who vividly experiences colors in specific spatial locations. We used a task where N.W. and control subjects were required to report the location of a gray square relative to a colored square. The color of the square was task-irrelevant. Participants responded to the following trial types: (1) central trials, where one stimulus appeared on the left and the other on the right side of fixation, and (2) relative location trials, where both stimuli appeared either on the left or on the right side of fixation. Results showed that the color of the target had a strong impact on N.W.'s responses on both trial types, but not on the controls' responses. These results show that the spatial representation underlying N.W.'s synesthetic experience is automatic and sensitive to the relative location of objects.

© 2016 The Authors. Published by Elsevier Inc. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

Synesthesia is characterized by an abnormal association in which a certain stimulus automatically induces an additional percept or association in another sensory modality. For example, letter and digits may elicit a vivid experience of colors or numbers may be visualized in specific spatial locations. The terms “inducer” and “concurrent” are used to refer to the event that triggers (e.g., letters) the specific sensory experience or association (e.g., colors), respectively. Among the most common types of synesthesia are the so-called grapheme-color synesthesia – in which letters, numbers, or days of the week are associated with specific colors (Alford, 1918; Cohen-Kadosh, Cohen-Kadosh, & Henik, 2007; Mattingley, Payne, & Rich, 2006; Mattingley, Rich, Yelland, & Bradshaw, 2001; Rich, Bradshaw, & Mattingley, 2005) – and spatial-form synesthesia, in which words, numbers, days of the week, or names of the months are visualized in specific spatial arrays (Eagleman, 2009; Galton, 1880; Piazza, Pinel, & Dehaene, 2006; Sagiv, Heer, & Robertson, 2006; Seron, Pesenti, Noël, Deloche, & Cornet, 1992; Gertner, Henik, & Kadosh, 2009; Arend, Gertner, & Henik, 2013;

Diesendruck et al., 2010; Jarick, Dixon, Maxwell, Nicholls, & Smilek, 2009).

An interesting aspect concerning spatial-form synesthesia is that it tends to co-occur with other types of synesthesia, as for example, grapheme-color synesthesia (Sagiv et al., 2006). Despite the fact that space is an important dimension characterizing different forms of the synesthetic experience, our knowledge about how these individuals represent space is still limited.

A central issue for understanding spatial processing in general refers to the coordinate system used to represent spatial locations. For example, we know that individuals with synesthesia represent numbers in specific spatial locations, but it is still not clear what frame of reference defines spatial locations in spatial-form synesthesia, or in other words what defines “left” and what defines “right” spatial locations. Space is represented according to a number of coordinate systems or frames of reference that can be, for example, viewer based or environmentally centered (Andersen, Snyder, Bradley, & Xing, 1997). Interestingly, viewer-based coordinates can occur with respect to left side versus right side of the midline of the observer's body, but they can also occur with respect to yet another set of coordinates centered on the object itself (Marr, 1982; Marr & Nishihara, 1978). In an object-based frame of reference, left and right are defined with respect to the object itself. This type of spatial coding is advantageous because it allows objects to be processed with structural invariance across different

* Corresponding author at: Department of Psychology, Ben-Gurion University of the Negev, P.O. Box 653, Beer-Sheva, Israel.

E-mail address: arend.psy@gmail.com (I. Arend).

orientations. Object-based spatial coding has been found in disorders of spatial attention, for example, in unilateral neglect (Behrmann & Moscovitch, 1994).

In the present study, we examine the spatial coordinate system that defines color-space association in synesthesia. We report on a single case of a synesthete (N.W.) who vividly experiences colors in specific spatial locations. Our aims are twofold: (1) to examine the impact of N.W.'s color-space association on her motor choices, in other words, to examine whether colors automatically elicit response locations; (2) to study the coordinate system or frame of reference that defines “left” space and “right” space in N.W.'s synesthetic experience. To achieve these goals, we used a task that required locating a colored square relative to a gray square. The specific color of the square was task-irrelevant. That is, the colors were not associated with any specific response. The following locations were possible: the colored square and the gray square could appear (1) on either the left side or the right side of the fixation cross (see Fig. 1, center condition); (2) both squares could appear on the left side of the fixation cross; (3) both squares could appear on the right side of the fixation cross (see Fig. 1, relative location condition). It is important to note that in the relative location conditions, the colored square could be located on the left side or on the right side of the gray square within the same visual field.

The present task shares a number of features with the Simon task (Nicoletti & Umiltà, 1989; Rubichi, Nicoletti, Iani, & Umiltà, 1997; Simon & Small, 1969). The Simon task involves an arbitrary mapping of color and response: Participants are asked to respond using their left and right hands for two different colors (e.g., press

left for blue and press right for green). The stimulus is presented on the left or right side of a fixation cross. Even though the spatial location of the stimulus is task-irrelevant, it affects individual's responses: When the location of the stimulus and the location of the response correspond (Simon compatible), response times (RTs) are faster in comparison to when the location of the stimulus and the response do not correspond (Simon incompatible). In the task used here, participants are presented with a gray and a colored square on the left or right side of a fixation cross. The task requires deciding the location of a gray square relative to a colored square (either blue or green in different trials). Different from the Simon task, there is no direct mapping involving the specific color of the square and the response. Because our task does not contain an arbitrary mapping involving color and response, controls are not expected to show a Simon-like effect. That is, there should be no effect involving the color of the target. We reason that if N.W.'s color-spatial association affects specific motor responses (blue → left and green → right), we should find faster RTs when color and spatial locations are congruent as opposed to when they are incongruent with her personal association. That is, N.W.'s synesthetic experience should produce a compatible Simon-like effect.

In addition, by manipulating the relative position of the colored target relative to the gray distractor within the visual field (see Fig. 1), we aim to explore how left and right spatial locations are defined in N.W.'s spatial representation. The effects of relative target location are particularly informative regarding how left and right locations are represented. For example, is the association blue → left coded with respect to N.W.'s body midline or does this

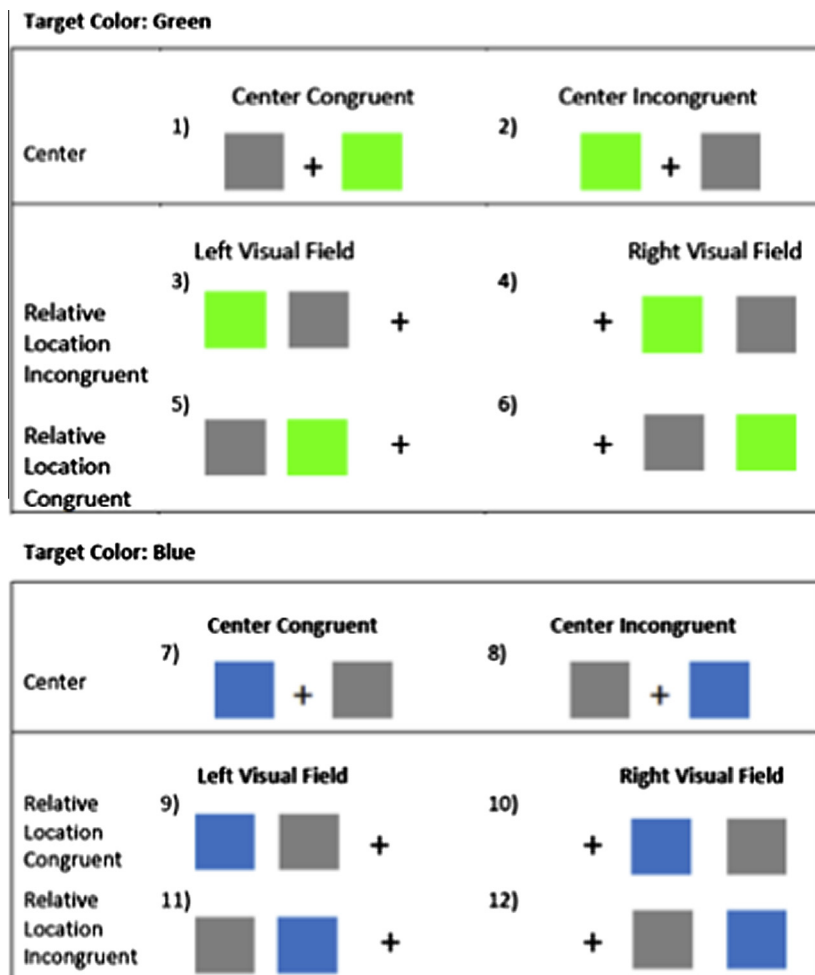


Fig. 1. Schematic representation of each trial type.

association appear when the color is processed relative to an object? The Simon effect has been shown to be sensitive to multiple frames of reference (Rubichi, Vu, Nicoletti, & Proctor, 2006; for a review). The effects of relative locations in the Simon effect were investigated by asking participants to press right and left keys in response to the shape or to the color of a stimulus. The stimulus appeared in one of two boxes presented on the left or right side of a fixation cross (Roswarski & Proctor, 1996, Experiment 2). The location of the stimulus was task irrelevant, and therefore, the automaticity of relative spatial codes was examined by computing the Simon effect across the visual field (left vs. right) and the relative target location (relative left or relative right). Results showed a reliable Simon effect across multiple frames of reference. However, the effect of relative spatial coding was modulated by target discriminability, suggesting that such coding does not occur automatically. Following these previous findings, we expect our control participants to be more accurate and faster when absolute and relative target locations, than when absolute and relative locations mismatch. This result would be consistent with the proposal that spatial coding occurs with respect to multiple frames of reference in nonsynesthetes. However, for controls, we expect no effect of target color.

2. Method

2.1. Participants

2.1.1. Synesthete

N.W. is a 24 year-old, right-handed woman who reports vividly experiencing the colors blue and green in the left and right side of space, respectively. N.W. first reported her association when she was taking part in an experiment for the Department of Psychology. The task required a response to a green color using the left hand and to a blue color using the right hand. Surprisingly, N.W. had to interrupt the testing session to tell the experimenter that she was unable to continue performing the task because the color-response mapping that she was asked to use in the experiment was not the “correct one.” She told the experimenter that for her, “Blue was always on the left and green was always on the right.” She actually wanted to rotate the keyboard in order to continue the task “so that the colors would be in the correct locations.” After this incident, we assessed N.W.’s color-space association. N.W. experiences colors along a horizontal axis. N.W. also reported associations involving numbers across space (from left to right) and names of the week in space. We tested N.W.’s spatial associations in two sessions, one year apart. N.W. was first interviewed on December 2012 and then again on December 2013. She was highly consistent in her report. She completed the Eagleman, Kagan, Nelson, Sagaram, and Sarma (2007) synesthesia battery.

2.1.2. Controls

Fifteen age-matched non-synesthetic controls (11 females, $M = 24.2$ years, $SD = 1.7$) received financial compensation for taking part in the study. All participants had normal or corrected-to-normal visual acuity and were not color blind. They reported no unusual color-space or color-number association. One participant was left-handed. The study was approved by the Ben-Gurion University Ethics committee. All participants gave written consent before participating.

2.2. Stimuli and procedure

Stimuli consisted of squares subtending were at a visual angle of approximately $1.3^\circ \times 1.3^\circ$ from a viewing distance of 50 cm from the screen. A colored square, green or blue, was presented together

with a gray square. RGB color code for green was 68, 227, 44, and for blue was 37, 41, 191. The squares were presented at a visual angle of 0.5° to the left or to the right of the fixation cross. The inter-distance between the two squares was at a visual angle of 0.3° . A white fixation cross was presented in the center of the display during the entire duration of the trial. To signal the start of the trial, a change occurred in the size of the fixation of the visual angle from $0.8^\circ \times 0.8^\circ$ to $0.5^\circ \times 0.5^\circ$. The background was black throughout the experiment.

A trial began with a fixation cross presented for a period of 1000 ms; next, a decrease in the size of the fixation cross for a period of 500 ms signaled the upcoming stimulus. The fixation cross remained in the center of the display throughout the trial following the methodology used in previous studies examining object-based effects (Tipper, Weaver, Jerreat, & Burak, 1994). The two squares were presented for 100 ms according to the conditions presented in Fig. 1. For the *center conditions*, the colored and the gray squares were presented on the left side and on the right side of the fixation cross (see Fig. 1, conditions 1 and 2 for green target, and conditions 7 and 8 for blue target). In the *relative location conditions*, both squares appeared either in the left or on the right visual field. The colored square appeared either on the left or right side of the gray square. Congruent relative conditions are those in which the relative location of the colored target matched that of N.W.’s association, irrespective of visual field (see Fig. 1, conditions 5 and 6 for green targets, and conditions 9 and 10 for blue targets). Incongruent relative conditions are those in which the relative location of the colored target mismatched that of N.W.’s association irrespective of visual field (see Fig. 1, conditions 3 and 4, for green targets, and 11 and 12 for blue targets). The task required responding, as quickly and as accurately as possible, to the location of the colored square relative to the gray square by pressing left or right keys of the computer keyboard (keys “x” and “m” for left and right positions, respectively).

The following conditions composed the full design: congruency, color, location, and frames, resulting in 16 experimental conditions. These conditions were mixed within blocks and were repeated nine times in each block, resulting in 144 trials per block. The experimental session consisted of two blocks (288 trials), which were preceded by 12 practice trials. Participants were encouraged to make a five minute break after 144 trials. N.W. completed 576 trials, divided into two sessions of 288 trials each. The 288 trials session took approximately 20 min to be completed.

3. Results

To compare N.W. with controls we used ANOVA (analysis of variance) and Crawford and Garthwaite’s procedure (2004; see also Crawford, Garthwaite, Howell, & Gray, 2004), designed to compare a single case with a control group. One-tail *t*-test is reported. Results for the *center condition* and the *relative location condition* are presented separately.

3.1. Center condition

3.1.1. Accuracy

Accuracy results for controls and N.W. are displayed in Fig. 2, panels A and B, respectively. The main focus of the present report is to examine the impact of N.W.’s color-space association on responses; therefore, congruent and incongruent trials are presented separately for blue and green targets (see Fig. 1). Congruent trials are those in which the location and the color of the target match N.W.’s associations. There are two types of congruent trials: congruent blue (blue on the left) and congruent green (green on

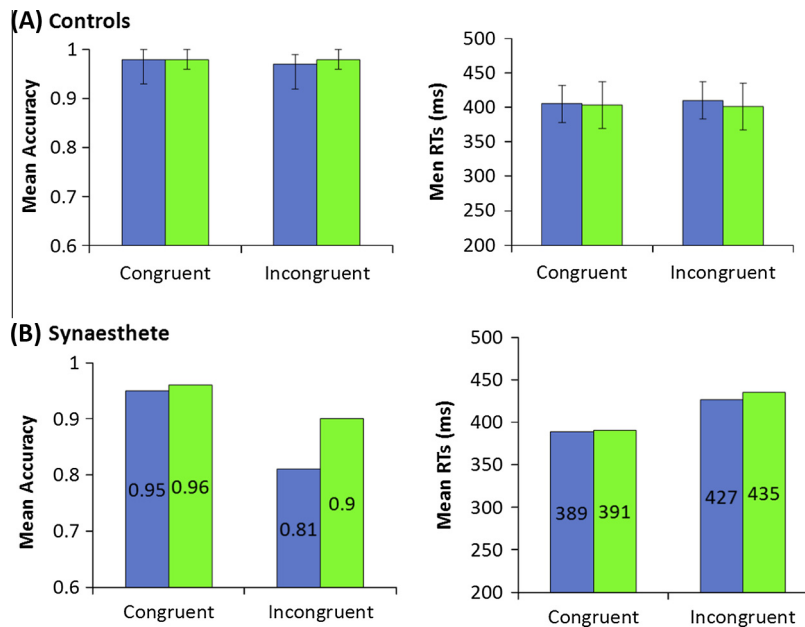


Fig. 2. Panel A and panel B show mean accuracy and mean RTs for the control sample and the synaesthete, respectively, as a function of congruency and target colors (blue and green). Error bars represent standard error of the mean. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the right); and two types of incongruent trials, incongruent blue (blue on the right) and incongruent green (green on the right).

Controls were overall highly accurate on the task (Mean = .98). For blue targets, N.W.'s performance for congruent and incongruent trials was significantly different from the control sample, $t(14) = 2.60$, $p < .01$; as well as for green targets, $t(14) = 1.78$, $p < .05$. These results clearly show that the color of the target automatically activates location information. That is, left responses are significantly less accurate when associated with green as opposed to blue. Similarly, right responses are significantly less accurate when associated with blue as opposed to green.

3.1.2. RTs

For the control sample, we conducted a repeated measured ANOVA taking congruity (congruent vs. incongruent) and color (blue vs. green) as factors on mean RTs. Results showed no significant main effect of congruity, $F(1, 14) = 1.11$, $p = .31$, $\eta_p^2 = .07$; and no interaction between the two factors, $F(1, 14) = 1.07$, $p = .33$, $\eta_p^2 = .07$. Results are shown in Fig. 2, panel A.

Comparison between N.W. and controls for blue targets showed a significant discrepancy between congruent and incongruent trials for blue targets, $t(14) = .79$, $p < .05$, as well as for green targets, $t(14) = 2.21$, $p < .02$. Results are shown in Fig. 2, panel B.

3.1.3. Interim discussion

As we mentioned in the Introduction, our task shares a number of features with the Simon task (Simon & Small, 1969). The logic behind stimulus–response association found in the Simon task is especially useful for the purpose of the present research because it allows us to study the impact of N.W.'s synesthesia on her responses. Results for both accuracy and RTs clearly show a Simon-like effect for N.W. and not for controls. That is, N.W.'s responses to the location of the target were significantly affected by the specific color of the target, even though she was not required to press a specific key to respond to blue and green. These results clearly show that N.W.'s space-color association resembles the arbitrary association of color and responses elicited by the experimental instructions in the Simon task. Note that, in the

Simon task, participants are asked to respond by pressing left or right keys to the color of the target. Color is relevant and target location is task-irrelevant. In contrast, for our task, color is task-irrelevant because participants must report the location of the colored square relative to the gray square. Even though the color of the target was not part of the response requirements, it affected N.W.'s responses, illustrating the automaticity of her synesthetic experience.

3.2. Relative location condition

Because there were no significant effects of relative location of the target on mean RTs, we will present only results for mean accuracy. For the control sample, we conducted repeated measures ANOVA taking visual field (left vs. right) \times relative location (left vs. right) \times color (blue vs. green) on mean accuracy. The only significant effect was the interaction between visual field and relative location of the target, $F(1, 14) = 32.37$, $p < .001$, $\eta_p^2 = .70$. As we expected, participants were faster when both visual field and relative location corresponded (i.e., a target presented on the left relative location and on the left visual field) as opposed to when they did not correspond (i.e., a target presented on the left relative location and on the right visual field). Therefore, relative location and visual field need to be considered when analyzing N.W.'s responses, so that the effects of the target color are not confounded by the mismatch between visual field and relative location.

We first analyzed N.W.'s performance in the matched condition. We compared her mean accuracy in responding to green and blue targets in the left visual field when the targets were located on the left relative location to that of controls (Fig. 3, left column, panels A and B respectively). Results clearly show that N.W.'s performance was significantly different from controls, $t(14) = 3.09$, $p < .001$. That is, N.W. made significantly more errors in responding to the green target when it appeared in the left visual field and in the left relative location in comparison to blue targets. The same analysis was carried out for the right visual field and right relative location. N.W.'s performance was again significantly different from controls, $t(14) = 4.47$, $p < .001$; her accuracy in responding to blue targets

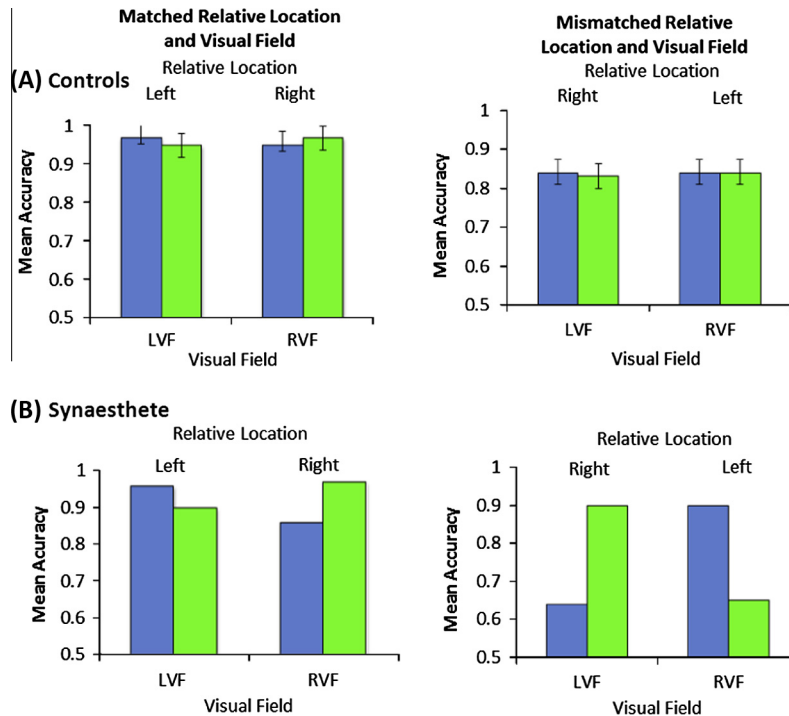


Fig. 3. Panel A and panel B show mean accuracy for the control sample and the synesthete, respectively, as a function of relative target location and visual field, separately for blue and green targets. The first column shows results for matched relative location and visual field and the second column shows results for mismatched relative location and visual field. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

was significantly lower than her response to green targets when the target appeared in the right visual field. That is, N.W.'s color-space association is sensitive to the relative location of the target.

We also compared N.W.'s performance with that of controls for the mismatched conditions. It is important to note that, even though controls were less accurate when the visual field and relative location of the target did not match, *their performance was not affected by the target color*. N.W.'s results for the mismatch condition (lower right panel) indicate that target color had a great impact on her responses. We compared her performance for blue versus green targets when both squares appeared in the left visual field and on the right relative location with the performance of controls. Results were statistically significant, $t(14) = 18.54$, $p < .001$. That is, N.W.'s "right" response accuracy was significantly better when the target was green, in comparison to when the target was blue, even though both targets appeared in the left visual field. A similar analysis was carried out for green versus blue targets when both squares appeared in the right visual field and in the left relative location. Results showed that N.W.'s performance was significantly different than controls, $t(14) = 12.16$, $p < .001$. That is, N.W.'s accuracy to respond "left" was higher when the target was blue than when the target was green, even though both targets appeared in the right visual field. These results show that spatial locations are represented in an object-based manner for N.W.

4. Discussion

In the present study, we report on a synesthete, N.W., who vividly experiences colors in specific spatial locations. Results revealed three novel findings regarding spatial representation in space-color synesthesia: (1) colors automatically activated left and right spatial locations for N.W., but not for controls. That is, N.W. was less accurate and slower in responding to the location

of the target when the target color was not consistent with her synesthetic experience; (2) N.W.'s color-space association is sensitive to the relative spatial location of the colors. That is, N.W.'s colors are not only associated with left and right locations when colors appear on the left or right side of the body-midline (center conditions), but also when the colors were presented on the left or on the right side of an object (relative location conditions); (3) N.W.'s color-space association follows an object-based representation. The object-based effects can be illustrated by the results for the mismatched conditions, which are depicted in Fig. 3 (panel B, lower right graph). N.W. was more accurate when responding "left" when the target was blue than when the target was green, even though the two targets were presented in the right visual field. Similarly, her accuracy in responding "right" was higher when the green target was presented on the right side of the gray object, even though both targets appeared in the left visual field.

One of our goals was to determine which coordinate system defines "left" and "right" in color-space synesthesia. Our results show that N.W.'s synesthetic experience accesses different frames of reference. For example, left and right locations are represented with respect to her body midline and also with respect to other objects (e.g., whether the gray square was on the left or on the right of another object). Previous studies in the context of the Simon effect have shown that spatial coding occurs with respect to multiple frames of reference (Roswarski & Proctor, 1996).

One explanation for how the relative coding effect emerges in color-space synesthesia is that synesthetic association may increase attention to the objects that represent their synesthetic experience. Therefore, similar to what is observed for control, spatial coding occurs as a function of attentional shifts, and it is sensitive to multiple frames of reference (Rubichi et al. (2006)). That is, spatial attention assesses the environmental locations and object-based locations of objects that are part of the synesthetic representation. Different from a typical Simon task, our task did not involve arbitrary stimulus-response mapping. Therefore, the

relative coding effects were only observed for the synesthete but not for the control sample. However, the control sample showed a clear advantage when absolute and relative location of the target matched relative when it mismatched, illustrating the formation of spatial codes as a function of multiple frames of reference (Roswarski & Proctor, 1996). Our results clearly illustrate that spatial coding in synesthesia shares the underlying mechanisms supporting spatial coding in nonsynesthetes. Furthermore, our results constitute the first demonstration for relative coding effects associated with colors. Therefore, it remains an open question whether a relative coding effect emerges in other types of space synesthesia. At present, our findings constitute a strong support for continuity in terms of underlying mechanisms of spatial coding between synesthetes and nonsynesthetes.

4.1. Spatial processing in synesthesia

How do the present findings relate to previous reports using Simon-like effects in synesthesia? The fact that N.W.'s association involving color and space produced a Simon-like effect corroborates our findings that show automatic activation of responses by numbers, analyzed in our previous study using a variation of the Simon task (Arend et al., 2013). In our previous study, we tested a group of number-form synesthetes in a Simon-color task where numbers were task-irrelevant and appeared simultaneously with the colored targets. We reasoned that, if the numerical spatial association has the potential to influence individual's actions, the task-irrelevant numbers should affect motor choices even though the participant is engaged in an ongoing action, namely, the Simon-color task. Results showed that the mere presence of numbers affected the synesthete's responses. RTs were consistently faster when target and response locations matched as opposed to when they mismatched. More importantly, synesthetes showed faster RTs in Simon incompatible trials when numbers followed the synesthetic number-form association. In the present study, there was no direct mapping involving the color of the target and the response. Participants were simply instructed to press the "left" or the "right" keys to indicate the location of the colored square relative to the gray square. Only N.W.'s responses were affected by the color of the target. Taken together, results from these two variants of the Simon task corroborate those from previous studies showing automaticity of space-form synesthesia (Jarick, Dixon, & Smilek, 2011; Jarick et al., 2009; Piazza et al., 2006).

Recently, the evidence for automaticity in spatial-form synesthesia has been challenged (see Price & Mattingley, 2013). In their review, Price and Mattingley identify a number of methodological limitations in tasks previously used to address automaticity in space-sequence synesthesia: SNARC tasks (Spatial Numerical Association Response Codes), spatial cueing, and numerical Stroop tasks. A full description of their constraints is beyond the scope of the present report because these paradigms differ substantially from the tasks reported here. However, of main relevance for studying cognitive processing in synesthesia is the criticism that the tasks mentioned by Price and Mattingley cannot speak to the issue of automaticity because they may be affected by short-term task instructions. That is, by top-down control. It is important to note that task requirements have been shown to affect performance of nonsynesthetes, but not the performance of synesthetes. The case study reported here challenges the notion that short-term task instructions affect synesthetic experience. The first time N.W. reported her synesthetic experience (see Section 2 for details), she was performing a cognitive task in exchange for course credit. It would have been beneficial for her to strategically modify her space-color association to be able to perform the task. She was highly motivated to modify her color space association to match that of the required task, but she was unable to do so. That is, even

though the experimenter suggested to N.W. to try to respond with the response mapping used in the experiment, she was unable to modify her association and told the experimenter that "... the colors were not in the right place..." N.W.'s self-report clearly illustrates that potential for a top-down influence in her color-space association is limited. Again, this observation is also consistent with previous descriptions of space-form synesthesia as less flexible and more automatic (Gertner et al., 2009). Learning new sequences would require a high degree of motivation and practice. Consistent with these observations is the fact that even though synesthetes may be better than controls at remembering features (e.g., colors) that are part of their synesthetic experience, they are not necessarily better in forming new associations (Pritchard, Rothen, Coolbear, & Ward, 2013).

The demonstration that spatial association can be characterized as automatic in synesthesia does not necessarily imply discontinuity in terms of the underlying mechanisms of spatial representations (Cohen Kadosh & Terhune, 2012). As it has been previously suggested, automaticity in synesthesia could reflect learning (Price & Mattingley, 2013) or over activation of brain circuits devoted in the normal brain to process different magnitude dimensions and space. An interesting topic for future research concerns the flexibility of the relative coding effects reported here across different types of synesthesia. In the same line, the effects of attention to particular inducers may provide insights on how spatial coding can help establish new spatial associations involving multiple representations.

4.2. Implications for the neurobiological basis of space synesthesia

The parietal cortex is known to host complex spatial representations. In a recent review looking at brain imaging studies on synesthesia (see Rouw, Scholte, & Colizoli, 2011), whole brain analysis showed higher activation patterns in both superior and inferior parietal cortices associated with the synesthetic experience, specifically to synesthesia involving color. Parietal activation has also been observed in number-form synesthesia (Tang, Ward, & Butterworth, 2008). The role of the parietal cortex in synesthesia was brought to light due to its part in feature binding and so was suggested as possibly supporting bindings between concurrent and inducers (Weiss & Fink, 2009). The fact that the parietal cortex is part of the neural network involved in different types of synesthesia corroborates the fact that different spatial representations may be efficiently accessed in synesthesia.

The relative coding effect reported here is consistent with continuity in terms of the brain mechanisms that underlie the association involving numbers and space for synesthetes and nonsynesthetes. We agree with the description provided by Rouw et al. (2011) that structural differences in the brain may account for the differences between synesthetes and nonsynesthetes in what can be a predisposition for the synesthetic trait. As suggested by the same authors, a predisposition for cross-activation (e.g., mediated by structural connectivity differences) between brain areas may exist, and the type of synesthesia is likely to be dependent on environmental factors (Simner et al., 2005). However, even though a predisposition may characterize synesthesia, it is also important to note that there is no direct correspondence between specific brain areas and the associated synesthetic experience. Structural and functional changes can underlie differences regarding the efficiency by which mechanisms can be applied to stored representations, without necessarily implying different mechanisms for different types of synesthesia. With this in mind, we interpret the spatial coding effects reported here to be the behavioral manifestation of complex spatial coding commonly observed in normal cognition.

Acknowledgment

This research was supported by the European Research Council under European Union's Seventh Framework Programme (FP7/2007–2013)/ERC Grant agreement number 295644 awarded to Avishai Henik.

References

- Alford, L. B. (1918). A report on two cases of synesthesia. *The Journal of Abnormal Psychology*, 13(1), 1.
- Andersen, R. A., Snyder, L. H., Bradley, D. C., & Xing, J. (1997). Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Annual Review of Neuroscience*, 20(1), 303–330.
- Arend, I., Gertner, L., & Henik, A. (2013). Perceiving numbers influences actions in number–space synesthesia. *Cortex*, 49(7), 1955–1962.
- Behrmann, M., & Moscovitch, M. (1994). Object-centered neglect in patients with unilateral neglect: Effects of left–right coordinates of objects. *Journal of Cognitive Neuroscience*, 6(1), 1–16.
- 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.
- Cohen Kadosh, R., & Terhune, D. B. (2012). Redefining synaesthesia? *British Journal of Psychology*, 103(1), 20–23.
- Crawford, J. R., & Garthwaite, P. H. (2004). Statistical methods for single case studies in neuropsychology: Comparing the slope of a patient's regression line with those of a control sample. *Cortex*, 40, 533–548.
- Crawford, J. R., Garthwaite, P. H., Howell, D. C., & Gray, C. D. (2004). Inferential methods for comparing a single case with a control sample: Modified *t*-tests versus Mycroft et al.'s (2002) modified ANOVA. *Cognitive Neuropsychology*, 21, 750–755.
- Diesendruck, L., Gertner, L., Botzer, L., Goldfarb, L., Karniel, A., & Henik, A. (2010). Months in space: Synaesthesia modulates attention and action. *Cognitive Neuropsychology*, 27(8), 665–679.
- Eagleman, D. M. (2009). The objectification of overlearned sequences: A new view of spatial sequence synesthesia. *Cortex*, 45(10), 1266–1277.
- Eagleman, D. M., Kagan, A. D., Nelson, S. S., Sagaram, D., & Sarma, A. K. (2007). A standardized test battery for the study of synesthesia. *Journal of Neuroscience Methods*, 159(1), 139–145.
- Galton, F. (1880). Visualised numerals. *Journal of the Anthropological Institute of Great Britain and Ireland*, 85–102.
- Gertner, L., Henik, A., & Kadosh, R. C. (2009). When 9 is not on the right: Implications from number–form synesthesia. *Consciousness and Cognition*, 18(2), 366–374.
- Jarick, M., Dixon, M. J., Maxwell, E. C., Nicholls, M. E., & Smilek, D. (2009). The ups and downs (and lefts and rights) of synaesthetic number forms: Validation from spatial cueing and SNARC-type tasks. *Cortex*, 45(10), 1190–1199.
- Jarick, M., Dixon, M. J., & Smilek, D. (2011). 9 is Always on top: Assessing the automaticity of synaesthetic number-forms. *Brain and Cognition*, 77(1), 96–105.
- Marr, D. (1982). *Vision: A computational investigation into the human representation and processing of visual information* (pp. 2–46). New York, NY: Henry Holt and Co., Inc.
- Marr, D., & Nishihara, H. K. (1978). Representation and recognition of the spatial organization of three-dimensional shapes. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, 200(1140), 269–294.
- Mattingley, J. B., Payne, J. M., & Rich, A. N. (2006). Attentional load attenuates synaesthetic priming effects in grapheme–colour synaesthesia. *Cortex*, 42(2), 213–221.
- Mattingley, J. B., Rich, A. N., Yelland, G., & Bradshaw, J. L. (2001). Unconscious priming eliminates automatic binding of colour and alphanumeric form in synaesthesia. *Nature*, 410(6828), 580–582.
- Nicoletti, R., & Umiltà, C. (1989). Splitting visual space with attention. *Journal of Experimental Psychology: Human Perception and Performance*, 15(1), 164.
- Piazza, M., Pinel, P., & Dehaene, S. (2006). Objective correlates of an unusual subjective experience: A single-case study of number–form synaesthesia. *Cognitive Neuropsychology*, 23(8), 1162–1173.
- Price, M. C., & Mattingley, J. B. (2013). Automaticity in sequence–space synaesthesia: A critical appraisal of the evidence. *Cortex*, 49(5), 1165–1186.
- Pritchard, J., Rothen, N., Coolbear, D., & Ward, J. (2013). Enhanced associative memory for colour (but not shape or location) in synaesthesia. *Cognition*, 127(2), 230–234.
- Rich, A. N., Bradshaw, J. L., & Mattingley, J. B. (2005). A systematic, large-scale study of synaesthesia: Implications for the role of early experience in lexical–colour associations. *Cognition*, 98(1), 53–84.
- Roswarski, T. E., & Proctor, R. W. (1996). Multiple spatial codes and temporal overlap in choice–reaction tasks. *Psychological Research Psychologische Forschung*, 59(3), 196–211.
- Rouw, R., Scholte, H. S., & Colzoli, O. (2011). Brain areas involved in synaesthesia: A review. *Journal of Neuropsychology*, 5(2), 214–242.
- Rubichi, S., Nicoletti, R., Iani, C., & Umiltà, C. (1997). The Simon effect occurs relative to the direction of an attention shift. *Journal of Experimental Psychology: Human Perception and Performance*, 23(5), 1353.
- Rubichi, S., Vu, K. P. L., Nicoletti, R., & Proctor, R. W. (2006). Spatial coding in two dimensions. *Psychonomic Bulletin & Review*, 13(2), 201–216.
- Sagiv, N., Heer, J., & Robertson, L. (2006). Does binding of synesthetic color to the evoking grapheme require attention? *Cortex*, 42(2), 232–242.
- Seron, X., Pesenti, M., Noël, M. P., Deloche, G., & Cornet, J. A. (1992). Images of numbers, or “When 98 is upper left and 6 sky blue”. *Cognition*, 44(1), 159–196.
- Simner, J., Ward, J., Lanz, M., Jansari, A., Noonan, K., Glover, L., & Oakley, D. A. (2005). Non-random associations of graphemes to colours in synaesthetic and non-synaesthetic populations. *Cognitive Neuropsychology*, 22(8), 1069–1085.
- Simon, J. R., & Small, A. M. Jr. (1969). Processing auditory information: Interference from an irrelevant cue. *Journal of Applied Psychology*, 53(5), 433.
- Tang, J., Ward, J., & Butterworth, B. (2008). Number forms in the brain. *Journal of Cognitive Neuroscience*, 20(9), 1547–1556.
- Tipper, S. P., Weaver, B., Jerreat, L. M., & Burak, A. L. (1994). Object-based and environment-based inhibition of return of visual attention. *Journal of Experimental Psychology: Human Perception and Performance*, 20(3), 478.
- Weiss, P. H., & Fink, G. R. (2009). Grapheme–colour synaesthetes show increased grey matter volumes of parietal and fusiform cortex. *Brain*, 132(1), 65–70.