Developmental Science
Developmental Science 12:3 (2009), pp 484–491 DOI: 10.1111/j.1467-7687.2008.00798.x

PAPER

Synaesthesia: learned or lost?

Roi Cohen Kadosh,[1] Avishai Henik[2] and Vincent Walsh[1]

1. Institute of Cognitive Neuroscience & Department of Psychology, University College London, UK
2. Department of Psychology, Ben-Gurion University of the Negev, Israel

Abstract

The question why synaesthesia, an atypical binding within or between modalities, occurs is both enduring and important. Two explanations have been provided: (1) a congenital explanation: we are all born as synaesthetes but most of us subsequently lose the experience due to brain development; (2) a learning explanation: synaesthesia is related to some learning process during childhood. Three recent studies provide conflicting support for these explanations. Two studies supported the idea that synaesthesia is learned by showing that the frequency of everyday language implicitly modulates the synaesthetic experience. Another study argued that synaesthesia reflects basic, innate magnitude representations. In this paper we reassess these points of view, and show that it is possible for both to be valid. These findings are integrated into an interactive specialization account of development in order to explain the neuronal mechanism underlying synaesthesia.

Introduction

Synaesthesia (from the Greek roots syn- 'union' and aesthesis- 'sensation') is a phenomenon involving atypical binding, in which certain stimuli evoke an additional percept between (e.g. vision-touch; Banissy & Ward, 2007, in which the first word relates to the inducer and the second word relates to the additional percept) or within modalities (e.g. grapheme-colour; Cohen Kadosh & Henik, 2007; Dixon, Smilek, Cudahy & Merikle, 2000; Hubbard & Ramachandran, 2005; Rich & Mattingley, 2002; Robertson & Sagiv, 2004). The synaesthetic experience is elicited by particular stimuli that would not evoke such experiences in most people. It is automatic, difficult to suppress and the nature of the synaesthetic experience itself is akin to that of a conscious perceptual event (Ward & Mattingley, 2006). A better understanding of the causal principles of this phenomenon may provide insights into the way in which sensory systems become organized developmentally, the way in which sensory and nonsensory information processing are integrated, and the origins of conscious sensory experience. Moreover, a better understanding of synaesthesia has implications for understanding normal and abnormal cognition (Cohen Kadosh & Henik, 2007; Sagiv & Ward, 2006).

A key question is why synaesthesia occurs. Are we all born as synaesthetes (i.e. congenital synaesthesia) but most of us subsequently lose the experience due to neural pruning (Maurer & Mondloch, 2006; Rouw & Scholte, 2007) or inhibitory interactions (Grossenbacher & Lovelace, 2001)? Alternatively, is synaesthesia due to some learning process during childhood (i.e. learning synaesthesia; Witthoft & Winawer, 2006), with the synaesthetes having a better memory or predisposition to develop synaesthesia. We do not intend to imply that there is a simple dichotomy, which might resemble the simplistic distinction between nature and nurture. A more likely picture is that synaesthesia involves multiple interacting constraints, including genes (Barnett, Finucane, Asher, Bargary, Corvin, Newell & Mitchell, 2008), brain and environment, which shape the neural structures that form the basis of mental representations (Westermann, Mareschal, Johnson, Sirois, Spratling & Thomas, 2007). Thus, the emergence of synaesthesia due to learning does not exclude the possibility that the synaesthete has a predisposition to develop synaesthesia given the right environmental experience. However, until this interaction takes place the synaesthete will not experience synaesthesia. In congenital synaesthesia infants might have synaesthesia due to initial cortical organization (e.g. lack of inhibition, anatomical connection pre-pruning). However, this form of synaesthetic experience may disappear during development, probably due to pruning (Maurer, 1997) or changes in the degree of inhibition or masking (Cohen Kadosh & Walsh, 2006; Knudsen, 2004; Grossenbacher & Lovelace, 2001).

Support for the learning account of synaesthesia

Recently, Beeli, Esslen and Jäncke (2007) examined the perceptual organization of people who experience grapheme

Address for correspondence: Roi Cohen Kadosh, Institute of Cognitive Neuroscience & Department of Psychology, University College London, 17 Queen Square, London WC1N 3AR, UK; e-mail: r.cohenkadosh@ucl.ac.uk

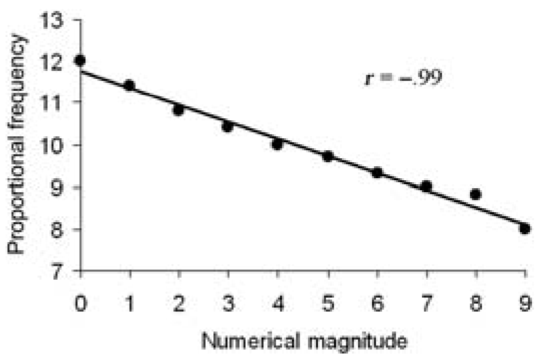

Figure 1 *The correlation between digit frequency (as reported by Beeli* et al.*, 2007), and numerical magnitude.*

in colour, i.e. people with grapheme-colour synaesthesia (e.g. the experience of 7 elicits the colour pink). They analysed the triggered colour perception of grapheme-colour synaesthetes according to saturation and luminance and examined the relationships between these components and the frequency of the letter or digit in everyday language.

For digits they found that an increase in frequency was correlated with an increase in the luminance level of the triggered perception. In contrast, they did not find any relationship between frequency and luminance for letters. Instead, they found a positive relationship between frequency and saturation. However, it seems that this correlation was mainly due to heteroscedasticity of the letter E (cf. Beeli *et al.*, 2007, Figure 1B). In a companion paper, Smilek, Carriere, Dixon and Merikle (2007) replicated Beeli *et al.*'s (2007) results of the connection between digit frequency and luminance level, and they also found a correlation between letter frequency and luminance. However, it seems that also in the latter case this result might be due to heteroscedasticity of the letter E (cf. Smilek *et al.*, 2007, Figure 1C).

Beeli *et al.*'s (2007) and Smilek *et al.*'s (2007) conclusion is straightforward: Because people are not normally aware of digit and letter frequencies in their language, the pairing between grapheme and colour in synaesthesia is due to implicit *learning* of the synaesthetic colour perception. For example, Beeli *et al.* (2007) concluded that 'The results for digit and letter frequency indicate that experience with graphemes may shape synaesthetic color perception' (p. 788). Similarly, Smilek *et al.* (2007) commented that '. . . the available evidence suggests the possibility that the quality of synaesthetic colors may be related to grapheme learning . . . ' (p. 794). Therefore, these studies might seem to provide support for the idea that synaesthetic experience is acquired during childhood.

Support for the congenital factor in synaesthesia

The idea that synaesthesia is learned is challenged by several factors that might provide evidence for the possibility that synaesthesia is congenital. The central problem with the notion of learning synaesthesia relates to the correlation between digit frequency and luminance as reported by both Beeli *et al.* (2007) and Smilek *et al.* (2007). The difficulty with this correlation is that there is a high correspondence between digit frequency and digit magnitude. We plotted both digit frequency and digit magnitude in Figure 1. It can be seen that there is almost a perfect correlation between digit frequency and magnitude ($r = -.99$, $t(10) = -22.22$, $p = .00000002$), thus clearly suggesting a possible confound.

This confounding factor leads to two possibilities that affect the interpretation and understanding of synaesthesia: (1) *There is a true correlation between digit frequency and luminance*. This result would, as Beeli *et al.* (2007) and Smilek *et al.* (2007) rightly argued, demonstrate that grapheme-colour synaesthesia is due to *learning* to associate the synaesthetic colour with digit frequency. (2) *The true correlation is between magnitude and luminance.* Because infants are able to process different magnitudes from infancy (Xu & Spelke, 2000; for a review see Cohen Kadosh, Lammertyn & Izard, 2008), this correlation supports the idea that synaesthesia is innate and rooted in infancy, and thus predates linguistic learning.

Several lines of evidence support the possibility that numerical magnitude rather than digit frequency is the important factor underlying the perceptual organization of luminance and digits. First, previous studies have shown that in non-synaesthete adults numerical magnitude, luminance level, and other magnitudes such as physical size are processed by the same brain region, the intraparietal sulcus (Cohen Kadosh, Henik, Rubinsten, Mohr, Dori, Van de Ven, Zorzi, Hendler, Goebel & Linden, 2005), and can cause mutual interference when in conflict (Cohen Kadosh & Henik, 2006). Second, developmental studies have shown that at the age of 2 years, but not later, non-synaesthete children associate brightness with small magnitudes (in this case object size), and darkness with large magnitudes (Smith & Sera, 1992). Third, Cohen Kadosh, Henik and Walsh (2007) examined the relationship between hue, saturation, luminance, and numerical magnitude (e.g. 1, 2, 3, etc.), rather than frequency. They found that in grapheme-colour synaesthetes digit–luminance association is based on magnitude. In contrast, days of the week, which embody ordinal but not cardinal information, showed no significant correlation with colour. Moreover, the relationship between the digits' numerical values and luminance strengthen when luminance was log transformed and hence followed the Weber-Fechner law. This psychophysical law has been reported previously for different types of magnitudes, including numerical magnitude (Dehaene, 2003), and it seems that at earlier developmental stages numerical magnitude is best represented as a log function and that the representation becomes more linear with time and proficiency (Booth & Siegler, 2006).

However, one may argue that the findings of Cohen Kadosh *et al.* (2007) may suffer from the same confound as Beeli *et al.*'s (2007) and Smilek *et al.*'s (2007) findings. Namely, one cannot be certain whether the luminance–magnitude organization is due to magnitude or frequency. In other words, due to the high correlation between magnitude and frequency, it is difficult to disentangle which component affects the synaesthetic colour, and therefore, whether the principle of organization behind synaesthesia is learned (e.g. linguistic frequency) or congenital (e.g. magnitude).

The current study

To disentangle the underlying mechanism of synaesthesia, one needs to dissociate the magnitude and frequency of the inducers, such as in the case of days of the week. Days of the week, especially in the Hebrew language, have a prominent ordinal nature because they are named in a purely ordinal manner: 'Sunday' is called 'First-day' (in Hebrew 'Yom Rishon'), 'Monday' is called 'Second-day' (in Hebrew 'Yom Sheni'), and so forth, with the exception of 'Shabat-day' for 'Saturday'. This special characteristic of the Hebrew language can be used to examine whether the synaesthetic experience is affected by linguistic frequency when cardinal scaling is replaced by ordinal scaling. Here we used data acquired from eight days-colour synaesthetes, who also experience digit-colour synaesthesia.

A previous paper documented that this group of synaesthetes exhibited a tight connection between numerical magnitude and the luminance component of the synaesthetic colour (Cohen Kadosh *et al.*, 2007). In contrast, they did not show the same relation between luminance and ordinal organization of the week's days. It is conceivable that if frequency matters, then the usage of frequency instead of ordinal information will yield a significant correlation. This result would provide support for frequency as the critical factor, and therefore, that synaesthesia is learned. In contrast, finding that frequency does not play a role might lead to the conclusion, together with other evidence from non-synaesthetes adults (Cohen Kadosh *et al.*, 2005), and children (Smith & Sera, 1992), that the synaesthetic experience is affected by magnitude, and therefore is congenital.

To explore this issue, we first collected norms for the frequency of days of the week in Hebrew. Since the days of the week are composed from two words, there is currently no data for their frequency in Hebrew. In addition, we also acquired the subjective frequency of each day as experienced by the day-colour synaesthetes. This allowed us to examine whether there are any differences between the synaesthetic group and the non-synaesthetic group in their rating of the frequency of the days, and whether the subjective experience modulates the synaesthetic colour more accurately than the sample's average rating.

Method

Norms for days of the week

Forty native Hebrew speakers (mean age = 33.27 years, SD = 11.59) were asked to score the relative frequency of each day in everyday language (writing and verbal) on a 1 to 7 scale. They could give the same score more than once. To avoid effects of order the days of the week were presented in a randomized order. In addition, in order to not bias the scoring by the names of the days (e.g. Yom Rishon (Sunday) – first day), which contain ordinal tags, half of the subjects were instructed to score 7 as the most frequent and 1 as the least frequent, and half were instructed to score 1 as the most frequent, and 7 as the least frequent. In addition, one might argue that the frequency of the days for day-colour synaesthetes might be different from frequency evaluated by the general population, or that the correlation of each colour component of each synaesthete is better correlated with his/her subjective frequency scaling. Therefore, data were acquired from seven participants (out of the eight day-colour synaesthetes in the current study) more than 2 years after the acquisition of each day-colour pair.

The frequency values for each subject, for each day, were entered into an analysis of variance (ANOVA) with days of the week (7 levels) as the within-subjects factor, and instruction (scoring in an ascending/descending order) and group (synaesthetes, non-synaesthetes) as between-subjects factors.

Assessing the correspondence between frequency and the synaesthetic experience

Eight synaesthetes (five females, mean age = 27 years, SD = 3.3) with normal or corrected-to-normal vision took part. Their synaesthetic experience is reported in detail elsewhere (Cohen Kadosh *et al.*, 2007). The synaesthetes were asked to choose the colour that matched their subjective colour induced by each day. Pairs of each day and colour were acquired together with the synaesthete who sat in front of a computer screen using Microsoft Paint. To keep the response unbiased, the values for each colour were acquired while entering the green-red-blue (RGB) values by different experimenters who were not aware of the study's purpose. To find the colour that fit synaesthetic experience, the synaesthetes were prompted to ask the experimenter to change the different RGB values until the colour matched their experience in the best way. These values were later converted to HSL (Hue-Saturation-Luminance) values.

To examine whether there is any correlation between frequency and HSL values, three correlations (between hue and frequency, saturation and frequency, and luminance and frequency) were calculated for each subject. Next, these r-values were Fisher transformed and two-tailed t-tests were performed to test whether the r-values

Table 1 *Frequency scores for each day of the week according to 40 participants, and search engine. SEM = standard error of mean*

Day	Frequency score	SEM	Search engine
Yom Rishon (Sunday)	5.22	.43	1,450,000
Yom Sheni (Monday)	3.62	.52	1,230,000
Yom Shlishi (Tuesday)	4.35	.42	1,270,000
Yom Revi'ee (Wednesday)	3.47	.39	1,280,000
Yom Chamishi (Thursday)	4.72	.49	1,390,000
Yom Shishi (Friday)	5.74	.44	1,470,000
Yom Shabat (Saturday)	6.16	.39	–

of the group deviated significantly from zero. The regression analysis for repeated measure data (Lorch & Myers, 1990) was not used in the current study since the number of observations per variable was too small to allow a reliable regression analysis.

Results

Norms for days of the week

The only significant effect was the main effect for the factor days of the week [$F(6, 216) = 7.56$, $p < .001$]. The results are presented in Table 1. None of the other factors (i.e. instruction, group) or the interactions were significant (all $Fs < .62$, $ps > .63$). When the frequency scores for the days of the week were correlated with their ordinal values, the correlation was not significant ($p = .19$). In contrast, the frequency score did correlate with results obtained in a web search engine (Google inc. <http://www.google.co.il/>). After excluding the Shabat-day (depending on the punctuation this day might have another meaning different from the Shabat-day (e.g. to strike, you returned)), there was a correlation of .93 [$t(4) = 4.93$, $p < .01$].

Assessing the correspondence between frequency and the synaesthetic experience

We calculated for each synaesthete the correlation between each colour component and the average frequency of the days of the week (Figure 2). The correlation between luminance and the average frequency was variable. A *t*-test confirmed this impression; the average *r*-value was almost zero (–.01), and was not significant [$t(7) = -.04$, $p = .97$]. In contrast, the correlations between hue and the average frequency and saturation and the average frequency appear to be more homogeneous. For hue and the average frequency, the *t*-test revealed a significant positive correlation (mean $r = .61$, $t(7) = 3.21$, $p = .01$). In contrast, for saturation and the average frequency the *t*-test revealed a significant negative correlation (mean $r = -.61$, $t(7) = -5.61$, $p < .001$).

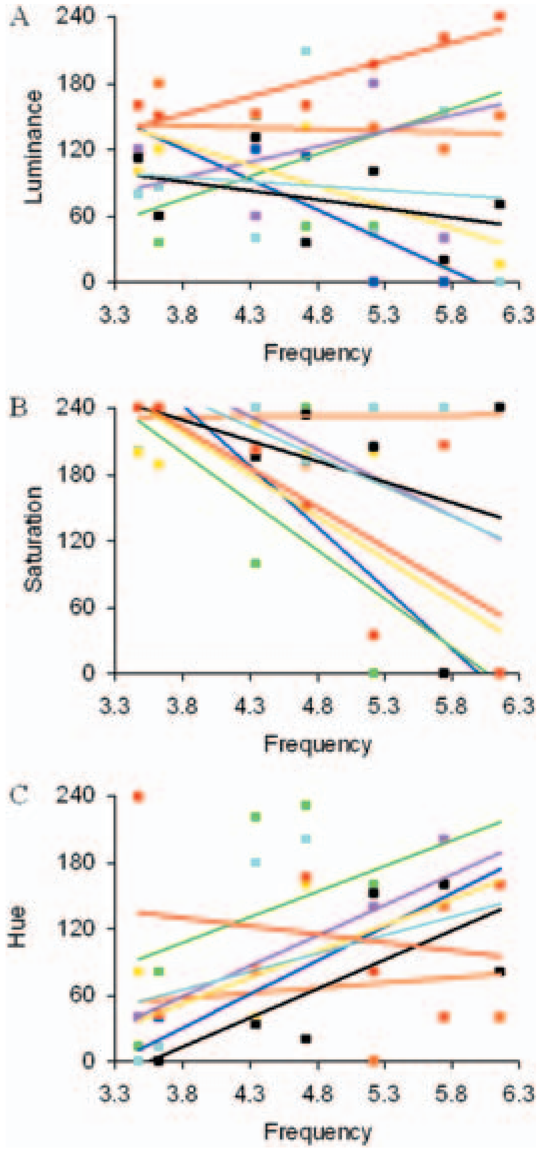

Figure 2 *Correlations between the average frequency of the days of the week (as described in Table 1) and luminance (A), saturation (B), and hue (C).*

Previous studies showed that the frequency of colour correlates with the frequency of the graphemes in language (Simner, Ward, Lanz, Jansari, Noonan, Glover & Oakley, 2005). We evaluated this issue also in the current case, but for the days of the week. We retrieved from the Word-frequency Database in Hebrew (Frost & Plaut, 2007) the frequency for each colour. We computed the correlation between the frequency of colour and the frequency of the days of the week, according to the same procedure mentioned above. We found a significant positive correlation between both frequencies (mean $r = .39$, $t(7) = 2.51$, $p < .05$).

In addition, we also examined whether the results would differ if the average frequency score of each day were replaced by the subjective score for each day given by each synaesthete. Since one synaesthete was not available for the subjective score procedure, only seven of the subjects were used. None of the correlations was significant in this case (all *p*s > .1).

Discussion

The current results shed new light on the question of whether synaesthesia is due to congenital or learning factors. We sketched two possibilities in the introduction: (1) *There is a correlation between digit frequency and luminance*. In line with this, Beeli *et al.* (2007) and Smilek *et al.* (2007) argued that grapheme-colour synaesthesia is due to *learning* to associate colours with digit frequency. (2) *The true correlation is between magnitude and luminance*. This correlation supports the idea that synaesthesia is not necessarily due to learning but is rooted in magnitude representation that exists in infancy.

We did not find that luminance correlated with linguistic frequency, rather, the correlation was close to zero (mean $r = -.01$). Notably, in our previous study the same synaesthetes showed a correlation between luminance and numerical magnitude (Cohen Kadosh, Henik & Walsh, 2007). Together these results indicate that the correlation between luminance and digits was not due to linguistic frequency, but rather due to magnitude, and support the idea that luminance level and magnitude share a common code from an early stage of development, therefore suggesting that magnitude rather than frequency is responsible for the association between luminance and digits. The association between luminance and magnitude seems to exist in synaesthetes and non-synaesthetes alike, probably due to shared representation for different magnitudes such as numbers, size, space, time, and luminance from birth (Walsh, 2003). However, due to cognitive and cortical development (Maurer & Mondloch, 2006) this link might, at least partly, dissipate in non-synaesthetes, therefore leaving its explicit traces in synaesthetes, and its implicit traces in non-synaesthetes (Cohen Kadosh & Henik, 2007, Smilek *et al.*, 2007).

However, we found that linguistic frequency does play a role in other aspects of the synaesthetic experience. Hue and saturation correlated with the frequency of days of the week. In addition, we also found that frequency of the colour (as a combination of HSL) correlates with frequency of the days of the week. While this has been shown previously for letters (Simner *et al.*, 2005), the current finding extends it to the semantic domain. Whether the critical factor for the correlation between frequency of the days of the week is hue or colour frequency is an open question. However, it seems that hue and saturation when taken together can explain a larger portion of the variance than colour name alone.

It is important to note that our data were based on adult synaesthetes and therefore the norms that we acquired were from adults as well. Future studies with children at different ages are necessary to examine whether these norms are different, and in this case whether the connection between the linguistic frequency and hue and saturation is changed as well.

The Interactive Specialization Approach to synaesthesia

In a previous study the same group of synaesthetes was tested. They showed that the luminance level of their synaesthetic experience is modulated by magnitude (Cohen Kadosh *et al.*, 2007). Moreover, in the current study other features of their synaesthetic experience for days of the week seemed to have been affected by linguistic frequency, which is acquired later. These findings are in line with other findings in the field of development (Thomas & Johnson, 2008). For example, it is agreed that there are multiple sensitive periods within one sensory modality (vision in the current study). Our results suggest that different sensitive periods reflect the development of different mechanisms, such as magnitude and linguistic frequency, rather than common mechanisms and principles in shaping synaesthesia.

One view of synaesthesia is that it is due to additional neuronal connections, probably due to lack of pruning (Maurer & Mondloch, 2006); another view suggests that synaesthesia is due to disinhibition (Grossenbacher & Lovelace, 2001) or unmasking (Cohen Kadosh & Walsh, 2006) between or within brain areas. We suggest a different concept for the emergence of synaesthesia, which encompasses both the connectivity and disinhibition accounts. This new account is rooted in the Interactive Specialization Approach to cognitive development (Johnson, 2001).

According to Interactive Specialization Approach, cortical functional specialization for cognitive functions emerges during human postnatal development as a result of initial biases and competitive interactions between different cortical and sub-cortical areas (Cohen Kadosh & Johnson, 2007; Johnson, 2001). We suggest that while there is cortical functional specialization during development in the case of non-synaesthetes, for synaesthetes certain cortical functional specialization is lacking. This can occur, for example, due to lack of synapses being eliminated during the sensitive period, resulting in additional inputs that do not contribute to the representation (Knudsen, 2004). The finding of increased white matter in synaesthesia, irrespective of whether this is the cause or a consequence of synaesthesia, seems to be compatible with the current explanation (Rouw & Scholte, 2007). We suggest that this failure in specialization leads to atypical binding of information between and especially within modalities. For example, in the current case, while infants show shared and domain-general mechanism for different magnitude representations (Brannon, Lutz & Cordes, 2006; Cohen Kadosh, Lammertyn & Izard, 2008; Feigenson, 2007; van Marle & Wynn, 2006), it seems that there is a specialization as a function of time (e.g. Droit-Volet, Clement & Fayol, 2008; Holloway & Ansari, 2008; Smith & Sera, 1992). In other words, the domain-general mechanism gradually becomes domain-specific, probably as a result of processing different kinds of input (Karmiloff-Smith, 1998) and different interactions with other brain areas. The same scenario might apply to linguistic development. A recent study showed that in non-synaesthete adults, language processing areas in the brain are involved in a visual perceptual task (Hai Tan, Chan, Kay, Khong, Yip & Luke, 2008). In Hai Tan *et al.*'s (2008) study, the ease with which a colour was named served as a manipulation of the linguistic processing. However, a possible confounding variable was the linguistic frequency of these colours. It might be that in synaesthesia the cross-talk between linguistic processing and colour perception is greater than in the normal population, again probably due to decreased specialization, in this case of language and colour perception.

Therefore, in the case of synaesthesia the failure in specialization, which is a general innate anomaly (probably of genetic origin; Barnett *et al.*, 2008), leads to the failure of the specialization for numerical magnitude starting from infancy. Later, a similar failure in specialization can trigger the development of other atypical cross-modal interactions, which may emerge later in life as a function of learning (e.g. day-colour in the current case), cortical development and organization.

One might predict that if indeed there is a lack of specialization then some synaesthetes should experience more than one type of synaesthesia. This prediction is supported by several studies (Rich, Bradshaw & Mattingley, 2005; Sagiv, Simner, Collins, Butterworth & Ward, 2006), and it seems that usually the other synaesthetic experience is of similar type. For example, synaesthetes who explicitly represent numbers in space are more likely to represent also other types of information in space such as days of the week, months, and years (Sagiv *et al.*, 2006). Synaesthetes are also more likely to have other atypical experiences such as Mitempfindung (German for 'sensing together'), which results in a tactile sensation to a location far away from the stimulation site (Burrack, Knoch & Brugger, 2006). Moreover, it seems that synaesthetes do not have only atypical experience in the explicit sense, but they might be subject to other types of synaesthesia while not being aware of it (Tyler, 2005). This occurrence of more than one type of synaesthesia in a single synaesthete also fits well with other atypical developmental syndromes (Karmiloff-Smith, 1998).

Interestingly, most brain imaging in synaesthesia research has focused on the atypical brain activation due to the additional experience (e.g. atypical activation of areas that are involved in colour processing) while neglecting activation in inducer-related areas. However, synaesthesia might also involve atypical activation in inducer-related areas (Cohen Kadosh, Cohen Kadosh & Henik, 2007), and future studies should examine atypical activation in inducer-related areas as well.

Other types of synaesthesia (e.g. vision-touch, hearing-colour) can be explained by the current framework. For example, people with vision-touch synaesthesia might experience vision due to touch as their visual cortex does not respond in a specialized fashion to vision as in non-synaesthetes (e.g. it does not mask neuronal populations that might be sensitive to touch). Indeed, it seems that a careful choice of task shows that the occipital cortex is sensitive to touch even in non-synaesthetes (Amedi, Jacobson, Hendler, Malach & Zohary, 2002), even though this tactile input is masked in their everyday life. Moreover, findings from congenitally blind participants show that their visual cortex is sufficient and necessary for tactile processing (Cohen, Weeks, Sadato, Celnik, Ishii & Hallett, 1999; Sadato, Pascual-Leone, Grafman, Ibanez, Deiber, Dold & Hallett, 1996). The interactive specialization account again can explain this latter atypical cross-modal interaction (Westermann *et al.*, 2007), and the similarity between atypical cross-modal interactions due to sensory deprivation and synaesthesia has been noted elsewhere (Cohen Kadosh & Walsh, 2006). Together, the interactive specialization account offers a parsimonious explanation of the principal mechanism behind these phenomena.

The current results show that adult synaesthetes share some characteristics with infants and younger children (the association between darkness and size). Therefore, we hope that by integrating synaesthesia into a developmental theory, we will facilitate research both in the developmental field and in the way that people approach synaesthesia in adult participants.

Acknowledgements

We would like to thank Kathrin Cohen Kadosh for her helpful comments. RCK is supported by a Marie Curie Intra European Fellowship.

References

Amedi, A., Jacobson, G., Hendler, T., Malach, R., & Zohary, E. (2002). Convergence of visual and tactile shape processing in the human lateral occipital complex. *Cerebral Cortex*, **11**, 1202–1212.

Banissy, M.J., & Ward, J. (2007). Mirror-touch synesthesia is linked with empathy. *Nature Neuroscience*, **10**, 815–816.

Barnett, K.J., Finucane, C., Asher, J.E., Bargary, G., Corvin, A.P., Newell, F.N., & Mitchell, K.J. (2008). Familial patterns and the origins of individual differences in synaesthesia. *Cognition*, **106**, 871–893.

Beeli, G., Esslen, M., & Jancke, L. (2007). Frequency correlates in grapheme-color synaesthesia. *Psychological Science*, **18**, 788–792.

Booth, J.L., & Siegler, R.S. (2006). Developmental and individual differences in pure numerical estimation. *Developmental Psychology*, **41**, 189–201.

Brannon, E.M., Lutz, D., & Cordes, S. (2006). The development of area discrimination and its implications for number representation in infancy. *Developmental Science*, **9**, F59–F64.

Burrack, A., Knoch, D., & Brugger, P. (2006). Mitempfindung in synaesthetes: co-incidence or meaningful association? *Cortex*, **42**, 151–154.

Cohen, L.G., Weeks, R.A., Sadato, N., Celnik, P., Ishii, K., & Hallett, M. (1999). Period of susceptibility for cross-modal plasticity in the blind. *Annals of Neurology*, **45**, 451–460.

Cohen Kadosh, R., Cohen Kadosh, K., & Henik, A. (2007). The neuronal correlate of bi-directional synaesthesia: a combined ERP and fMRI study. *Journal of Cognitive Neuroscience*, **19**, 2050–2059.

Cohen Kadosh, R., & Henik, A. (2006). A common representation for semantic and physical properties: a cognitive-anatomical approach. *Experimental Psychology*, **53**, 87–94.

Cohen Kadosh, R., & Henik, A. (2007). Can synaesthesia research inform cognitive science? *Trends in Cognitive Sciences*, **11**, 177–184.

Cohen Kadosh, R., Henik, A., Rubinsten, O., Mohr, H., Dori, H., Van de Ven, V., Zorzi, M., Hendler, T., Goebel, R., & Linden, D.E.J. (2005). Are numbers special? The comparison systems of the human brain investigated by fMRI. *Neuropsychologia*, **43**, 1238–1248.

Cohen Kadosh, R., Henik, A., & Walsh, V. (2007). Small is bright and big is dark in synaesthesia. *Current Biology*, **17**, R834–R835.

Cohen Kadosh, K., & Johnson, M.H. (2007). Developing a cortex specialized for face perception. *Trends in Cognitive Sciences*, **11**, 367–369.

Cohen Kadosh, R., Lammertyn, J., & Izard, V. (2008). Are numbers special? An overview of chronometric, neuroimaging, developmental and comparative studies of magnitude representation. *Progress in Neurobiology*, **84**, 132–147.

Cohen Kadosh, R., & Walsh, V. (2006). Cognitive neuroscience: rewired or crosswired brains? *Current Biology*, **16**, R962–R963.

Dehaene, S. (2003). The neural basis of the Weber-Fechner law: a logarithmic mental number line. *Trends in Cognitive Sciences*, **7**, 145–147.

Dixon, M.J., Smilek, D., Cudahy, C., & Merikle, P.M. (2000). Five plus two equals yellow. *Nature*, **406**, 365.

Droit-Volet, S., Clement, A., & Fayol, M. (2008). Time, number and length: similarities and differences in discrimination in adults and children. *Quarterly Journal of Experimental Psychology*, **61**, 1827–1846.

Feigenson, L. (2007). The equality of quantity. *Trends in Cognitive Sciences*, **11**, 185–187.

Frost, R., & Plaut, D. (2007). The word-frequency database for printed Hebrew. Retrieved 22 October 2007, from http://word-freq.mscc.huji.ac.il/index.html.

Grossenbacher, P.G., & Lovelace, C.T. (2001). Mechanisms of synesthesia: cognitive and physiological constraints. *Trends in Cognitive Sciences*, **5**, 36–41.

Hai Tan, L., Chan, A.H.D., Kay, P., Khong, P.-L., Yip, L.K.C., & Luke, K.-K. (2008). Language affects patterns of brain activation associated with perceptual decision. *Proceedings of the National Academy of Sciences, USA*, **105**, 4004–4009.

Holloway, I., & Ansari, D. (2008). Domain-specific and domain-general changes in children's development of number comparison. *Developmental Science*, **11**, 644–649.

Hubbard, E.M., & Ramachandran, V.S. (2005). Neurocognitive mechanisms of synesthesia. *Neuron*, **48**, 509–520.

Johnson, M.H. (2001). Functional brain development in humans. *Nature Reviews Neuroscience*, **2**, 475–483.

Karmiloff-Smith, A. (1998). Development itself is the key to understanding developmental disorders. *Trends in Cognitive Sciences*, **2**, 389–398.

Knudsen, E.I. (2004). Sensitive periods in the development of the brain and behavior. *Journal of Cognitive Neuroscience*, **16**, 1412–1425.

Lorch, R.F., & Myers, J.L. (1990). Regression analyses of repeated measures data in cognitive research. *Journal of Experimental Psychology: Learning, Memory and Cognition*, **16**, 149–157.

Maurer, D. (1997). Neonatal synaesthesia: implications for the processing of speech and faces. In S. Baron-Cohen & J.E. Harrison (Eds.), *Synaesthesia: Classic and contemporary readings* (pp. 224–242). Malden, MA: Blackwell Publishers.

Maurer, D., & Mondloch, C.J. (2006). The infant as synaesthete? In Y. Munakata & M.H. Johnson (Eds.), *Attention and performance XXI: Processes of change in brain and cognitive development* (pp. 449–471). Oxford: Oxford University Press.

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**, 53–84.

Rich, A.N., & Mattingley, J.B. (2002). Anomalous perception in synaesthesia: a cognitive neuroscience perspective. *Nature Reviews Neuroscience*, **3**, 43–52.

Robertson, L.C., & Sagiv, N. (Eds.) (2004). *Synesthesia: Perspectives from cognitive neuroscience*. New York: Oxford University Press.

Rouw, R., & Scholte, H.S. (2007). Increased structural connectivity in grapheme-color synesthesia. *Nature Neuroscience*, **10**, 792–797.

Sadato, N., Pascual-Leone, A., Grafman, J., Ibanez, V., Deiber, M.-P., Dold, G., & Hallett, M. (1996). Activation of the primary visual cortex by Braille reading in blind subjects. *Nature*, **380**, 526–528.

Sagiv, N., Simner, J., Collins, J., Butterworth, B., & Ward, J. (2006). What is the relationship between synaesthesia and visuo-spatial number forms? *Cognition*, **101**, 114–128.

Sagiv, N., & Ward, J. (2006). Crossmodal interactions: lessons from synesthesia. In S. Martinez-Conde, L.M. Martinez, J.M. Alonso, P.U. Tse, & S.L. Macknik (Eds.), *Visual perception (Progress in brain research series)* (pp. 259–271). London: Elsevier Science.

Simner, J., Ward, J., Lanz, M., Jansari, A., Noonan, K., Glover, L., & Oakley, D. (2005). Non-random associations of graphemes to colour in synaesthetic and non-synaesthetic populations. *Cognitive Neuropsychology*, **22**, 1069–1085.

Smilek, D., Carriere, J.S.A., Dixon, M.J., & Merikle, P.M. (2007). Grapheme frequency and color luminance in grapheme-color synaesthesia. *Psychological Science*, **18**, 793–795.

Smith, L.B., & Sera, M.D. (1992). A developmental analysis of the polar structure of dimensions. *Cognitive Psychology*, **24**, 99–142.

Thomas, M.S.C., & Johnson, M.H. (2008). New advances in understanding sensitive periods in brain development. *Current Directions in Psychological Science*, **17**, 1–5.

Tyler, C. (2005). Varieties of synesthetic experience. In L.C. Robertson & N. Sagiv (Eds.), *Synesthesia: Perspectives from*

cognitive neuroscience (pp. 34–44). New York: Oxford University Press.
vanMarle, K., & Wynn, K. (2006). Six-month-old infants use analog magnitudes to represent duration. *Developmental Science*, **9**, F41–F49.
Walsh, V. (2003). A theory of magnitude: common cortical metrics of time, space and quantity. *Trends in Cognitive Sciences*, **7**, 483–488.
Ward, J., & Mattingley, J.B. (2006). Synaesthesia: an overview of contemporary findings and controversies. *Cortex*, **42**, 129–136.
Westermann, G., Mareschal, D., Johnson, M.H., Sirois, S., Spratling, M.W., & Thomas, M.S.C. (2007). Neuroconstructivism. *Developmental Science*, **10**, 75–83.
Witthoft, N., & Winawer, J. (2006). Synesthetic colors determined by having colored refrigerator magnets in childhood. *Cortex*, **42**, 175–183.
Xu, F., & Spelke, E.S. (2000). Large number discrimination in 6-month-old infants. *Cognition*, **74**, B1–B11.

Received: 10 December 2007
Accepted: 27 April 2008