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Grapheme-color synesthesia subtypes: Stable individual differences reflected in posterior alpha-band oscillations

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Grapheme-color synesthesia is a condition in which seeing letters and numbers produces sensations of colors (e.g., the letter R may elicit a sky-blue percept). Recent evidence implicates posterior parietal areas, in addition to lower-level sensory processing regions, in the neurobiological mechanisms involved in synesthesia. Furthermore, these mechanisms seem to differ for “projectors” (synesthetes who report seeing the color “out there in the real world”) versus “associators” (synesthetes who report the color to be only an internal experience). Relatively little is known about possible electrophysiological characteristics of grapheme-color synesthesia. Here we used EEG to investigate functional oscillatory differences among associators, projectors, and non-synesthetes. Projectors had stronger stimulus-related alpha-band (~10 Hz) power over posterior parietal electrodes, compared to both associators and non-synesthetes. Posterior alpha activity was not statistically significantly different between associators from non-synesthetes. We also performed a test-retest assessment of the projector-associator score and found strong retest reliability, as evidenced by a correlation coefficient of .85. These findings demonstrate that the projector-associator distinction is highly reliable over time and is related to neural oscillations in the alpha band.

Keywords: Synaesthesia; Grapheme-color; Brain Networks; Alpha-band; Individual differences.

In grapheme-color synesthesia, neurologically healthy individuals experience colors when seeing or hearing letters or numbers (e.g., the letter X may be associated with the color purple). It is a “real” phenomenon in that it is not driven by psychoactive substances or psychosis. Indeed, the experiences are consistent over time, and the perceptual nature of the experiences affect performance on a variety of low-level perceptual as well as higher-level cognitive tasks (Baron-Cohen, Wyke, & Binnie, 1987; Hubbard & Ramachandran, 2005; Palmeri, Blake, Marois, Flanery, & Whetsell, 2002; Smilek, Dixon, Cudah, & Merikle, 2002, 2001). Despite a sharp increase in

research on synesthesia in recent years, much is still unknown about the condition. There is a genetic predisposition to developing synesthesia (Asher et al., 2009; Tomson et al., 2011), as well as an influence of learning on the specific synesthetic associations (Barnett et al., 2008; Simner et al., 2005). Both structural (Hänggi, Beeli, Oechslin, & Jäncke, 2008; Jäncke, Beeli, Eulig, & Hänggi, 2009; Rouw & Scholte, 2007) and functional (Hubbard & Ramachandran, 2005; Nunn et al., 2002; Rich et al., 2006) brain differences are observed between the synesthetic and the non-synesthetic brain. Most of the research focus has been on finding specific

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(typically, sensory processing-related) brain functions that set synesthetes apart from non-synesthetes (Hubbard & Ramachandran, 2005; Hupe, Bordier, & Dojat, 2012; Rich et al., 2006). However, an overview of many neuroimaging results suggests that differences in a network of brain areas, rather than in a single brain area (or single brain function) underly synesthesia (Hubbard, Brang, & Ramachandran, 2011; Rouw, Scholte, & Colizoli, 2011).

Of the non-sensory brain areas implicated in synesthesia, the parietal cortex seems to play a major role. The posterior parietal cortex has larger gray matter in synesthetes compared with non-synesthetes (Rouw & Scholte, 2010), exhibits activations during synesthetic experiences (Paulesu et al., 1995; Steven, Hansen, & Blakemore, 2006), and leads to disruptions in synesthetic experiences when transiently interrupted by TMS (Esterman, Verstynen, Ivry, & Robertson, 2006; Muggleton, Tsakanikos, Walsh, & Ward, 2007). Based on these findings, it has been proposed that the parietal cortex may be involved in “hyperbinding” multisensory processes in synesthetes, in addition to other neighboring regions, including the superior temporal sulcus (Esterman et al., 2006; Grossenbacher & Lovelace, 2001; Robertson, 2003).

The EEG literature on synesthesia is relatively small (see Hubbard, 2007), but has highlighted two main effects in the time course of synesthesia-related activation (Jäncke, 2013): Modulation of early components in response to a synesthesia-evoking stimulus, as well as later, higher-order, cognitive processes in response to priming (Barnett et al., 2008; Beeli, Esslen, & Jäncke, 2008; Brang et al., 2011a; Cohen Kadosh, Cohen Kadosh, & Henik, 2007; Gebuis, Nijboer, & Van der Smagt, 2009; Goller, Otten, & Ward, 2009; Niccolai, Wascher, & Stoerig, 2012; Schiltz et al., 1999; Sinke et al., 2014; Teuscher, Brang, Ramachandran, & Coulson, 2010). While the parietal involvement is supported in some studies (Jäncke, Rogenmoser, Meyer, & Elmer, 2012), inconsistencies have also been reported (Schiltz et al., 1999). Next to the differences in methodology and behavioral tasks, inconsistencies across studies may also be related to the relatively small number of subjects tested in some of these experiments. Furthermore, given the proposed differences in connectivity in synesthesia (Hubbard et al., 2011; Ramachandran & Hubbard, 2001; Rouw et al., 2011), local network functioning such as oscillations may provide more sensitive measurements than localized ERPs in terms of neurological differences between synesthetes and non-synesthetes.

For example, Jäncke and Langer (2011) used resting-state EEG and graph theory analyses to show that the parietal cortex is a stronger hub region (stronger functionally interconnected) in synesthetes as compared with non-synesthetes. Van Leeuwen and colleagues (2013) used MEG to show that during an attention task, attention-modulated lateralized alpha-band (~10 Hz) oscillations over parietal cortex differentiated synesthetes from controls, and the strength of the lateralization (alpha power over left vs. right hemispheres) correlated with a bias in task performance attributable to synesthesia. On the other hand, Volberg, Karmann, Birkner, and Greenlee (2013) reported a complex set of local and long-range EEG connectivity results, including synesthesia-related differences in high-frequency activity recorded over the parietal/occipital cortices. Functional connectivity patterns have been investigated in a few fMRI studies (Dovern et al., 2012; Neufeld et al., 2012; Tomson, Narayan, Allen, & Eagleman, 2013). In addition to consistent findings, there are also some inconsistencies across these studies. For example, some studies suggest greater differences between synesthetes and controls in the prefrontal areas (Schiltz et al., 1999).

Functional connectivity patterns have also been obtained in fMRI studies. For example, Dovern et al. (2012) used ICA on resting state fMRI and found both a global and a specific, visual and frontoparietal, increase in intrinsic network connectivity in synesthetes. A few studies analyzed functional connectivity in the fMRI signal during synesthetic (inducing vs. non-inducing) experiments. Neufeld et al. (2012), for example, found no differences between tone-color synesthetes and non-synesthetes in the connectivity of auditory and visual brain areas, but stronger connectivity in left inferior parietal cortex with visual and auditory areas in synesthetes. Similarly, Sinke et al. (2012) found increased connectivity between left inferior parietal cortex and visual areas in grapheme-color synesthetes. In contrast, a study by Tomson and colleagues (2013) did not find evidence for a role for parietal regions in synesthesia, but rather, for visual regions. Thus, in addition to consistent findings (an emphasis on visual and parietal areas in the connectivity studies), there are also some inconsistencies across these studies (that is, the exact same regions are not always obtained). Inconsistencies across studies may, among other things, be related to differences amongst the synesthetes themselves (for example, the aforementioned Tomson et al. study investigated sequence-color synesthesia). That is, heterogeneity

in the subject sample may lead to null or inconsistent findings.

Grapheme-color synesthesia can be decomposed into two subtypes based on self-reported phenomenological experiences (Dixon, Smilek, & Merikle, 2004; Smilek et al., 2002). “Associators” experience the color internally (in their “mind’s eye”) only, whereas “projectors” also report seeing an external visual experience (as if it were present in the outside world). The distinction between these subtypes is more than simply experiential, as evidenced, for example, by results from the “synesthetic Stroop” task. In this variant of the Stroop task, a grapheme is presented in a color that is congruent or incongruent to the synesthetic color. Projectors are faster at naming synesthetic than veridical colors while associators show the reverse pattern (Dixon et al., 2004; Ward, Li, Salih, & Sagiv, 2007). Furthermore, there are regularities of which shapes evoke which colors, and these regularities were found to be stronger for projectors than for associators (Brang, Rouw, Ramachandran, & Coulson, 2011b). Additionally, in a visual detection task, synesthetic colors improved the detection of visual letters or shapes, as measured through decreased reaction times. There are individual differences in these tasks (Hubbard & Ramachandran, 2005), with projectors showing stronger effects (Ward et al., 2007). Still, the behavioral and neurological characteristics of the projector-associator distinction remain debated (Rothen, Meier, & Ward, 2012; Ward, Jonas, Dienes, & Seth, 2010), perhaps in part because behavioral differences are not always obtained (Edquist, Rich, Brinkman, & Mattingley, 2006; Gebuis et al., 2009). Some studies examining the projector-associator distinction included only a small number of subjects, which may have contributed to the uncertainty about the nature of this possible subtype distinction.

The differences in cognitive task performance have led researchers to postulate differences in neuroanatomical architecture between associator and projector grapheme-color synesthetes. Indeed, increased connectivity obtained in synesthetes near the fusiform gyrus was stronger in projectors than in associators (Rouw & Scholte, 2007). Furthermore, projectors have increased gray matter in modality-specific cortical areas such as visual cortex and Heschl’s gyrus, as well as in prefrontal areas and superior precuneus in the parietal cortex (Rouw & Scholte, 2010). In contrast, associators have increased gray matter volume and increased activation in the temporal cortex surrounding and

including the hippocampus, and in the angular gyrus (Rouw & Scholte, 2010).

It is possible that the two subtypes of grapheme-color synesthesia are related to different neurocognitive strategies for processing graphemes and their associated colors, such that the evoked color relates mostly to direct activation of early and relatively low-level sensory processes in projector synesthetes, while the evoked color relates more strongly to feedback of later and relatively high-level multi-sensory or conceptual processes in associators (see also the “higher” versus “lower” distinction by Ramachandran & Hubbard, 2001; Hubbard & Ramachandran, 2005). Consistent with this idea, effective connectivity analyses, measured with dynamic causal modeling of fMRI data, provided evidence that V4 activation was driven by the fusiform gyrus (“bottom-up pathway”) in projectors but by the parietal lobe (“top-down pathway”) in associators (van Leeuwen, Den Ouden, & Hagoort, 2011).

The electrophysiological mechanisms of these differences remain largely unexplored, but it is possible that alpha is a signature of the mechanism that distinguishes associators from projectors (van Leeuwen et al., 2013). For example, alpha oscillations in sensory cortical areas have been implicated in gating percepts into and out of attention (Jensen, Gips, Bergmann, & Bonnefond, 2014; Jensen & Mazaheri, 2010). A previous study showing alpha activity differences in synesthesia (van Leeuwen et al., 2013) focused on task-related alpha differences in lateralized attention leaving open the question whether there are synesthesia-related differences in alpha that are task-independent, i.e., stable trait-like individual differences. An advantage of this approach is that obtained effects cannot be attributable to possible differences in task performance strategies.

The purpose of our study here is twofold. First and foremost, we sought to investigate whether cortical oscillation characteristics would differentiate projectors, associators, and controls. To this end, synesthete and matched non-synesthete controls performed a simple letter font discrimination (italics vs. roman) task in order to evoke EEG responses. We designed the task such that it would elicit synesthetic experiences while leaving task performance unaffected by those experiences. Second, we used this opportunity to examine the test-retest reliability of the questionnaire that measures whether a grapheme-color synesthete is classified as a projector or an associator. Briefly, we found (1) that projectors, relative to associators and non-synesthetes, showed

enhanced parietal cortex alpha-band oscillations, and (2) that the projector-associator questionnaire had excellent test-retest reliability, as reflected in a correlation coefficient of .85 despite the test-retest interval of months to years. Overall, our findings clearly demonstrate that there are two distinct “flavors” of grapheme-color synesthesia that are consistent over time and that reflect biological differences in cortical oscillatory dynamics.

METHODS

Subjects

We tested 43 female participants with normal or corrected-to-normal vision and no history of neurological or psychiatric disease. Subjects were recruited from an existing subject pool, from which MRI results (DTI and VBM) were previously reported for eight and 13 subjects, respectively (Rouw & Scholte, 2007, 2010). Synesthetes were included based on retest consistency of their individual synesthetic grapheme-color associations on an unexpected retest at least three weeks after initial testing. In the EEG experiment, each synesthete was presented with a personalized set of stimuli, based on the strength of the synesthetic color experience. From the list of graphemes, each synesthete indicated eight graphemes that elicit the strongest color experience, and eight graphemes that elicit a weak color experience. Synesthetes also chose eight graphemes that evoked no synesthetic (color) experience; these graphemes could also be symbols (e.g., #). Each synesthete was matched with a control subject based on age, sex, handedness, and level of education. The total sample comprised 10 associator synesthetes, 12 projector synesthetes, and 21 control subjects. Controls were matched for age (Mean = 28, range = 18–54, $SD = 8$), level of education and handedness (95% were right-handed). Projectors and associators were categorized based on their score on the projector-associator questionnaire (PA; Rouw & Scholte, 2007). The questionnaire measures the type of synesthetic experience, in particular differentiating experiences that are “inside my head only” from externally perceived synesthetic color. The total score ranges from -4 to 4 and reflects associator (< 0) or projector type (> 0) of synesthetic experience. In the present sample, the PA score ranged from -2.83 to 4.0 and the mean equaled 0.57 ($SD = 2.15$) for grapheme-color synesthetes.

For the questionnaire in English, Dutch, German, and Polish, see <http://www.uva.nl/overde-uva/organisatie/medewerkers/content/r/o/r.rouw/r.rouw.html>.

Task

While we recorded EEG, subjects performed a typography judgment, in which they reported whether presented single graphemes were in italicized or roman (i.e., non-italicized) font (Rouw & Scholte, 2007) by pressing a key with, respectively, index finger or middle finger of their dominant hand. The task was designed to (1) focus attention to the stimuli, and (2) not interfere or interact with the synesthetic experiences. Stimuli appeared for 500 ms (visual angle equaled 2°) in light-gray font on a gray background, to minimize contrast effects. After each stimulus, an isoluminant gray image appeared for 750–1250 ms, which served as an inter-trial interval. Electrophysiological signals were recorded while subjects performed the letter font-discrimination task. Targets were eight graphemes consisting of letters, digits, or symbols eliciting either a strong, a present-but-weak, or no synesthetic experience, and were presented in random order in blocks of 240 stimuli. As the symbols used to elicit no synesthetic experience differed greatly from the letters and digits in frequency and familiarity (e.g., an ampersand), these trials were not included in the present analysis. Furthermore, initial inspection of the results revealed no differences between letters associated with a strong and weak experience, and these letters were thus combined in the present analyses. Each stimulus was presented five times in roman and five times in italics per block. After a practice block of 100 stimuli, subjects completed five experimental blocks. Each block lasted around 6.5 minutes, resulting in a total of 1200 trials. Because letter-color associations differ between grapheme-color synesthetes, stimuli were selected on an individual basis prior to the task. Experiments were approved by the Ethics Committee of the University of Amsterdam, and all participants read and signed an informed consent form before starting the experiment.

EEG data collection

EEG data were acquired with Biosemi 64-channel (Active Two EEG system) at 256 Hz from 64 channels placed according to the international 10–20

system and from both earlobes (used as reference). Offline, EEG data were high-pass filtered at 0.5 Hz and then epoched from -1.5 to +2 seconds surrounding each trial. All trials were visually inspected and those containing EMG or other artifacts not related to blinks were manually removed. Independent components analysis was computed using eeglab software (Delorme & Makeig, 2004), and components containing blink/oculomotor artifacts or other artifacts that could be clearly distinguished from brain-driven EEG signals were subtracted from the data.

EEG analyses

Time-frequency decomposition

All analyses were performed in MATLAB 2012b. Single-trial data were first decomposed into their time-frequency representation by multiplying the power spectrum of the EEG (obtained from the fast-Fourier-transform) by the power spectrum of complex Morlet wavelets ($e^{i2\pi ft} e^{-t^2/(2\sigma^2)}$), where t is time, f is frequency, which increased from 1 to 15 Hz in 30 logarithmically spaced steps, and σ defines the width of each frequency band, set according to $4/(2\pi f)$, and then taking the inverse fast-Fourier-transform. From the resulting complex signal, an estimate of frequency-band-specific power at each time point was defined as the squared magnitude of the result of the convolution Z ($\text{real}[z(t)]^2 + \text{imag}[z(t)]^2$) (Cohen, 2014). Power was normalized using a decibel (dB) transform ($\text{dB power} = 10 \cdot \log_{10}[\text{power}/\text{baseline}]$), where the baseline activity was taken as the average power at each frequency band, averaged across conditions, from -300 to -100 ms pre-stimulus. Conversion to a dB scale ensures that data across all frequencies, time points, electrodes, conditions, and subjects are in the same scale and thus comparable. Error trials were excluded from EEG analyses.

EEG statistics

Statistics were performed using two-sample t -tests, comparing each time-frequency-electrode point between pairs of groups (associators vs. controls, projectors vs. controls, associators vs. projectors). Due to the large number of comparisons with strong autocorrelations amongst neighboring time-frequency-electrode points, we used permutation testing to evaluate the statistical significance. At

each of 1000 iterations in the permutation test, group labels were randomly assigned to each subject. A cluster-based correction was applied to address multiple comparisons issues (Maris & Oostenveld, 2007). To define time-frequency-electrode windows for plotting the results, we averaged the data over all subjects and conditions, and identified the global maximum and minimum power values. From there, regions of interest were selected, as shown in Figure 2.

PA test-retest

The synesthetes received a retest in order to examine consistency of their PA scores. For two out of the 22 synesthetes included in the current analyses there was only one PA measurement; they were classified as projector or associator based on their single PA score. The average interval between test and retest was 26 months (range: 16–38 months).

Seven synesthetes in this study participated in a previous study (Rouw & Scholte, 2007). We used the same PA score as the “original score” reported in that study for these seven subjects, where one question of the “projector” type was removed from analyses due to low correlation with the total projector score. All other subjects completed a PA questionnaire with that question replaced by an improved question. The old question stated that the color appeared only somewhere in the outside world; the new question removed the reference word “only.” In hindsight, it is possible that projectors object to this word “only” as they also “know,” or see inside their head, the synesthetic color.

RESULTS

Projector-associator score

The Kolmogorov-Smirnov test indicated that the distributions of both the original PA scores ($D = .15$, $df = 20$, $p = .20$) and the PA retest ($D = .14$, $df = 20$, $p = .20$) did not deviate significantly from a normal distribution. The mean and standard deviation of original PA scores were ($M = 0.6$, $SD = 2.24$) and from retest scores ($M = -0.03$, $SD = 2.18$). The test and retest scores were strongly correlated: $r(18) = .85$, $p < .001$). Examining the similarity of subjects based on their order rather than absolute score (non-parametric test) also showed strong correlation between the two scores $r_s(18) = .88$, $p < .001$) (Figure 1).

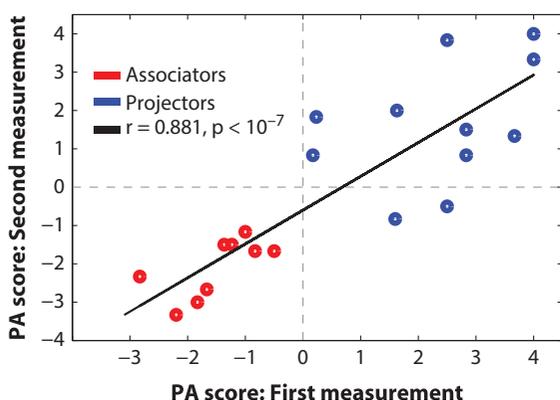


Figure 1. Test-retest reliability of the PA questionnaire is illustrated as the high correlation between the scores on two repeated measurements, separated by 16–38 months. Each dot represents a subject, and the subjects are categorized as associators or projectors based on their scores in the first measurement period. (Note that only one PA score was available from two subjects).

As an exploratory follow-up analysis, we computed the test-retest correlation separately for each group. In the associators ($N = 9$), the correlation was $.68$, $p = .045$; in the projectors ($N = 11$), the correlation was $.41$, $p = .211$. Although these two correlation coefficients were not significantly different from each other ($Z = .729$, $p = .233$) (Cohen & Cohen, 1983), and the number of subjects was small in these analysis, numerically it seems that the test-retest reliability may be somewhat stronger for associators.

From the 20 subjects with two test scores, 18 scored in the same category in both tests (90%). Taken together, the correlation and categorization results imply that using PA categories via this questionnaire is a valid approach, but a large enough sample should always be included in both categories.

EEG time-frequency power

Averaged over all subjects, the task elicited a suppression of bilateral parietal-occipital alpha-band power and an increase in midfrontal theta-band power (see Figure 2).

Based on the group-averaged results of task-related EEG activity, we selected electrodes FCz and the average of PO7 and PO8 for further inspection of possible group differences (see starred electrodes in Figure 2). Because we did not have a priori hypotheses concerning the time-frequency windows in which group differences may occur, we tested for group differences at each time-frequency pixel, and

corrected for multiple comparisons, using a threshold of $p = .01$ in combination with cluster correction (Maris & Oostenveld, 2007). Furthermore, because we performed three comparisons (all combinations of the three groups), we further reduced the p -value threshold to $p = .0033$ ($.01/3$). At electrodes PO7/8 (Figure 3), significant differences in alpha-band power were observed between projectors and associators and between projectors and non-synesthetes (here the significance also extended into the beta band). At electrode FCz (Figure 4), similar results were obtained, except the differences between non-synesthetes and associators was significant in the lower alpha and theta bands.

In addition to the topographically constrained analyses, we also performed topography-wide analyses in which we assessed the differences between groups in the average power of the alpha (8–15 Hz) and theta (3–6 Hz) bands. The results are presented at 200, 400, and 600 ms to allow visualization of the temporal progression of the effects. Electrodes showing significant effects (task vs. baseline in Figures 5a and 6a, and group differences in Figures 5b and 6b) at $p < .05/64$ (thus Bonferroni correcting for multiple comparisons over electrodes) are encircled in black contours. No differences between associators and controls were statistically significant in this analysis.

DISCUSSION

Reliability of PA questionnaire

The projector-associator (PA) distinction reveals individual differences in how synesthesia is experienced. There has been some debate concerning the validity and reliability of PA questionnaires. The consistency of the PA score over time reported here is therefore important for two reasons.

First, previous work has reported insufficient test-retest consistency of a PA questionnaire (Skelton, Ludwig, & Mohr, 2009), with a four-month test-retest interval, although an illustrated version increased consistency (Skelton et al., 2009). One possible explanation of the discrepancy between these and the current results is the smaller number of subjects and the smaller number of questions used in the Skelton et al. study. It might also be related to the questions included in the questionnaire, as “the Colored Letters and Numbers” (CLaN; Rothen, Tsakanikos, Meier, & Ward, 2013) showed good test-retest consistency, after an average of a four-

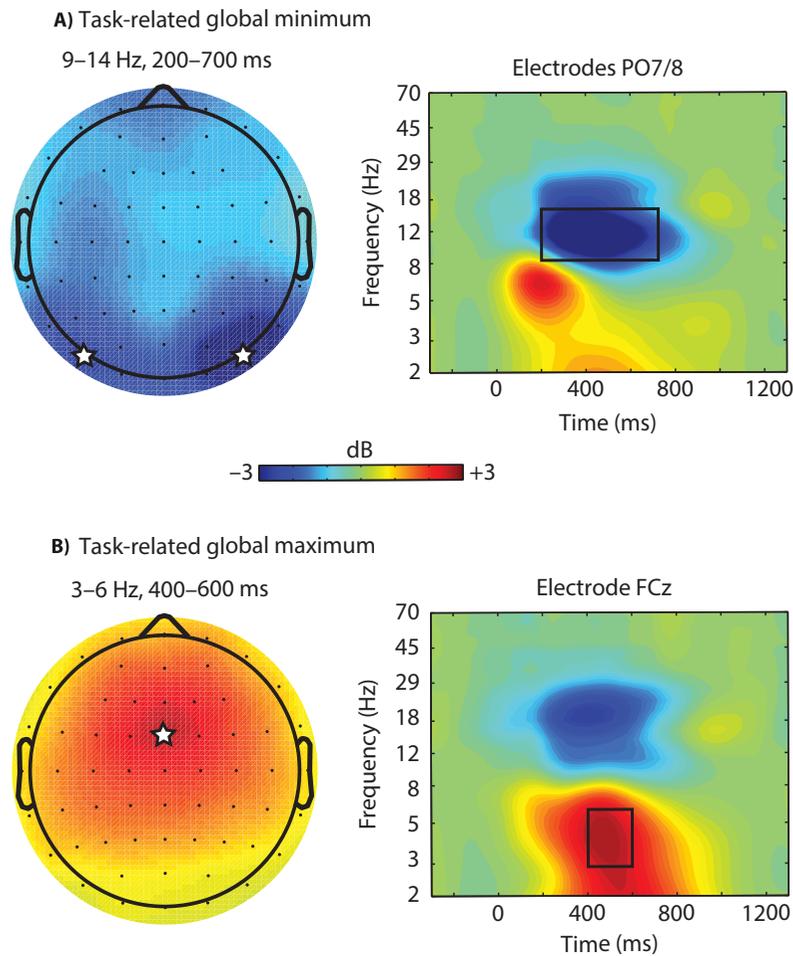


Figure 2. Grand-averaged (over all subjects and groups) task-related time-frequency power effects. The two most prominent task features were a bilateral posterior suppression of upper alpha-band power (panel A) and an increase in mid-frontal theta-band power (panel B). In both panels, the time-frequency power plots are drawn from electrodes indicated by white stars, and the topographical maps are from the time-frequency windows indicated by black boxes on the time-frequency power plots.

month interval. The current study shows, for the first time, that a highly consistent PA score can be obtained with years between test and retest. Furthermore, most subjects scored in the same category in both tests (90%). This indicates that the PA questionnaire can be used to reliably assign PA values (continuous or categorical) to grapheme-color synesthetes. We do, however, still recommend testing a sufficient number of subjects in any study on synesthesia, to help minimize the possibility of measurement error or sampling variability from influencing behavioral and neuroimaging findings.

Second, the construct validity of PA questions is currently a topic of debate. The current questionnaire simply makes a distinction between an experience of the color internally (“inside my head”) versus seeing it externally (“seeing in the outside world”)

(respectively, this corresponds to associators and projectors). Ward et al. (2007) suggested that differences in phenomenology extend beyond the projector-associator dichotomy. Each of these factors can be further divided, with “surface projectors” and “space-projectors” (whether the color is projected onto the written type-face of the inducer, or onto an externalized near-by space) as projector types, and “see-associators,” and “know associators” (is there a sensory experience of “seeing” color or is there only “knowing” that a particular color is associated with the grapheme) as associator types. This can be viewed as two orthogonal factors: A combination of the “Projector-Associator” factor, and an “ability to form a visual mental image” factor (Simner, 2013). The CLaN questionnaire had 16 items loading on four different factors. These factors were localization,

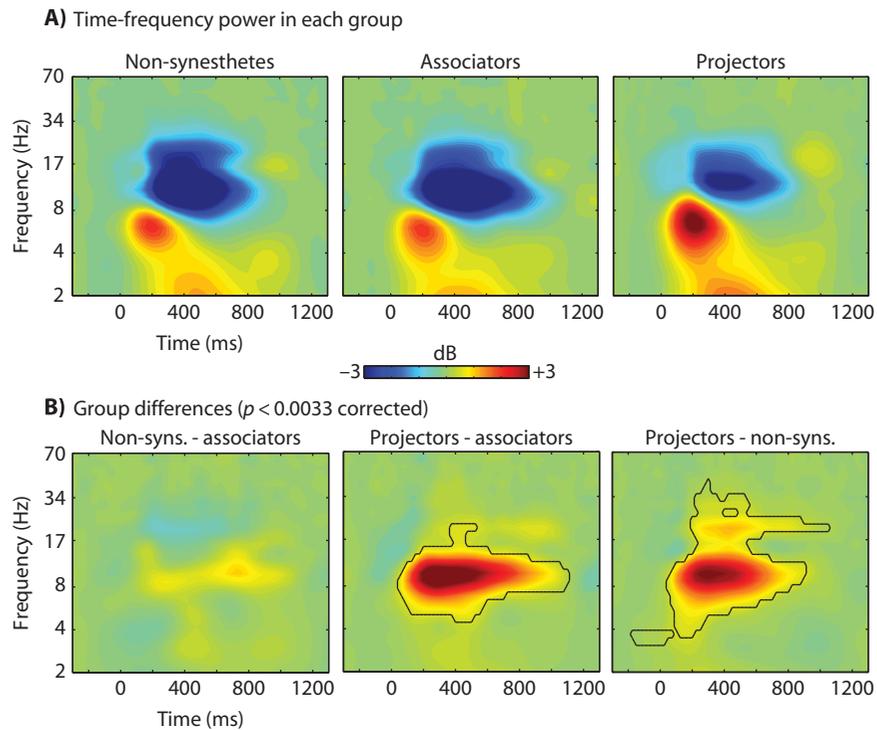


Figure 3. Time-frequency power plots of task-related effects at electrodes PO7 and PO8 (averaged together; see white stars in Figure 2a), plotted separately for each group (panel A) and for group contrasts (panel B). Black contours outline regions in which the group effect exceeded the statistical threshold.

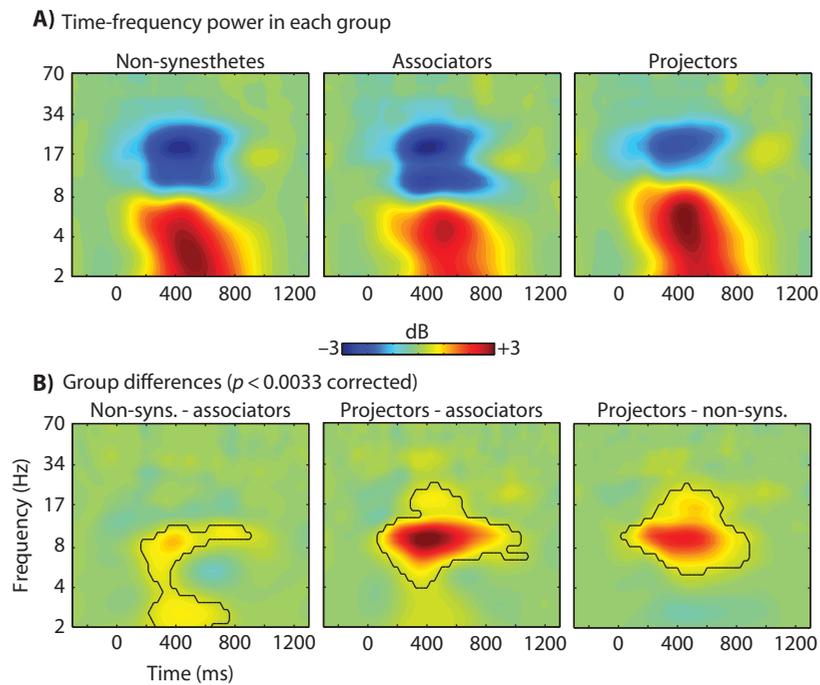


Figure 4. As Figure 3 except for midfrontal electrode FCz (see white star in Figure 2b).

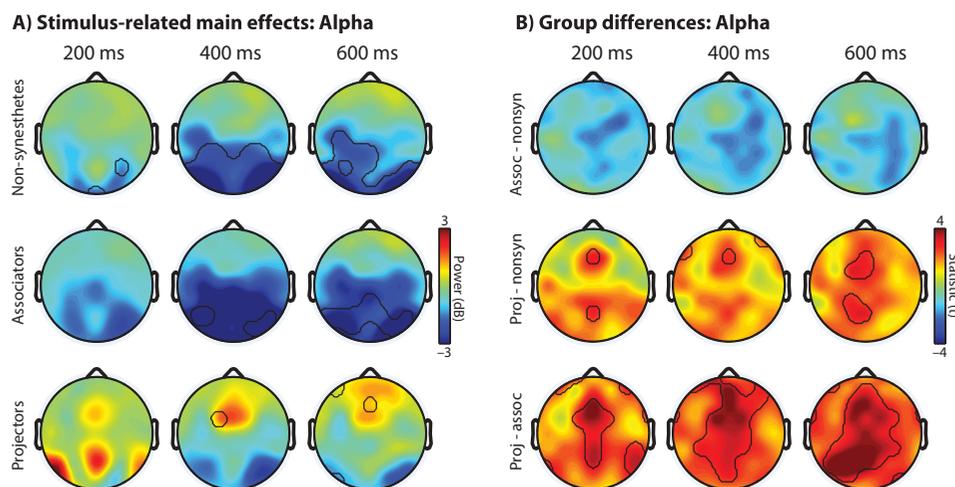


Figure 5. Topographical analyses revealed significant (black outlined regions) differences in alpha-band (8–15 Hz) power between task vs. baseline for each group separately (panel A), and group differences (panel B).

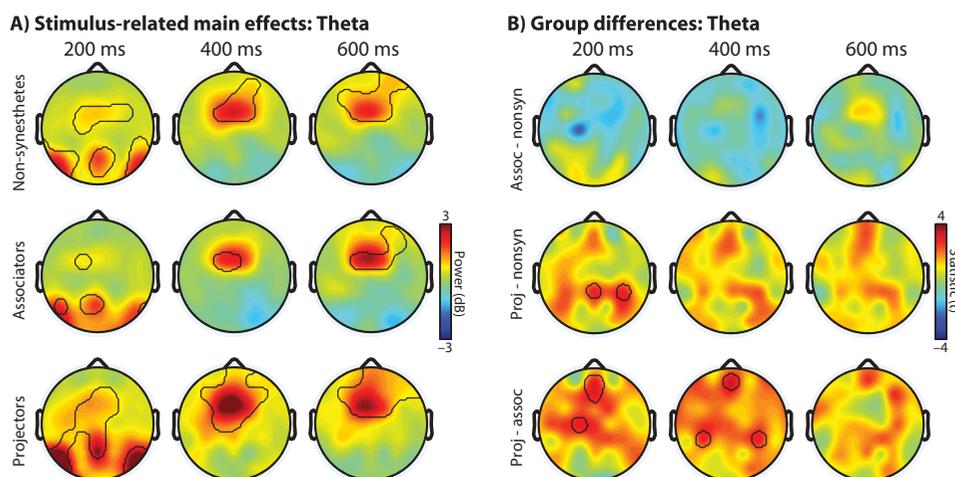


Figure 6. As Figure 5 except for theta-band power.

automaticity/attention, deliberate use, and longitudinal changes. The first of these factors seems similar to our PA factor, although the nature of the distinction is slightly different. A high score on the factor indicates that the synesthetic color has an external location, but it is less clear what phenomenology is related to a low score (Rothen et al., 2013). These factors were externally validated, and the questionnaire showed good test-retest reliability and construct validity. It would be interesting to study whether differences in neurobiological mechanisms are also obtained related to individual differences on these other questionnaires. Still, and most importantly, regardless of the specific questionnaire used to identify subtypes of synesthesia, the current results

stress the relevance of the PA distinction in synesthesia research, and the PA group composition is likely to affect any comparisons of synesthetes versus controls.

Synesthesia and EEG oscillations

The most striking finding in the EEG results was the robust difference in stimulus-related alpha-band power in projectors compared to associators and non-synesthete controls. This effect suggests a biological difference in cortical functional organization that is unique to grapheme-color projectors. These differences in alpha oscillations are also striking considering that the task was orthogonal

to the phenomenon of synesthesia. That is, unlike in cognitive/perceptual tasks often used to study synesthesia, in which the color can either boost or impair performance, in our task, color associations were unrelated to task performance. This is an advantage of the present study, because the group differences can only be attributed to their self-reported synesthetic experience, and cannot be attributed to cognitive or task-strategic differences that might result from utilizing their color percepts in different ways to solve the task. Thus, we interpret our results to indicate that the alpha- and theta-band effects reflect stable trait-like individual differences rather than task-specific strategies.

Alpha-band oscillations have been suggested to be a neural mechanism by which sensory-related processing is actively inhibited (Jensen et al., 2014; Jensen & Mazaheri, 2010). This is because alpha oscillations create narrow temporal windows in which neurons can fire, thus constraining the regional neural processing and output. It is possible that the increased alpha for projectors reflects a suppression of parietal top-down pathways, which in turn allows for stronger bottom-up processing. This interpretation is consistent with fMRI findings showing that associators have relatively stronger parietal-to-V4 effective connectivity (van Leeuwen et al., 2011). On the other hand, because our task did not require or manipulate bottom-up or top-down processing, additional studies will be necessary to build off the present results and examine situations in which bottom-up versus top-down processing might be beneficial or detrimental to task performance.

When comparing controls and grapheme-color synesthetes without separating subtypes, it is possible that group differences are mainly driven by the projectors within one group. Note that EEG has low sensitivity to subcortical structures including the thalamus and hippocampus. Thus, group differences in subcortical structures, which may be more apparent for associators than for projectors (Rouw & Scholte, 2010), will be difficult to measure with EEG. On the other hand, null effects in a group comparison should be interpreted with caution, and there may be true associator-vs.-control posterior alpha-band differences that were too subtle to be detected in our data, despite some differences in frontal activity as measured at electrode FCz.

In conclusion, we provided evidence that the projector-associator distinction in grapheme-color synesthesia is consistent over time and is related to cortical neural oscillations, most prominently in the alpha band over posterior scalp regions.

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