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Absolute Pitch and Synesthesia: Two Sides of the Same Coin? Shared and Distinct Neural Substrates of Music Listening

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ABSTRACT

People with Absolute Pitch can categorize musical pitches without a reference, whereas people with tone-color synesthesia can see colors when hearing music. Both of these special populations perceive music in an above-normal manner. In this study we asked whether AP possessors and tone-color synesthetes might recruit specialized neural mechanisms during music listening. Furthermore, we tested the degree to which neural substrates recruited for music listening may be shared between these special populations. AP possessors, tone-color synesthetes, and matched controls rated the perceived arousal levels of musical excerpts in a sparse-sampled fMRI study. Both APs and synesthetes showed enhanced superior temporal gyrus (STG, secondary auditory cortex) activation relative to controls during music listening, with left-lateralized enhancement in the APs and right-lateralized enhancement in the synesthetes. When listening to highly arousing excerpts, AP possessors showed additional activation in the left STG whereas synesthetes showed enhanced activity in the bilateral lingual gyrus and inferior temporal gyrus (late visual areas). Results support both shared and distinct neural enhancements in AP and synesthesia: common enhancements in early cortical mechanisms of perceptual analysis, followed by relative specialization in later association and categorization processes that support the unique behaviors of these special populations during music listening.

I. BACKGROUND

A. Introduction

Central to the study of music perception and cognition is the question of how individuals may differ in the way they hear music. Two populations of people who are known to perceive music differently are people with Absolute Pitch and people with Synesthesia. Both these phenomena are more common among people in creative industries and commonly co-occur in the same individuals, suggesting that the two conditions may share similar neural substrates.

B. Absolute Pitch

Absolute Pitch (AP) is the ability to identify the stable pitch class of any given tone without an external reference. Its has been associated with exceptional musical talent due to its possession by famous musicians in history such as Mozart (Ward, 1999). Despite being a rare trait, AP is distributed non-uniformly across populations: East Asians are more likely to possess AP (Gregersen, Kowalsky, Kohn, & Marvin, 1999), and AP tends to run in families (Baharloo, Service, Risch, Gitschier, & Freimer, 2000), suggesting that genetic factors play a role in AP possession. However, learned factors also play a major role in AP: Timbre and pitch range of one's learned instrument can influence the accuracy of note naming ability (Miyazaki, 1989), AP acuity is correlated with fluency in tone languages (Deutsch, Dooley, Henthorn, & Head, 2009), and subjects who start musical training at a young age are more likely to possess AP (Baharloo, et al., 2000; Brown, Sachs, Cammuso, & Folstein, 2002; Gregersen, et al., 1999). However, AP can be found in nonmusicians as it has been observed using methods that do not depend on knowledge of pitch categories (Smith & Schmuckler, 2008). Some have noted that autistic traits are more likely to persist in AP possessors (Brown et al., 2003), suggesting that there may be an association between AP and autism. Due to its interesting etiology and the interplay between genetic and developmental factors, AP is thought to be a model for understanding the influence of genes and development (Zatorre, 2003).

The neural substrates of AP have received increased interest in recent years, perhaps in part due to the possibility of an association between AP and disorders such as autism. Neuroanatomical studies have observed increased leftward hemispheric asymmetry in the planum temporale (Keenan, Thangaraj, Halpern, & Schlaug, 2001; Schlaug, Jancke, Huang, & Steinmetz, 1995; Zatorre, Perry, Beckett, Westbury, & Evans, 1998). Diffusion tensor imaging (DTI) of white matter has shown increased connectivity from the superior temporal gyrus (STG) in AP possessors, with white matter connectivity in the left hemisphere connections between STG and middle temporal gyrus (MTG) being correlated with AP acuity (Loui, Li, Hohmann, & Schlaug, 2011). The role of the left STG is also supported by functional MRI, ERP, and MEG studies, which showed significantly higher activity in the left superior temporal and left prefrontal regions during the encoding and retention of pitch in AP possessors (Hirata, Kuriki, & Pantev, 1999; Itoh, Suwazono, Arao, Miyazaki, & Nakada, 2005; Schulze, Gaab, & Schlaug, 2009; Zatorre, et al., 1998).

C. Synesthesia

Synesthesia is a condition in which external stimulation in one modality induces involuntary concurrent percepts in another modality. For example, in grapheme-color synesthesia, letters or numbers trigger color percepts, whereas in tone-color synesthesia (or colored music synesthesia), color percepts are triggered by musical stimuli. Synesthesia is found in 1-4% of the population but is most common among musicians, writers, artists, and other people in the creative industries (Ramachandran & Hubbard, 2001), and historically the phenomenon has been a source of inspiration for composers such as Messiaen, Skryabin, and Liszt (Cytowic & Eagleman, 2009). Multiple theories have been proposed to explain the phenomenon of synesthesia. The hyperconnectivity theory (Ramachandran & Hubbard, 2001) proposes that synesthesia arises from increased cross-wiring or cross-activation between different stages of modality-specific processing – for instance, tone-color synesthetes may have cross-wired or cross-activated brain regions responsible for pitch and color perception. In contrast to the hyperconnectivity theory, the disinhibited feedback hypothesis (Grossenbacher & Lovelace, 2001) suggests that the processes that usually inhibit the convergence between inducer and concurrent percepts are not in place in synesthetes. Support for disinhibited feedback comes from behavioral studies showing the effect of synesthetically induced percepts on perception of visual stimuli; these effects are attention-dependent and can be attenuated by applying brain-stimulation over sensory integration regions in the parietal lobe (Esterman, Verstynen, Ivry, & Robertson, 2006; Rich & Mattingley, 2003; Smilek, Dixon, Cudahy, & Merikle, 2001). Support for the hyperconnectivity theory comes from cortical thickness and DTI studies in grapheme-color synesthetes showing increased connectivity (Hanggi, Wotruba, & Jancke, 2011; Rouw & Scholte, 2007), as well as by MEG and TMS studies showing increased activation and excitability in visual association areas (Brang, Hubbard, Coulson, Huang, & Ramachandran, 2010; Terhune, Tai, Cowey, Popescu, & Cohen Kadosh, 2011). Further evidence for cross-activation comes from fMRI studies that showed activation in late visual areas (V4), known to be involved in the perception of color, in response to spoken words for auditory-visual synesthetes (Nunn et al., 2002) and color-inducing letters for grapheme-color synesthetes (Sperling, Prvulovic, Linden, Singer, & Stirn, 2006).

Synesthesia, like Absolute Pitch, is both genetic and environmental: although it runs in families, it is heterogeneous and polygenetic (Asher et al.; Brang & Ramachandran, 2011; Tomson et al., 2011). There is also a well-documented role of early experience in synesthesia, as seen in grapheme-color synesthetes from lexical effects on concurrently perceived color (Rich, Bradshaw, & Mattingley, 2005) as well as a correlation between perceptual similarity of graphemes and their concurrent colors (Brang, Rouw, Ramachandran, & Coulson, 2011). Less is known about the role of experience in tone-color synesthesia, but there are associations between pitch height and brightness of concurrent colors that are also observed, though to a smaller extent, in non-synesthete controls (Ward, Huckstep, & Tsakanikos, 2006).

II. AIMS

AP and synesthesia are above-normal perceptual experiences that have much in common. Both phenomena refer to the specific tendency to perceive one-to-one mappings between sensory stimuli and perceptual or conceptual categories. Both are rare conditions that have uneven distributions in the population, and both are sensitive to genetic and environmental or experiential factors. Finally, a significant proportion of synesthetes also report having AP and vice versa (Cytowic & Eagleman, 2009), suggesting an association between the two phenomena. We hypothesize that AP and tone-color synesthesia are explained by partially shared neural mechanisms. An overarching model that ties together the two enhanced perceptual phenomena would be powerful both for our theoretical understanding of perception and its neural correlates, and for the increased availability of empirical data on hand to address each phenomenon. The aim of this study is to test whether and to what extent tone-color synesthetes use similar neural mechanisms as absolute pitch possessors relative to controls during music listening.

III. METHOD

A. Subjects

Fifteen AP possessors (AP), 15 tone-color synesthetes (SYN), and 30 matched controls (15 for each special population: Non-AP, Non-SYN) were recruited via advertisements online and at local schools and conservatories. Control subjects for each group were matched for age, sex, ethnicity, IQ, and number of years and age of onset of musical training. Demographics and musical training information of each subject group are given in Table 1.

Group	Age ±SD	Years music train	Onset music train	Ethnicities (White/Black/Asian/ Hispanic)	Scaled IQ
AP	25±5	16±6	6±3	10/0/5/0	120±5
Non-AP	26±5	17±7	6±2	9/0/6/0	118±4
SYN	24±5	14±6	8±3	11/2/1/1	120±4
Non-SYN	25±5	13±6	8±3	12/1/1/1	119±5

Table 1. Subject characteristics in AP, AP-control, Synesthete, and Synesthete-control groups.

B. Behavioral testing

After obtaining informed consent, a survey was administered to all subjects to assess their linguistic and musical background. To control for possible between-group differences in IQ, we conducted Shipley's verbal and abstract tests (Shipley, 1940), which have been shown to be a predictor of IQ (Paulson & Lin, 1970).

All subjects completed an AP test (Keenan, et al., 2001) and four subtests of the synesthesia battery (Eagleman, Kagan, Nelson, Sagaram, & Sarma, 2007). The AP test involved 52 trials. Each trial consisted of a 500 ms single pure tone with fundamental frequency ranging from 370 Hz (F#3) to 740 (F#4). Subjects' task was to label each pitch by writing down the note name on an answer sheet upon hearing each note. The inter-tone interval was 2 s. In accordance to previous studies (Bermudez & Zatorre, 2009), subjects were classified as AP possessors if they scored a mean deviation of 1.0 semitone or less.

Subjects also completed four subtests of the synesthesia battery: the grapheme-color, musical pitch-color, musical chords-color, and musical instruments-color subtests. In each trial of the grapheme-color subtest, subjects were given a letter or a number, accompanied by a color palette on the screen; their task was to choose the color that they most closely associated with the given letter or number. In each trial of the musical pitch-color, musical chords-color, and musical instruments (timbre)-color subtests, subjects were given a piano note, a three-note chord played on a piano, and an excerpt played on a Western instrument respectively; these were again accompanied by an on-screen color palette, and subjects' task was to choose the color they most closely associate with the musical sound. There were 36 graphemes, 13 pitches, 12 chords, and 18 instrument timbres used as test items; each test item repeated three times in random order. The subject's color choices were quantified in RGB color values and the variance between the three occurrences of the same test item was calculated and averaged to form a single synesthetic score. Subjects with a synesthetic score below 1.0 were classified as synesthetic (Eagleman, et al., 2007)(also see synesthete.org).

C. fMRI stimuli

Musical clips that were presented in the fMRI were chosen from a larger battery of musical stimuli that had been previously rated for emotional valence and arousal (Bachorik et al., 2009) and were shown to elicit consistent and reliable arousal ratings. Audio stimuli consisted of 12-second clips of music from different genres, with rise and fall times of 500 ms respectively. All audio stimuli were loudness-normalized to avoid arousal effects being due to differences in loudness alone.

D. fMRI acquisition

All images were acquired in a 3T General Electric scanner. A T1-weighted anatomical image with a voxel resolution of 0.93 x 0.93 x 1.5 mm was acquired in addition to three runs (with 26 acquisitions each) of gradient echo echo-planar imaging (EPI) using a sparse temporal sampling paradigm (Gaab, Gaser, Zaehle, Jancke, & Schlaug, 2003; Ozdemir, Norton, & Schlaug, 2006). The T2*-weighted EPI sequence had an effective repetition time (TR) of 15 s, an echo time (TE) of 30 ms, an acquisition time (TA) of 1.8 s for 26 axial slices with an acquisition matrix of 64 x 64 resulting in a voxel size of $3.8 \times 3.8 \times 4$ mm^3. Twenty-six whole brain volumes were acquired in each of three functional runs, each of which included 2 dummy volumes to allow time for steady state magnetization resulting in a total of 72 acquisitions (3 runs x 24 acquisitions) across the Music and Rest conditions. Order of Music and Rest trials was counterbalanced. In the Music condition, subjects listened to 12-second musical sound clips, followed by a 500 ms burst of white noise. Subjects' task was to make judgments on the level of emotional arousal in each sound clip after the short noise burst via a button-press. In the Rest condition, subjects heard silence followed by the 500ms noise burst, which was monaurally presented in a counterbalanced order. Upon hearing the noise burst, subjects' task was to indicate via button-press whether the noise came from the left ear or the right. The purpose of the fMRI task was to identify regions related to listening to music with different levels of emotional arousal. These activated regions would then be compared between APs, synesthetes, and each of the control groups.

E. fMRI data analysis

FMRI data analysis was done in MATLAB and the SPM5 toolbox (Friston et al., 1994). Images were realigned, normalized using SPM5's EPI template, and smoothed using an 8 mm Gaussian kernel. Each trial was modeled using a Finite Impulse Response (FIR) at the first level. Based on each subject's behavioral responses, trials from the Music condition were further divided into trials that were rated as High-arousal and Low-arousal. High-arousal, Low-arousal, and Rest trials were modeled separately at the first level. The two contrasts of interest, Music vs. Rest, and High- vs. Low-arousal, were computed for each subject. Each contrast for each subject was then entered into a second-level analysis comparing between AP and non-AP subjects, between SYN and non-SYN subjects, and between AP and SYN subjects for Music vs. Rest and for High- vs. Low-arousal conditions.

IV. RESULTS

A. Music vs. Rest shows enhanced activity in APs and synesthetes

A comparison between Music and Rest conditions showed that music elicited robust activations for all subjects in auditory areas in the bilateral superior temporal gyrus (STG) and prefrontal regions, but the volumes of activations were larger for both the AP and SYN groups compared to the control groups (Fig. 1).

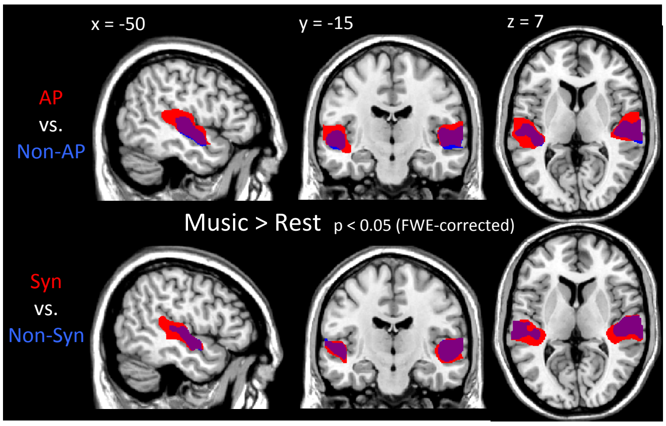

Fig. 1. Activations for Music vs. Rest trials at the p < 0.05 (FWE-corrected) level overlaid on a T1 template, showing similarities and differences between AP subjects (red) and controls (blue), and between tone-color synesthetes (red) and their controls (blue).

B. Reversed hemispheric asymmetries in APs and Synesthetes

Comparing activations for the Music vs. Rest contrast for AP and SYN groups revealed differences in hemispheric asymmetry in activated regions between groups: while both groups showed bilateral activations in STG, AP subjects showed more left-hemisphere prefrontal and anterior temporal activations than SYN subjects. In contrast, SYN subjects showed more right prefrontal and anterior temporal activations. This dissociation in left-right asymmetry for music-induced activity between AP and SYN groups is shown in Fig. 2.

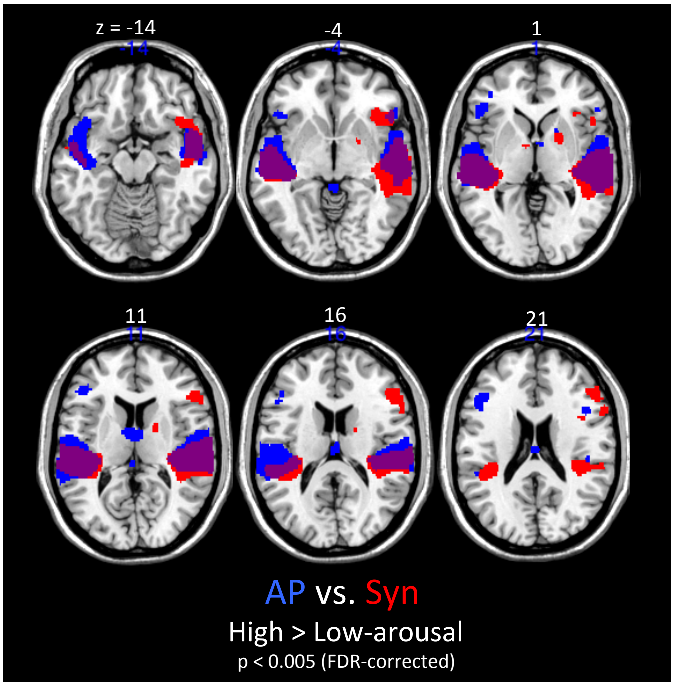

Fig. 2. Activations for the Music vs. Rest contrast ($p < 0.005$ FDR-corrected) comparing AP subjects (blue) and tone-color synesthetes (red) overlaid on a T1 template. Prefrontal regions show reversed patterns of asymmetry between groups: left prefrontal regions were more activated in AP subjects whereas right prefrontal regions were more activated in synesthetes.

C. High-arousal vs. low-arousal music elicits modality-specific enhancements

Music that was rated as high-arousal elicited more activation in bilateral STG (secondary auditory areas) in the AP group compared to controls. The same contrast for synesthetes and their controls also showed an increase in bilateral STG activation in synesthetes. In addition, a significant cluster of activity was observed for the synesthetes in the lingual gyrus (late visual area) in the synesthetes (Fig. 3).

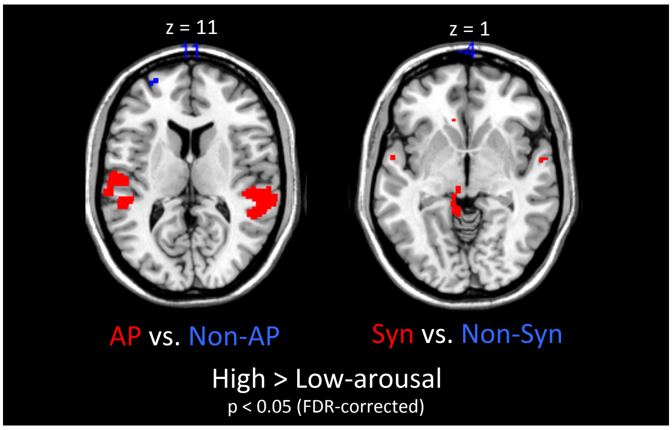

Fig. 3. Activations for AP and controls and SYN and controls during high-arousal music compared with low-arousal music ($p < 0.05$ FDR-corrected) overlaid on a T1 template. Significantly higher activity is seen in STG for AP subjects and in STG and lingual gyrus for synesthetes.

A direct contrast between synesthetes and controls, and between AP subjects and controls, showed that the unique effect of AP during the High- vs. Low-arousal contrast was centered around the left STG, whereas the unique effect of Synesthesia during the same contrast was centered around the bilateral lingual and inferior temporal gyri (Fig. 4). The increased left STG activation in the AP group may subserve heightened pitch categorization during music listening, whereas the increased activation of visual areas in the SYN group may explain why tone-color synesthetes report the subjective experience of seeing colors and other concurrent percepts while hearing music.

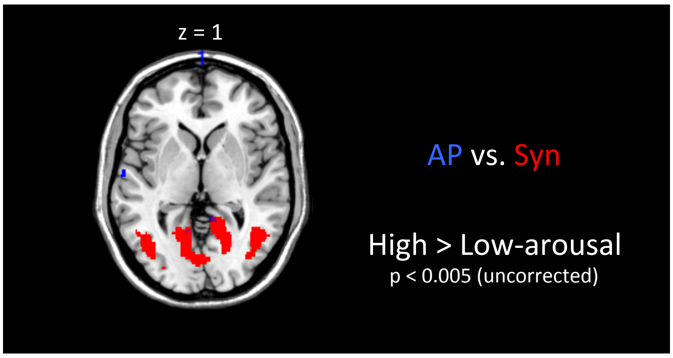

Fig. 4. Activations for SYN vs. controls (red) and for AP subjects vs. controls (blue) during the High > Low-arousal contrast ($p < 0.005$ uncorrected), showing increased activations in the left STG for the AP group and increased activations in the lingual gyrus and the inferior temporal gyrus for the SYN group.

V. CONCLUSIONS

Results support both shared and distinct neural mechanisms of AP and synesthesia. AP possessors and tone-color synesthetes show similar additional activations for the early cortical processing of music compared to non-APs and non-synesthetes, but distinct patterns of functional activations for perceptual associations, categorizations, and affective processing. The early cortical enhancements center on the bilateral STG, regions known to be important in pitch processing (Loui, Alsop, & Schlaug, 2009; Loui, et al., 2011; Mathys, Loui, Zheng, & Schlaug, 2010). These early additional activations feed towards dissociated hemispheric specializations, with leftward asymmetry in AP and rightward asymmetry in synesthetes. Later stages in processing, that reflect the top-down task demands of affective judgment of arousal in music, showed further enhancements centering around late auditory areas (STG) and late visual areas (lingual gyrus), but with increased auditory processing in AP and increased visual processing in synesthetes. The enhancement of STG activity in AP may subserve sound categorization, whereas enhanced lingual gyrus activations in synesthetes may subserve the subjective experience of seeing colors when hearing sounds. Taken together, fMRI results from music listening suggest that AP and tone-color synesthesia may be two sides of the same coin: the same general mechanism of enhanced sensory activation feeds into auditory experience in AP and visual experience in synesthetes. We expect that the same biological and/or experiential prerequisites may be in place early on in development for a single overall group of individuals to develop heightened abilities of perceptual association. This heightened perceptual association may give rise to AP as well as tone-color synesthesia depending on attentional processes that play a role in the conscious evaluation of unconsciously processed triggers such as letters, timbres, and musical pitch (Rich & Mattingley, 2003, 2009). These findings have strong implications for individual differences in the experience of music, and are applicable towards other special populations who may perceive music differently, such as highly trained musicians, highly creative people, and individuals with autistic spectrum disorders.

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