

CHAPTER 6

ABSOLUTE PITCH

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DEFINITIONS AND INCIDENCE

ABSOLUTE pitch (AP) is the unique ability to identify the pitch class of any given tone without a reference (Ward, 1999). While the ability is thought to be rare, with estimates ranging from 0.01% to 1% (Lenhoff, Perales and Hickok, 2001; Levitin and Rogers, 2005; Ward, 1999; Ward and Burns, 1982), the ability is unevenly distributed across populations, with some aspects of absolute memory for pitch that may be much more common across all individuals (Levitin, 1994). Among “The Greatest” Western classical composers as identified by *The New York Times* (2011), historical evidence has identified more than half as AP possessors. While this does not imply that AP is sufficient or even necessary for exceptional musical creativity, this high occurrence of AP among great composers has led some to suggest that AP is an “ultimate in musical endowment” (Ward, 1999), or one of many possible indices of genius, musical creativity, and/or exceptional ability in the musical domain.

THE ORIGINS OF ABSOLUTE PITCH

The debate on the origins of AP has seen views ranging from fully innate to fully environmental, with multiple accounts of interactionist views in between. Because of these intriguing controversies, neuroscientists have turned to the study of neural underpinnings of AP as a model for understanding the interactions between genes and the environment on neurocognitive functions (Zatorre, 2003).

AP is known to have strong genetic associations. AP possessors are extremely likely to have siblings who also possess AP, even in families where parents do not play instruments (Baharloo, Johnston, Service, Gitschier and Freimer, 1998). Furthermore, AP is most commonly found in people of East Asian ethnic descent (Gregersen, Kowalsky, Kohn and Marvin, 1999). From a survey in which subjects self-reported AP, Gregersen et al. noted a strong correlation between the prevalence of AP and the percentage of students who

reported their ethnic background as “Asian or Pacific Islander,” as well as higher rates of AP possession in students at music conservatories (Gregersen et al., 1999). However, more recent evidence shows that the East Asian advantage extends even to relative pitch (RP) tasks, and therefore the genetics of East Asian descent may not fully or specifically explain the origins of AP (Hove, Sutherland and Krumhansl, 2010). Genome-wide studies showed linkage between AP and several chromosomes especially chromosome 8, suggesting that AP has genetic associations but is polygenetic, that is, it is a trait that involves contributions from multiple genes (Theusch, Basu and Gitschier, 2009).

One possible account for the increased incidence of people with East Asian descent in AP etiology comes from the tone language hypothesis: East Asian languages, many of which rely on tones to convey meaning, may be providing a background of early learning for AP development, perhaps in an analogous mechanism as early onset of musical training. This is supported by findings that tone language speakers are much more likely to have AP (Deutsch, Henthorn and Dolson, 2004); furthermore the accuracy of AP is associated with fluency in tone language (Deutsch, Dooley, Henthorn and Head, 2009). Several effects of musical instruction are also noted: the fixed-do instruction system for solfège are thought to train AP more than the movable-do system; however these may be confounded with the country and culture in which musical training occurs (Deutsch, 2013).

In addition to the effects of solfège instruction, plenty of evidence exists for the role of learning in AP development. The classic studies by Miyazaki showed effects of timbre and register on pitch identification: while most AP possessors are most accurate in the middle range of the keyboard, violinists are more accurate in the upper register, cellists in the lower registers, and pianists are more accurate for the white keys than the black keys (Miyazaki, 1989). Baharloo et al. tested for AP using a pitch identification task with sine wave tones and piano tones and showed an advantage for piano tones. They further identified subcategories of AP behavior among all AP possessors ranging from AP-1 (most accurate on both piano tones and sine wave tones) to AP-4 (subjects who scored well above chance, but much less accurately especially on piano tones). Across all categories, AP possessors reported beginning formal musical training at a much younger age, with nearly all AP possessors reporting first formal musical training at or before 6 years of age (Baharloo et al., 1998). This effect of early musical training is well replicated and lends support to the critical period hypothesis, which states that a window of opportunity for AP development exists early in life if given frequent exposure to pitch information (Deutsch, Henthorn, Marvin and Xu, 2006). A recent pharmacological study (Gervain et al., 2013) showed that people on valproate, a commonly used drug for epilepsy and bipolar disorder that can change the critical period by manipulating cellular processes of neuroplasticity, were able to learn AP slightly better than placebo controls, thus providing strong evidence for the critical period hypothesis.

In addition to effects of pitch register and timbre, there is now considerable evidence that accuracy in identifying each pitch class is associated with the frequency of occurrence of each pitch class in music that the subjects might be exposed to in their lifetime. A robust association was observed between note count in the classical repertoire and accuracy of note naming for each pitch class (Deutsch, 2013; Deutsch, Le, Shen and Li, 2011). This association suggests that there are statistical learning properties in the acquisition of AP, rather than the pitch class of AP acting as a perceptual magnet as proposed by others (Athos et al., 2007).

TESTING FOR ABSOLUTE PITCH

AP possessors typically do not realize they possess any unusual perceptual functions until they are told that their peers do not possess the same abilities. Music teachers may identify AP possessors from among their students during formal musical training, such as by noting that the student is exceptionally adept at ear training and musical dictation (Dooley and Deutsch, 2010). Nevertheless, formal tests of pitch identification or categorization are necessary to establish AP possession in a robust manner.

Concerning the testing of AP, one important debate surrounds the issue of labeling. Since the reporting mechanism for AP testing requires that the listener reports back the pitch class, and these pitch classes are generally learned through musical training, then one must need to have musical training to have AP. Many approaches have been adopted to circumvent this confound (Hulse, Cynx and Humpal, 1984; Ross, Olson, Marks and Gore, 2004; Saffran and Griepentrog, 2001; Smith and Schmuckler, 2008). Based on results from testing for AP with methods that do not require musical training, Ross, Gore and Marks (2005) concluded that AP may be relatively independent of musical experience. Furthermore, Ross et al. determined that there are multiple types of AP, with the two categories being APE (AP encoders), who possess the ability to encode the frequency of auditory stimuli perceptually, and HTM (heightened tonal memory), who recognize target stimuli by comparing the stimuli with their memory of specific auditory events. According to Ross et al., early learning favors HTM but may not affect the onset of APE, or “genuine” AP, per se (Ross et al., 2005). This categorical view stands in contrast with Athos et al. (2007), who tested a large sample of participants online and reported that AP ability was bimodally distributed (Athos et al., 2007); however, this bimodal distribution is probably due to self-selected sampling among participants of the online study.

Bermudez et al. (2009) disputed the claim of bimodal distribution of AP; they further showed that a circular arrangement of pitch class categories is the most unbiased way to assess AP performance. Additionally, they observed that measuring the mean deviation from the target response (in semitones) provides a relatively robust estimate of acuity of AP. Finally, they showed that recording reaction time could be useful for teasing apart “true” AP possessors from those who might be using RP to solve the pitch categorization task (Bermudez and Zatorre, 2009). Based on these observations, we have developed an online AP test that reports results immediately and can be used for personal testing as well as formal research purposes (<www.musicianbrain.com/aptest>). The source code for our AP test is now available online (West and Loui, 2013) for download and validation across different platforms and with different testing equipment, and we hope that it will be shared by other researchers in the music psychology community.

One question that has received relatively little attention, at least from the published literature, concerns transfer abilities of AP to other skills. AP possessors are known to have a large digit span (Deutsch and Dooley, 2013), suggesting that having AP may generalize toward an increased working memory capacity in extramusical domains of audition. Another functional study investigated the transfer abilities of AP to other skills, specifically linguistic skills in lexical-semantic processing (Oechslin, Meyer and Jancke, 2010b). This study is unique in that it specifically tests for the transfer of AP ability to nonmusical tasks, and does

so by incorporating behavior and functional neuroimaging to investigate the relevant neural correlates that might be shared between pitch and speech perception. It would be an important follow-up to see which aspect of speech acquisition (phonology, lexical-semantics, etc.) might correspond most closely to the acquisition of AP during development.

NEURAL CORRELATES

Following the debate on innateness and the roles of learning on development, the research has turned to address the neural correlates of AP. In relating the research on neural correlates of AP to its innate and/or developmental origins, it is important to note that finding neural correlates of AP does not establish “innateness.” Much of what we know about the human brain supports the central thesis of neuroplasticity: that experience can shape the brain in its structure (structural neuroplasticity) and function (functional neuroplasticity). Nonetheless, understanding the neural substrates of AP can help disentangle the cognitive processes that contribute to AP by offering reasonable inferences from the neural data to their psychological implications. Furthermore, understanding how AP plays out in the brain can help us better trace the development of this intriguing phenomenon from a basic mechanistic perspective, while offering more data to tease apart the confounding influences of ethnicity, linguistic experience, and musical training factors. To date, findings from cognitive neuroscience studies on AP can be categorized methodologically into electrophysiology, structural neuroimaging, and functional neuroimaging.

ELECTROPHYSIOLOGICAL EVIDENCE

Event-related brain potentials are derived from averaging electroencephalography (EEG) responses to provide time-sensitive neural responses to perceptual or cognitive events such as listening to sounds. In the study of AP, the first event-related potential (ERP) evidence for differences in pitch processing among AP subjects came from Klein, Coles, and Donchin (1984). AP was behaviorally verified in this study by a pitch-labeling task with pure tones, in which AP subjects made fewer errors than the control group in labeling pitch class, without the same benefit in pitch height (i.e., AP possessors made as many octave errors as controls: a well-replicated finding). An EEG experiment was then conducted using the classic “odd-ball” paradigm, in which two stimuli, one frequent and one rare, were presented while EEGs were recorded. The experiments were conducted both in the auditory modality, in which stimuli were pure tones of different frequencies, and in the visual modality as a control, in which stimuli were letters presented on a screen. Viewing or hearing the rare stimuli elicited the P₃₀₀ (a positive waveform around 300 milliseconds after the onset of the stimulus), which is thought to reflect the psychological processes of maintaining and updating working memory. While AP subjects showed a visual P₃₀₀ that was indistinguishable from controls, the auditory P₃₀₀ was greatly reduced in the AP subjects, with one out of the seven AP possessors not showing any P₃₀₀ effect at all. Results suggest that the AP possessors might be using some working memory-independent strategy to process musical tones. In contrast to

the common working-memory-dependent mechanism, AP possessors may have relied on a pre-existing framework of pitch categories to store the pitch information. However, later studies did find P300 in AP subjects (Bischoff Renninger, Granot and Donchin, 2003; Hirose et al., 2002), implying that the use of working-memory processes in AP may be quite sensitive to differences in task instructions (e.g., detection versus identification of rare tones in an experiment), as well as to individual differences in strategies used to solve the task at hand.

NEUROANATOMICAL EVIDENCE

In the first study to investigate brain structure associated with AP, Schlaug, Jancke, Huang, and Steinmetz (1995) compared nonmusicians and musicians specifically in the planum temporale (PT), a well-defined portion of the posterior superior temporal gyrus (STG), which is a known hub of auditory processing. Results from magnetic resonance imaging (MRI) scans showed an enlarged left PT in musicians, with most of the effect of musicianship on the resultant leftward PT asymmetry being explained by possessors of AP. This classic finding of exaggerated leftward PT asymmetry in AP musicians has been replicated subsequently (Keenan, Thangaraj, Halpern and Schlaug, 2001); however, at the time AP possessors were not identified by formal testing, but by self-report confirmed by review of school examination records for pitch discrimination task performance. Authors interpreted these results as indicative that “outstanding musical ability is associated with increased leftward asymmetry of cortex subserving music-related functions.” (Schlaug et al., 1995). Although we now know that AP may not be invariably associated with outstanding musical ability, the initial finding of an association between PT asymmetry and AP has fueled many more studies. In a notable follow-up study, Keenan et al. traced the PT in nonmusicians, non-AP musicians, and AP musicians. Results showed that leftward PT asymmetry, characterized by higher left PT volume and lower right PT volume, was most characteristic of the AP musicians (Keenan et al., 2001). Considering PT surface area rather than asymmetry, it was the absolute size of the right PT, instead of the left PT, that best predicted musical group membership. These results may indicate that pruning (i.e., reduction in volume during early development) of the right PT results in the increased leftward PT asymmetry, and thus is a developmental marker of AP ability. While the triggers of such an early developmental pruning are yet unclear, the authors suggest that genetic factors coding for hemispheric asymmetry might be at play, and furthermore that young children with an increased leftward PT asymmetry might acquire AP if exposed to musical training early in development. Although the data from this and other neuroanatomical studies are unable to address this hypothesis directly, it is notable that the hypothesis put forth by Keenan et al. offers an interactionist view of the etiology of AP, whereby a genetic predisposition and a background of early musical exposure are both required for AP to develop.

In addition to gray matter volume and surface area, cortical thickness has become a variable of interest in recent years that may yield information about developmental changes and differences in specific brain regions that are associated with behavioral attributes. Recent results from cortical thickness comparisons between AP and non-AP possessors converged with PT findings in showing that a region in the left STG was thicker in cortical volume among AP possessors compared to non-AP controls matched for musical training (Dohn

et al., 2013), thus adding support to the findings of increased left superior temporal volume from a convergent method.

FUNCTIONAL NEUROIMAGING

In designing functional neuroimaging studies, an important consideration comes from equating stimulus parameters versus equating task difficulty between subjects who perform at different levels given the same stimulus parameters. When given a standard pitch identification task, for instance, AP subjects are expected to dramatically outperform their non-AP counterparts. This may lead to differences in brain activity that are associated with psychological functions that are unrelated to AP-specific behavior, such as frustration and/or apathy on the part of non-AP possessors and mind-wandering or even boredom on the part of AP possessors. To circumvent these problems in experiment design, studies targeted at understanding functional differences in brain activity between AP and control groups have focused on tasks that require listening to pitches, but that focus on a behavioral output that is orthogonal to the feature of pitch class per se. One such study made use of a task in which subjects simply had to press a key after each pair of tones, as well as an interval judgment task in which subjects had to discriminate between major and minor intervals—a task that could be solved using relative pitch. Results from positron emission tomography (PET) scans showed hyperactivity (increased activation) among AP subjects in the dorsolateral prefrontal cortex (DLPFC) in PET scans during the tone task (Zatorre, Perry, Beckett, Westbury and Evans, 1998). This same region in the DLPFC was active during the major/minor discrimination tasks that involved relative pitch in non-AP possessors. The authors suggest that recruitment of DLPFC in both groups means that a single general working memory system, regardless of whether it is for absolute or for relative pitch processing, may be recruited in all subjects. While non-AP subjects may depend on this working memory mechanism only during tasks that specifically require working memory, AP subjects may be constantly engaging the same mechanism whenever they encounter pitched information. Thus, working memory is less task-dependent for AP subjects. This may be consistent with results from the EEG literature (Klein et al., 1984), which suggests a release from working-memory dependence in AP subjects.

More recently, Schulze et al. performed a functional magnetic resonance imaging (fMRI) study comparing pitch memory in AP subjects and matched controls. Subjects listened to sequences of tones and had to judge whether the first and last pitches were same or different. In performing this task, both AP and non-AP musicians showed activations in the classic secondary auditory regions including bilateral STG and superior temporal sulcus (STS), and the inferior parietal lobe as well as frontal lobe (inferior frontal gyrus) and motor control regions (supplementary motor area). Importantly, AP musicians showed more activation in the left STS, an area important for categorization, during the early perceptual encoding phase. In contrast, the non-AP musicians showed more activity in the parietal lobe, which might be more involved in a spatial binding strategy between pitch and spatial configuration (Schulze, Gaab and Schlaug, 2009). Taken together, these results suggest that AP musicians possess an enhanced ability for auditory categorical perception that may be relatively automatic or at least early in the perceptual-cognitive pathway. The neural mechanisms that

enable this auditory categorical perception process are likely centered on the superior temporal areas (STG and STS). While this finding places the bulk of the uniqueness of AP on an automatic categorization ability rather than on a constant working-memory mechanism, working-memory release may be an emergent property of such an automatic categorization mechanism.

As further evidence for increased activity that subserves heightened ability in AP possessors, Oechslin et al. also compared AP musicians, RP musicians, and nonmusicians in a lexical-semantic task and found left-lateralized enhancements in AP possessors in the posterior STS during the processing of segmented speech (Oechslin et al., 2010b). In contrast, both AP and RP musicians showed stronger bilateral activity in the posterior middle temporal gyrus (MTG) in all conditions. These results suggest that while musical training leads to bilateral enhancements in the MTG during all sound processing, AP is more specifically associated with the rapid access and assignment of sound categories, a function probably favoring the left STS.

In another fMRI study to investigate functional differences that were not specific to memory, we looked at emotional judgments to familiar musical stimuli. Subjects were presented with short clips of musical segments and told to rate the arousal level of each clip. Results showed increased activation in AP possessors in the STG extending into STS, in the precentral gyrus which is involved in motor output of the task, and in the hippocampus, amygdala, and ventral tegmental area, which are known to play roles in memory and reward processing. All these enhanced functional activations in auditory and emotional and reward-sensitive regions were observed without any differences in behavioral output (as AP subjects and non-AP subjects performed similarly in the emotional ratings task), suggesting that: (1) AP subjects may find music intrinsically more rewarding, and (2) there may be differences in functional connectivity that are intrinsic to AP, not related to any specific task (Loui, Zamm & Schlaug, 2012b).

STRUCTURAL CONNECTIVITY

While a generation of studies in cognitive neuroscience have focused on identifying regional differences in the brain that are associated with behavior, in recent years cognitive neuroscience has shifted toward looking for differences in brain connectivity, both in structure (e.g., identifying white matter connections between gray matter regions) and in function (e.g., identifying correlations between areas of activation), in order to define brain networks that subservise behavioral characteristics such as AP. One approach in understanding the role of brain connectivity in AP comes from comparing the microstructure of white matter between AP possessors and matched controls using diffusion tensor imaging (DTI), a type of MRI specifically tuned to the diffusion properties of white matter.

Oechslin et al. compared AP musicians, RP musicians, and nonmusicians in a DTI study by tracing the superior longitudinal fasciculus, which includes the arcuate fasciculus (AF), a prominent white matter pathway that runs between the superior temporal lobe and the frontal lobe (Oechslin, Imfeld, Loenneker, Meyer and Jancke, 2010a). Fractional anisotropy (FA a standard parameter in DTI analysis that measures the direction-dependent diffusion of water within biological tissue), which is related to the integrity of white matter, showed

leftward asymmetry in AP subjects, consistent with the structural neuroimaging results. However, among AP subjects FA also showed negative correlation with error rates in an AP test, suggesting that integrity of white matter was lower in AP possessors. To account for these results the authors proposed the “pioneering axon theory” which states that development of peripheral white matter (in contrast to core regions of white matter) is influenced considerably by environmental factors, such as musical training, over a long period in post-natal life.

If peripheral white matter development is influenced by environmental factors, then one would expect the volume of white matter in the periphery of the AF to be larger in musicians with more years of training. In a DTI study we compared AP and controls, matched for gender, ethnicity, linguistic background, and age of onset and number of years of musical training, in white matter connectivity in peripheral regions where the AF overlaps with other white matter tracts, specifically between the STG and MTG. These regions of interest that were selected due to their known roles in auditory perception and categorization respectively (Loui, Li, Hohmann and Schlaug, 2011). AP subjects showed higher volume in identified tracts of white matter between the STG and MTG in both hemispheres. Furthermore, the volume of tracts identified STG-to-MTG pathways in the left hemisphere was significantly correlated with mean deviation in semitones, a measure of AP acuity (Bermudez and Zatorre, 2009; Loui et al., 2011). Although tracts in the right hemisphere were larger in the AP group, tract volume in the right hemisphere was not significantly correlated with behavioral measures of AP acuity. Taken together, these results suggest that white matter within the temporal lobe of the left hemisphere reflects group differences between AP and non-AP groups as well as individual differences within the AP group, whereas the right temporal lobe is sensitive to between-group differences (AP vs. non-AP) but not to individual differences within the AP group per se.

The pattern of results for between-group differences, but not within-group differences, was somewhat replicated more recently (Dohn et al., 2013) when regions close to the right STG and MTG were shown to be significantly higher in FA in a whole-brain comparison between AP and non-AP groups. Although the significant regions from that analysis were labeled in the automated diffusion imaging algorithm (tract-based spatial statistics (TBSS); see Smith et al., 2006) as parts of the inferior longitudinal fasciculus and inferior frontal occipital fasciculus, it is likely that the peripheral aspects of the superior longitudinal fasciculus extended into those voxels but were not labeled as such by the automated probabilistic TBSS algorithm.

FUNCTIONAL CONNECTIVITY

One approach to investigating whole-brain connectivity comes from graph theory and small-world network analysis (Bassett and Bullmore, 2006). To introduce the idea of small-world networks, consider your social network: the set of all your acquaintances up to now. These acquaintances may cluster together into your elementary/primary school friends, your high school friends, and your university friends. Occasionally, one of your university friends may know your primary school friend—a phenomenon called “the small-world phenomenon.” The same statistics used to analyze these “small-world networks” are also used

in graph theory to understand how brain regions interact with each other. For instance, the network statistic of “degree” refers to number of connections: intuitively to continue the social network example, a person who is “popular,” that is, who has many friends, has a high number of connections, hence a high degree. The network statistic of “clustering” refers to the proportion of connections that are also connected to each other: intuitively, a person who has high clustering is “cliquish,” that is, has friends who are also friends with each other. Using these graph theory statistics applied to regions of interest across the whole brain, we observed that the AP brain was characterized by higher degrees and higher clustering compared to well-matched controls; furthermore these measures of degree and clustering reflected the acuity of AP: the highest-performing AP subjects had higher degree and clustering than the mostly-accurate AP subjects, both of whom had higher network statistics than the non-AP controls (Loui et al., 2012b). Importantly, these network statistics provide novel support for the thesis of hyperconnectivity in AP: what characterizes this enhanced perceptual categorization ability is enhanced functional as well as structural connectivity.

NEUROPSYCHOLOGICAL EVIDENCE

One question that is often raised concerning AP is whether AP shares characteristics with other special populations, specifically populations with neurological or psychiatric disorders (e.g., autism, Williams syndrome, obsessive-compulsive disorder) or populations with exceptional or enhanced abilities (e.g., synesthesia, exceptional creativity). Lenhoff et al. identified five cases of children with Williams syndrome who also scored at AP levels in pitch categorization testing (Lenhoff et al., 2001). However, this AP processing advantage among children with Williams syndrome was not replicated in a larger sample (Levitin et al., 2004), despite findings of higher emotional engagement with music among Williams syndrome patients compared to controls. Another question concerns whether there is a possible relationship between AP and autism. In two studies, it was shown that persons with autism had enhanced pitch sensitivity, scoring similar to AP levels and potentially with more accurate veridical mapping of acoustic frequency to pitch class categories (Bonnell et al., 2003; Bonnell et al., 2010; Mottron et al., 2013). In a study comparing AP possessors and controls in tests for autism, Dohn, Garza-Villarreal, Heaton, and Vuust (2012) showed that AP possessors tested higher than non-AP controls in some subscales of the autism spectrum quotient (AQ), compared to non-AP possessors and nonmusicians. This may suggest an association between AP and the enhanced perceptual abilities in autism (Bonnell, et al., 2003; Mottron, et al., 2013). However, Dohn et al. (2012) found no differences in social and communication scores on the AQ between AP subjects and the other two groups; thus while AP possessors might have the hypercategorization acuity that resembles some autism traits, they do not share the lack of social and communicative skills that define autism.

Synesthesia is another trait that may share commonalities with AP. Synesthesia is a fusion of the senses whereby the perception of some stimuli automatically trigger concurrent percepts in another modality, for example, in music-color synesthetes, the perception of music triggers concurrent sensations of color. Overlearned sequences such as letters, numbers, and days of the week are relatively common triggers of synesthetic sensations (Eagleman, 2009; Pariyadath, Plitt, Churchill and Eagleman, 2012). As pitch classes are also a form of

ordinal sequential categories that can be overlearned, the view of AP may share properties with synesthesia in that it is a categorization triggered by overlearned sequences. While synesthetic subjects' processing of these overlearned categories was localized to the right MTG, AP subjects appear to recruit more left hemispheric STG and MTG areas during music listening (Loui, Zamm and Schlaug, 2012a), suggesting that AP and synesthesia might be two sides of the same coin: left–right hemispheric analogues of each other. Similarities between neural structure of AP and synesthesia extend toward white matter: a recent DTI study on music–color synesthetes (Zamm, Schlaug, Eagleman and Loui, 2013) showed increased FA in the inferior frontal occipital fasciculus especially in the right hemisphere—a white matter pathway that also showed increased FA in AP subjects from a whole-brain approach (Dohn et al., 2013).

Another piece of evidence from special populations comes from blind musicians and provides a special window into structural and functional neuroplasticity. Blind musicians are more likely to be AP possessors (Gaab, Schulze, Ozdemir and Schlaug, 2006), suggesting that neuroplasticity may kick in for brains that have pressure to rewire extensively throughout life, such as from the lack of sensory input in the visual modality. This pressure to rewire may give rise to changes in the brain, such as in the visual cortex and sensory-integration regions in the parietal lobe, that store and enhance the mental framework that binds pitches to their learned categories.

TYING IT TOGETHER: THE DIATHESIS STRESS MODEL

A holy grail of research in AP has been to unravel the origins of such a unique behavioral phenomenon, using behavioral work, cross-cultural comparisons, and genetic methods coupled with emergent techniques from cognitive neuroscience. Although the nature–nurture debate has been underlying this discussion for many years, few have brought in literature from translational medicine to explain the phenomenon of AP, perhaps because AP is regarded as a blessing rather than a curse: an exceptional ability rather than a neurological or psychiatric disorder. Nevertheless, existing models of thinking about the etiologies of psychiatric disorders may be useful in our conceptualization of the origins of AP. Diathesis stress models (Zuckerman, 1999), first formulated to explain the onset of schizophrenia (Zubin and Spring, 1977), posit that there is some genetic or dispositional vulnerability that predisposes individuals to a disorder, followed by a stressor or life events that bring upon the disorder. Thus there are dual requirements for the disorder to come to pass. While this diathesis stress model is well cited for many psychiatric disorders (Walker and Diforio, 1997), few have specifically addressed the influence of these two routes to development of exceptional abilities such as AP. It is likely that AP is caused by the convergence of the two pathways of influence: disposition (or vulnerability) and exposure (or experience). Dispositionally, the influences could be ethnicity, family history of AP, polymorphisms in genes that may code for hemispheric asymmetry of the temporal lobe or the presence of other factors such as synesthesia. Developmentally, influences are most sensitive within a critical period (or sensitive period) and could include tone language background, musical training, and/or extensive

pressure for the brain to rewire, as in the case of blind musicians, thus bringing upon neural pruning and/or use-dependent cross-activation or cross-wiring in the brain. The two pathways of influence most likely interact at the level of the neuroanatomy and functional differences in specific neural networks such as those for working memory and sound categorization. A combination of at least one predisposition and at least one developmental factor is probably required for the neural determinants of AP.

CONCLUSIONS

Taken together, the best available evidence suggests that AP is an enhanced perceptual phenomenon that enables relatively automatic and working-memory-independent categorization ability. It stems from an interaction between innate and experiential factors, shares some commonalities with other special populations, and is characterized by enhanced neural networks as evidenced by increased gray matter volume, cortical thickness, and white matter connectivity, as well as higher efficiency in small-world functional connectivity. While AP is thought to be a relatively circumscribed trait, future studies are needed to establish the degree to which this unique ability may transfer toward extramusical domains of life.

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