Absolute pitch: a model for understanding the influence of genes and development on neural and cognitive function

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Absolute pitch (AP), the ability to identify or produce the pitch of a sound without any reference point, is discussed here as a possible model system for understanding the neurobiology of complex cognitive functions. AP is of interest because it may reflect an atypical organization of sensory representations. Indications are that it depends on both genetic factors and exposure to musical training during childhood, supporting the idea of a sensitive period. Functional and structural neuroimaging studies suggest special roles for working memory and associative memory mechanisms in AP, and results from these studies indicate that there may be structural markers of AP in asymmetries of cortical areas. AP seems to depend on the nervous system's response to experiential, maturational and genetic factors, making it a good candidate model for understanding how these interactions play out in cognitive development generally.

Why is a fairly obscure phenomenon, known to musicians as 'perfect' or 'absolute' pitch (AP), drawing interest from cognitive neuroscientists and geneticists? There are two reasons: first, it provides an avenue into understanding how specialized abilities are linked to brain function and distributed in the population; and second, AP is one of the cleanest examples of a human cognitive ability that arises from the interaction of genetic factors and environmental input during development. In particular, unlike most other cognitive functions (including language and memory, which are influence by multiple factors and interact with many general brain functions), AP is distributed relatively discretely in the population, and its expression is neatly encapsulated, as it seems unrelated to most other cognitive functions. Moreover, it seems to be closely linked to the timing of environmental exposure to music during childhood. Thus, it could well turn out to be an interesting model system for investigating the general mechanisms of neural development and cognition.

AP basics

To start, how does one test for AP? In its simplest form, it is sufficient to administer appropriately controlled tests that require a listener to identify the name of a musical note in some way (for a quick test of AP ability, go to: www.zlab.mcgill.ca)[1,2]. The key is that people with AP can quickly and effortlessly identify the precise position of a tone in the scale without reference to any other tone (hence the term 'absolute'). Everyone has at least some degree of AP, as it is fairly easy to identify a tone as belonging, say, to the range of a piccolo rather than a bass guitar. In fact, even people with no musical training are surpris-

ingly good at remembering and singing the pitch of a favorite pop tune[3]. A listener with true AP, however, can perform such feats with an order of magnitude better accuracy (**Fig. 1**). That is, whereas most people can identify general ranges of pitch within the audible spectrum, perhaps achieving a total of 6–8 categories[4], AP possessors have much narrower fixed categories, approaching 70 or more[1].

The situation is made a little more complicated by the fact that pitch is generally thought to have two dimensions, height and chroma[5], such that chroma repeats every octave and corresponds to musical scale steps. It may therefore be more appropriate to say that AP represents absolute chroma, especially because musicians with AP make occasional octave errors. In addition to their narrow, fixed pitch-chroma categories, AP possessors have easily retrievable labels for each of these categories, accounting for their ability to quickly call out the name of the musical note they hear, which is the basis for most tests of AP ability.

AP ability is thus a notable exception to the usual cognitive limit on the number of perceptual categories for stimuli that differ in a single dimension along a continuum. Typically, subdivisons along such an axis are restricted by what George Miller[6] called the "span of absolute judgment," which has a limit of 7 (or so) categories. This limit is true for pitch as well as intensity, brightness and weight. It is sometimes suggested that color is like AP because people have relatively fixed color names and don't make relative judgments (nobody needs to compare an apple to a cucumber to determine that the former is red). But this is a false analogy, not only because colors of real objects are multidimensional, but also because color (or 'hue' to be precise) presents the same processing limitations as pitch does for people without AP: given stimuli varying along a single hue dimension, observers can only broadly categorize a limited range of colors and are actually quite poor at accurately labeling specific shades[7]. (Ever try to identify the precise color of your

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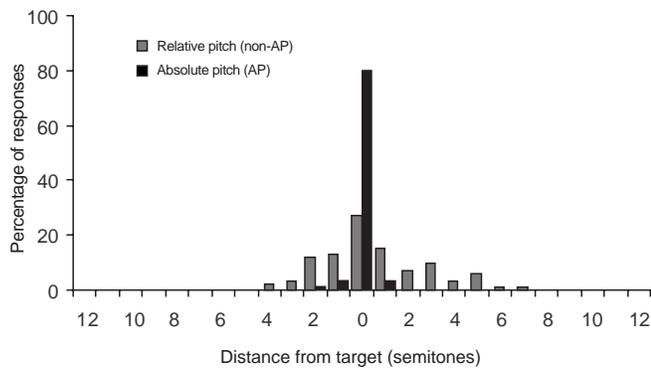
Figure 1 Distributions of pitch-name responses to randomly presented tones, plotted as distance from correct response (*e.g.*, a response of "C-sharp" to the target tone "C" would be a distance of one semitone). Data from a musically trained individual with relative pitch, but without AP (gray bars) and from a possessor of AP (black bars). The mode of the distribution for the non-AP subject is at zero, indicating that more correct note-name responses were given than responses at more distant points, but note that the response distribution of the AP subject has a much smaller variance than that of the non-AP musician, indicating the presence of narrow, precise fixed-pitch categories. Data replotted from ref. 22.

bedroom wall at the paint store?) The fact that absolute identification is much worse than side-by-side discrimination is another consequence of Miller's memory limitation, and is the case for both color and pitch—unless one has the atypical ability for absolute identification.

From cognitive studies, AP can thus be seen to require two separable cognitive components: very narrow fixed pitch categories and the association of these categories with verbal labels. These skills may be considered as a perceptual encoding ability plus a conditional associative memory component (more about the latter below). It is useful to note that the labels need not be verbal: AP may also be demonstrated by several other codes[8], including auditory imagery and sensorimotor responses (*e.g.*, playing a certain tone on a given instrument). Thus, even musicians from an aural tradition, illiterate in musical notation, could still show AP if given the opportunity to reproduce a sounded note by playing it on their instrument.

It has been suggested, though not yet proven, that one can develop (or be born with) the perceptual ability to encode fine pitch categories but never learn the pitch-name associations because of a lack of musical training. Such a person would presumably have a sort-of 'latent' AP. It is certainly possible that such people exist, but few or none of them have apparently ever attempted to learn the associations as adults, for true AP ability seems to depend on early learning.

AP acquisition

So how does one acquire AP? In this case, the famous adage that the way to get to Carnegie Hall is 'practice, practice' does not seem to apply. Clearly, musical training is essential for AP to manifest itself, but most importantly, it must happen early in life[9–11]. Without training before a certain age (the upper limit of which is uncertain, but probably around 9–12 years of age), it is essentially impossible to develop true AP ability. Training can certainly improve performance on AP-like tasks among non-AP listeners, but despite heroic efforts on the part of both musicians and psychoacousticians, there are hardly any well-documented cases in which true AP was successfully learned without early musical training[2].

Early training can only be part of the story, though, for most people who receive musical training from a young age do not develop AP.

Some investigators suggest that the nature of the training is important, pointing to the fact that much musical training involves teaching of *relative* pitch, that is, the relationships between notes rather than the specific pitches used. Thus, when we learn to transpose a tune from one key to another, we are learning about pitch relations and not about the pitches themselves. Moreover, experience with musical instruments may be detrimental to establishing AP if the instrument used is not a fixed-pitch instrument (such as a violin) or if several different instruments are played, as there would be no guarantee that they were all tuned to the same standard. Some have suggested that everyone is born with the capacity to learn AP, but that it is lost in most of us because of these factors. Studies with infants do indicate a capacity for using absolute over relative pitch cues in certain tasks[12], an interesting finding in itself; but there is no evidence that all infants are born with a large number of fixed-pitch categories. Perhaps more people would develop AP if given appropriate training, yet some children show AP despite the experience of hearing out-of-tune pianos and songs sung in many keys, whereas others don't ever develop it, despite training that is intended to emphasize note names. The type of training, therefore, does have some influence[13], but it cannot account for all of the variance in the population. In fact, what is striking about AP is that the ability often develops without explicit tutoring; mere exposure to tones and their labels can be enough. AP possessors regularly report that AP came so naturally for them that they assumed everyone else had it too.

Curiously, some musicians with AP actually have difficulty making relative judgments, apparently because for them the absolute values of the notes are so salient[14]. This suggests that there is a primacy to the absolute representation that can interfere with tasks such as transposition, raising interesting questions about the nature of the training that such people may have received and its interactions with the development of categories. To resolve these questions, we need systematic longitudinal studies in which the type of training is manipulated and its effects on absolute or relative pitch assessed.

Rather than asking what type of training is relevant, a more fundamental question is which neural events are responsible for this fairly fixed developmental time course. Neuroscience abounds with examples of neurodevelopmental processes with sensitive or 'critical' periods during which environmental input is necessary for a skill to emerge. An analogy is often drawn between AP and second-language learning in this respect, but perhaps a better example is ocular dominance columns, as more neuroscientific details are known in this case. Ocular dominance columns refer to the columnar segregation of neurons in visual cortex that respond differentially to one eye or the other. The process by which ocular dominance columns develop is keenly dependent on environmental input during a specific time-window in development, but it is also now clear that ocular dominance columns are present even before any visual experience, presumably guided by molecular mechanisms that are under genetic control[15]. Thus, there may be distinct developmental phases of neural activity associated with genetically driven versus environmentally driven events. Whether or not a similar process occurs in AP is not known, but it seems that the AP phenomenon could be used to understand cognitive function and neural development if we can get a fix on two things: its genetic basis (if any) and its neural substrate.

AP and genetics

At this point, a likely—though yet unproven—candidate to explain the unequal distribution of AP in the population is genetics (see ref. 16 for an early suggestion to this effect). More recently, there have been two findings that point to a genetic component. First, there are significant

associations between siblings who demonstrate AP[17]. Early training is itself familial (sibs of people with early musical training often have such training too), but even when one controls for this environmental factor, there remains a high rate of familial aggregation: the sibling recurrence rate is about 8–15%, which is similar to numbers for much more complex traits thought to have a heritable component, such as schizophrenia (~9% sibling recurrence rate). This observation is compatible with many non-genetic explanations as well, so more direct evidence is needed to confirm these highly suggestive findings. Parenthetically, it is interesting to note that the other side of the musical coin may have a genetic basis. Poor ability to process melodies—termed 'congenital amusia' when it is extreme[18]—shows a higher incidence in identical than fraternal twins[19]. It is therefore not far-fetched to suppose that a genetic factor may be at play with AP as well. Of course, even clear proof of a genetic link would not mean that other factors were unimportant.

The second hint of a genetic factor is that AP may be differentially distributed across different human populations, with persons of Asian descent, for example, having a much greater incidence of AP than those of other backgrounds[13]. One might be tempted to attribute such findings solely to sociocultural variables, were it not for the observation that the higher rate of AP is found across several Asian ethnicities that are distinct from one another culturally (e.g., Chinese, Korean and Japanese). Furthermore, the higher Asian incidence of AP persists even after factoring out as a covariate that Asian children, on average, experience musical exposure at an earlier age than non-Asian children and often receive training that is thought to foster AP. Note that this effect is unrelated to speaking tonal languages, as neither Korean nor Japanese is a tonal language, and the higher incidence has been reported among Asian-Americans who often speak only English. Once again, these data speak to the importance of environmental factors, but even when these are controlled, certain populations seem to show a different distribution of AP skill, and genetic differences may offer one possible explanation.

Genetic influences in AP will be identified in due course, if they exist, using more rigorous methods and larger samples. But what this will contribute to our understanding of the mechanisms of AP depends upon how much we can understand about how genetics may influence specific aspects of neural development. In other words, what are the putative genes coding *for*? In the example of ocular dominance columns, some developmental processes may be under genetic control independent of experience, but ultimately, how the columns are turned into functional units depends upon environmental interactions. In AP, genetic influences may have to do with a neural substrate related to analysis of pitch, or with enabling associations to be made between sounds and their internal representations. We don't know yet, but to find out, we first need a better model of the neural correlates of AP.

Neural correlates of AP

This question has been addressed using both functional and structural imaging approaches. The pattern of brain activity in people with AP shows some interesting differences from that in equally trained musicians who don't have AP. According to early studies using event-related potentials (ERPs), listeners with AP show an absent[20] or reduced[21] electrical scalp component that is thought to index the updating of working memory. In other words, whereas typical listeners show an electrophysiological response to a certain pitch change, indicating that some type of 'on-line' memory system has been refreshed, AP possessors do not show this response. This is presumably because their memory representations consist of fixed, absolute values for each pitch, and
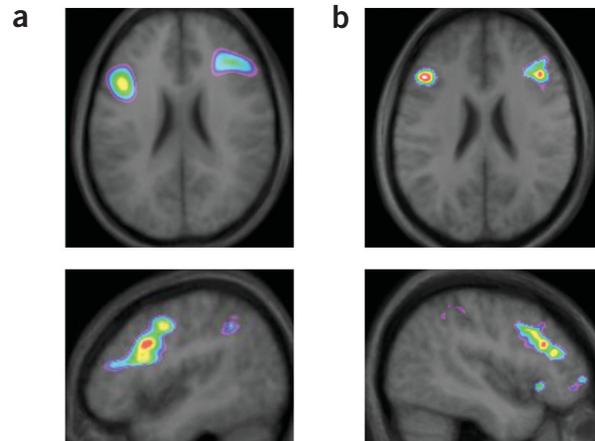

Figure 2 Images from PET and fMRI. (**a**) Horizontal (top) and sagittal left-hemisphere (bottom) views showing sites of cerebral blood flow increases measured with PET in the dorsolateral frontal cortex in AP musicians while they listened to individual tones[22]. (**b**) Comparable views (right hemisphere shown in bottom image) of fMRI activation sites in dorsolateral frontal cortex in a group of non-musicians who were taught to identify chords by making an arbitrary button press (Bermudez, P. and Zatorre, R., *Soc. Neurosci. Abstr.* 673.4, 2002). Note the overall similarity of brain activity patterns, suggesting that processing of associative memory cues makes use of similar neural resources in each case.

thus a pitch representation requires encoding into working memory, but no updating once it's in memory. A related phenomenon has been observed using measures of cerebral blood flow, such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI): an area of the right frontal cortex believed to be important for monitoring pitch information in working memory is more active among musicians lacking AP than in those with AP[22]. Thus, instead of requiring continuous maintenance of a sensory trace, AP possessors apparently use their categorical representation of tones in such tasks.

Conversely, a different area of the frontal lobe, the posterior dorsolateral cortex, responds preferentially in subjects with AP, as compared to control musicians, when they are listening to tones[22]. This area, known to be involved in establishing and maintaining conditional associations in memory[23], is a logical candidate region for the link between a pitch and its label in individuals with AP. The best evidence for this interpretation is that the same area is active in both subjects with AP and those without AP when they are asked to label pairs of tones that form musical intervals such as major or minor, whereas only the AP subjects show such activation when listening to single tones, presumably because only AP subjects can label the latter. Additional support for this explanation is that similar regions of frontal cortex can be recruited, even in non-musicians, once they are taught to identify chords with arbitrary labels (Bermudez, P. and Zatorre, R.J. *Soc. Neurosci. Abstr.* 673.4, 2002) (**Fig. 2**). Thus, it seems that for some reason, the associative function of this part of the frontal lobe is somehow facilitated in people with AP such that they form sound-label associations more readily.

These findings thus help to demystify AP by showing that working-memory and associative-learning aspects of AP draw on neural resources that are reasonably well understood. This still does not explain, however, the component of AP related to fixed-pitch categories. Part of the answer to this issue may lie in the function of subcortical nuclei important for periodicity coding and coincidence detection, such as the inferior colliculus[24], which could provide input based on intrinsic oscillations to auditory cortex in AP subjects.

Progress is now being made in understanding the nature of neural coding of pitch in auditory cortex[25], and it is likely that pitch representation in AP will be explained when we better understand the interactions between subcortical inputs and the cortical processing of spectral and temporal aspects of pitch[26].

The presence of behavioral and physiological differences between people with and without AP leads to the question of whether brain anatomy might also differ. The picture emerging from several studies is that there are indeed significant differences in the degree of lateral asymmetry of structures concerned with auditory processing in the superior temporal cortex. Persons with AP tend to show an exaggeration of the typical leftward asymmetry of this area of the brain, as compared to both musicians without AP and non-musicians[22,27]. The correct interpretation of this effect, however, remains uncertain. Whereas initial indications were that the increased asymmetry might reflect relative enhancement of left-hemisphere auditory cortical structures, the latest evidence suggests instead that it may be a relative reduction in volume of right-hemisphere structures that accounts for the differences[28]. Thus, beyond size itself, there may be more complex interactions between gross morphological features and underlying cortical function. In any case, anatomical differences are important to the extent that they serve as an indication of possible genetic or epigenetic factors; as asymmetries in this part of the brain have been reported to exist even before birth[29], perhaps they are indices of a propensity for developing AP under appropriate environmental conditions. Longitudinal studies are therefore of great interest to unravel this issue.

Future outlook

Ultimately, these various lines of research will have to converge if we are to fully understand AP and its origins. But we can already see avenues that may prove useful: if there are two separable components to AP—fine representation of pitch into fixed categories and ready association between pitches and labels—we can then test the relative susceptibility of each component to environmental and genetic influences. If we know that there are specific patterns of brain activity associated with AP, we can investigate how these arise and whether they are unique to AP. If we know that there are anatomical markers of AP, we can ask how these arise in development, and we can probe how the anatomy translates into function. Although it may appear to be a trivial ability as compared to other cognitive skills, it is precisely because AP is relatively encapsulated and easily measurable that its neural basis may be more amenable to study. Further, because it seems to result from interactions between experiential and maturational factors, as do many complex functions, AP may serve as model for understanding how cognitive functions in general emerge from the interplay of genes, brain structure, brain function, development and environment.

1. Ward, W.D. in *The Psychology of Music* edn. 2 (ed. Deutsch, D.) 265–298 (Academic, San Diego, 1999).
2. Takeuchi, A. & Hulse, S. Absolute pitch. *Psychol. Bull.* **113**, 345–361 (1993).
3. Levitin, D. Absolute memory for musical pitch: evidence from the production of learned melodies. *Percept. Psychophys.* **56**, 414–423 (1994).
4. Pollack, I. The information of elementary auditory displays. *J. Acoust. Soc. Am.* **24**, 745–749 (1952).
5. Krumhansl, C.L. *Cognitive Foundations of Musical Pitch* (Oxford Univ. Press, New York, 1990).
6. Miller, G.A. The magical number seven, plus or minus two: some limits on our capacity for processing information. *Psychol. Rev.* **63**, 81–97 (1956).
7. Bornstein, M.H. in *Categorical Perception: the Groundwork of Cognition* (ed. Harnad, S.) 287–300 (Cambridge Univ. Press, Cambridge, UK, 1987).
8. Zatorre, R.J. & Beckett, C. Multiple coding strategies in the retention of musical tones by possessors of absolute pitch. *Mem. Cognit.* **17**, 582–589 (1989).
9. Miyazaki, K. Musical pitch identification by absolute pitch possessors. *Percept. Psychophys.* **44**, 501–512 (1988).
10. Sergeant, D. Experimental investigation of absolute pitch. *J. Res. Mus. Ed.* **17**, 135–143 (1969).
11. Baharloo, S., Johnston, P., Service, S., Gitschier, J. & Freimer, N. Absolute pitch: an approach for identification of genetic and nongenetic components. *Am. J. Hum. Genet.* **62**, 224–231 (1998).
12. Saffran, J.R. & Griepentrog, G.J. Absolute pitch in infant auditory learning: evidence for developmental reorganization. *Dev. Psychol.* **37**, 74–85 (2001).
13. Gregersen, P., Kowalsky, E., Kohn, N. & Marvin, E. Early childhood music education and predisposition to absolute pitch: teasing apart genes and environment. *Am. J. Med. Genet.* **98**, 280–282 (2000).
14. Miyazaki, K. & Rakowski, A. Recognition of notated melodies by possessors and non-possessors of perfect pitch. *Percept. Psychophys.* **64**, 1337–1345 (2002).
15. Katz, L. & Crowley, J.C. Development of cortical circuits: lessons from ocular dominance columns. *Nat. Rev. Neurosci.* **3**, 34–42 (2002).
16. Bachem, A. Various types of absolute pitch. *J. Acoust. Soc. Am.* **9**, 146–151 (1937).
17. Baharloo, S., Service, S., Risch, N., Gitschier, J. & Freimer, N. Familial aggregation of absolute pitch. *Am. J. Hum. Genet.* **67**, 755–758 (2000).
18. Peretz, I. *et al.* Congenital amusia: a disorder of fine-grained pitch discrimination. *Neuron* **33**, 185–191 (2002).
19. Drayna, D., Manichaikul, A., de Lange, M., Snieder, H. & Spector, T. Genetic correlates of musical pitch recognition in humans. *Science* **291**, 1969–1972 (2001).
20. Klein, M., Coles, M. & Donchin, E. People with absolute pitch process tones without producing a P300. *Science* **223**, 1306–1308 (1984).
21. Wayman, J., Frisina, R. & Walton, J. Effects of musical training and absolute pitch ability on event-related activity in response to sine tones. *J. Acoust. Soc. Am.* **91**, 3527–3531 (1992).
22. Zatorre, R.J., Perry, D.W., Beckett, C.A., Westbury, C.F. & Evans, A.C. Functional anatomy of musical processing in listeners with absolute pitch and relative pitch. *Proc. Natl. Acad. Sci. USA* **95**, 3172–3177 (1998).
23. Petrides, M. Functional organization of the human frontal cortex for mnemonic processing: evidence from neuroimaging studies. *Ann. NY Acad. Sci.* **769**, 85–96 (1995).
24. Langner, G., Albert, M. & Briede, T. Temporal and spatial coding of periodicity information in the inferior colliculus of awake chinchilla (*Chinchilla laniger*). *Hearing Res.* **168**, 110–130 (2002).
25. Lu, T., Liang, L. & Wang, X. Temporal and rate representations of time-varying signals in the auditory cortex of awake primates. *Nat. Neurosci.* **4**, 1131–1138 (2001).
26. Zatorre, R.J., Belin, P. & Penhune, V.B. Structure and function of auditory cortex: music and speech. *Trends Cogn. Sci.* **6**, 37–46 (2002).
27. Schlaug, G., Jäncke, L., Huang, Y. & Steinmetz, H. *In-vivo* evidence of structural brain asymmetry in musicians. *Science* **267**, 699–701 (1995).
28. Keenan, J., Thangaraj, V., Halpern, A. & Schlaug, G. Absolute pitch and planum temporale. *Neuroimage* **14**, 1402–1408 (2001).
29. Witelson, S. & Pallie, W. Left hemisphere specialization for language in the newborn: neuroanatomical evidence of asymmetry. *Brain* **96**, 641–646 (1973).