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REVIEW ARTICLE

Absolute Pitch: Interplay of Genetics, Brain Structure, and Early Experience

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ABSTRACT: Absolute pitch (AP) is the rare ability to identify or produce musical notes without an external reference. The origins of AP remain debated. In this review, we integrate evidence across genetics, brain structure and function, and early experience. Work in vocal-learning animals and human genetics points to gene networks, including FoxP2 and downstream partners, that shape the cortico-striatal circuits required for precise auditory–motor mapping. Structural and functional imaging in humans shows differences in the planum temporale and adjacent auditory cortex in individuals with AP, often with stronger leftward asymmetry and altered microstructure, consistent with early-tuned category representations for pitch. Behavioral and developmental studies in humans indicate that early music training and exposure to tonal languages increase the likelihood and stability of AP, in line with a sensitive-period account and with learning-by-labelling mechanisms. Taken together, AP most likely arises from the interaction between biological predisposition and structured early input. Genetic programmes establish circuits with high resolution for pitch, and early labelling experiences consolidate these circuits into a durable skill. We outline key gaps, including causal links in humans, cross-species generalisation, and measurement heterogeneity, and propose longitudinal and interventional designs to resolve mechanisms and to test gene-environment models.

KEYWORDS: Neuroscience, Cognitive Neuroscience, Absolute Pitch, Auditory Perception, *FoxP2* Gene.

Introduction

Absolute pitch (AP) is a striking yet uncommon human ability. Some individuals can identify or produce a musical note with no external reference, an ability that continues to intrigue neuroscience and cognitive science. Its rarity, its apparent effortlessness in expert listeners, and its tight link between perception make AP a natural target for theories of auditory cognition.[1,2] Operationally, AP refers to assigning stable pitch-class labels or producing the corresponding tones without a reference. This differs from relative pitch, which estimates intervals from a heard standard and relies on short-term memory and comparison. The labelling component is central: AP requires mapping continuous frequency input onto discrete categories that remain stable across timbre and register.[3]

AP also serves as a framework for probing how biology and experience interact across development. Evidence from early musical training and tone-language exposure supports the idea of sensitive periods during which pitch categories are more easily acquired. In parallel, neuroimaging and intervention studies show that training reshapes plasticity.[4,5] Despite decades of work, a core controversy remains: Is absolute pitch largely a genetic predisposition, or is it a skill learned through early environmental exposure? Converging lines of evidence include familial aggregation and genetic hints, on the one hand, and large prevalence differences tied to tone-language background and age of onset of musical training, on the other.[6,7] This review weighs these strands to clarify how far each account can go and where they intersect.

Discussion

FoxP2 in Songbirds: The Zebra Finch:

When investigating complex biological processes such as vocal learning, researchers often turn to animal models that share similar auditory systems with humans. The zebra finch is an excellent example, serving as a powerful model organism for studying the genetics, neurobiology, and behavior of vocal communication. Such research has shown stark similarities between the songbird and human brain, particularly in the functionality of Area X in the zebra finch and the striatum in the human brain. Both structures serve an important role in the auditory system (Figure 1). Furthermore, the Pallium area (green) appears on the peripheral part of the brain in both organisms. Due to this homology, the zebra finch provides an accurate model that reflects certain functions of the human brain and can therefore be a favoured subject for study.

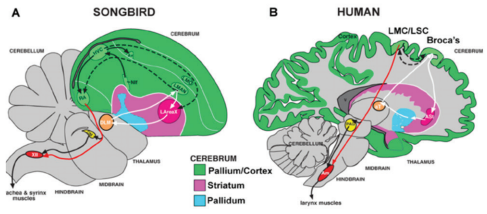

Figure 1: Auditory Pathways in Humans and Zebra Finches. This figure compares the auditory pathways of humans and zebra finches, illustrating key similarities in the organization of their vocal and auditory circuits. Panel A: zebra finch male brain section displaying connectivity of anterior (LMAN, area X) and posterior (HVC, RA) song pathways. Panel B: human brain section showing vocal pathway connectivity including the LMC/LSC and part of the anterior striatum (ASt) that shows convergence with songbird RA and area X. Black arrows, connections and regions of the posterior vocal motor pathway; white arrows, connections and regions of the anterior vocal pathway; dashed arrows, connections between the two pathways.[8]

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Songbirds are heavily dependent upon accurately processing and imitating different sound patterns. Starting from a very young age, zebra finches are required to copy their tutor's songs. Figure 2 shows the auditory pathway of the Zebra Finch. Solid black lines show the pathway necessary for the production of sound and melody. Some crucial regions in the zebra finch's auditory pathway include Area X, the thalamus, and the Lateral Magnocellular Nucleus of the Anterior Nidopallium (LMAN). These areas form part of the anterior forebrain pathway, which is essential for pitch processing.

FoxP2, a highly conserved transcription factor, is essential for establishing the neural circuits that support human speech and language. Mutations in this gene have been linked to verbal dyspraxia, a condition characterized by difficulties in articulating and sequencing speech sounds. This highlights its key role in motor control and vocal learning. Its close paralogue, *FoxP1*, works alongside *FoxP2* to modulate shared gene networks that drive neuronal differentiation and synaptic development. Operating together, these genes help model the cortico-striatal pathways required for precise auditory–motor integration. Songbirds, which rely on comparable vocal learning mechanisms, therefore, offer an excellent model for insights into the evolutionary and functional significance of *FoxP2* in vocal behavior.

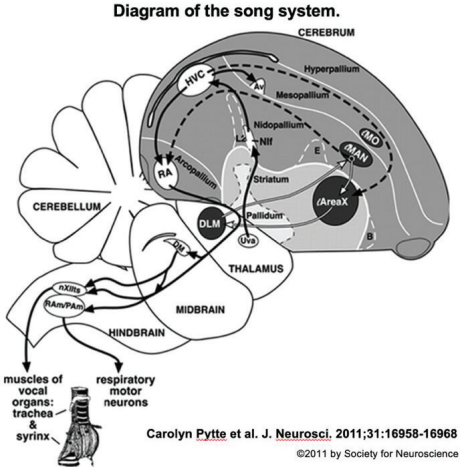


Figure 2: Auditory Pathway of Zebra Finch. Auditory pathway of Zebra Finches, Solid black lines show the pathway necessary for the production of song. Dashed and white lines together show the anterior forebrain pathway necessary for song learning and adult song maintenance.[9]

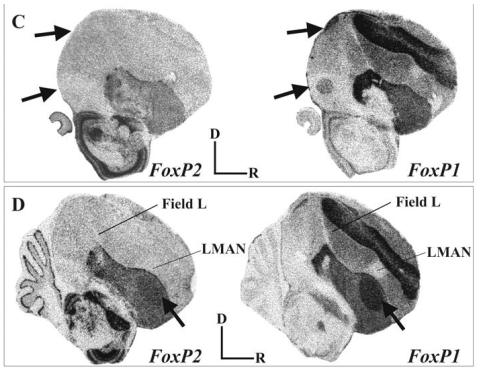


Figure 3: Expression of *FoxP2* and *FoxP1* mRNA in the Adult Zebra Finch Brain. Brightright-field photomicrographs which show *in situ* hybridization (ISH) results for *FoxP2* (left) and *FoxP1* (right) mRNA in adult male zebra finch sagittal section sections. [10]

Figure 3 displays bright-field photomicrographs that show situ hybridization (ISH) results for *FoxP2* (left) and *FoxP1* (right) mRNA in adult male zebra finch brain sections. Panels A and B highlight *FoxP2* expression in Area X, the Thalamus, and the cerebellum, confirming that *FoxP2* is active in brain regions that contribute to auditory processing. In contrast, *FoxP2* was not strongly expressed in LMAN or the Mesopallium, suggesting a more targeted role for *FoxP2* in Zebra Finches' auditory system.

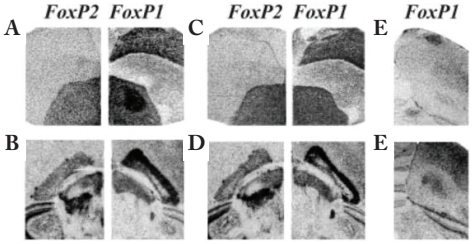
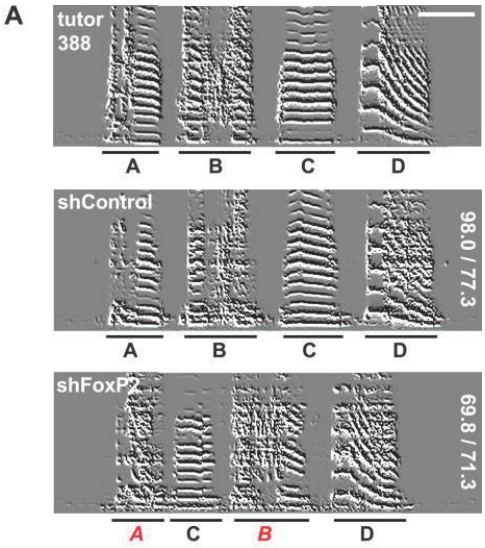


Figure 4: Sexually Dimorphic Expression of *FoxP1* and *FoxP2* in Zebra Finches In 35–day –old male birds (A, B, E) distinct expression patterns of *FoxP1* and *FoxP2* are already present, with *FoxP1* showing higher expression in the song nucleus area X (A) and in HVC (E). In contrast, images from 35–day –old females (C, D, F) highlight the sexually dimorphic expression of *FoxP1* , while *FoxP2* does not display such differences. Notably, females do not show the elevated *FoxP1* expression in the striatum where area X is found in males (compare A and C, right).[11]

Figure 4 compares the presence of *FoxP2* and *FoxP1* in male (A, B, E) and female (C, D, F) brains. In zebra finches, only males sing and have specialized brain regions like Area X. Clearly, there is no significant difference in *FoxP2* expression between juvenile males and females, suggesting that *FoxP2*'s roles extend beyond song production alone and that its presence impacts other aspects of the zebra finch's auditory system. In contrast, *FoxP1* shows a much larger difference in expression between the sexes, supporting its sexually dimorphic nature and its link to male-specific functions and vocal learning.



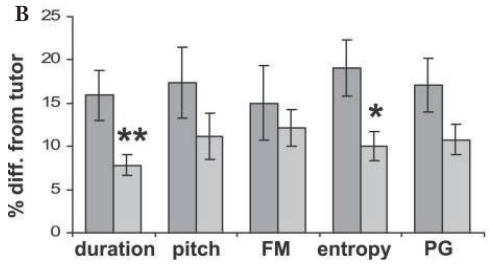


Figure 5: Result of *FoxP2* Knockdown on Results showing comparisons of syllable imitation in knockdown and control pupils. (A) Representative sonograms of *FoxP2* knockdown and control pupils, both tutored by male 388 (scale bars indicate 100 ms, frequency range 0–8,600 Hz). Syllables are marked with black underlines and l. The identity of pupil syllables was assessed by comparing them to tutor syllables using SAP software. Red italics indicate syllables that were copied inaccurately. Imprecise imitation is obvious in syllable A and syllable B. Similarity and accuracy scores are shown along the right edge of the sonograms. (B) Comparison of syllable duration and mean acoustic features (FM and PG) between pupil syllables and their tutor counterparts. The *FoxP2* knockdown pupils (dark grey bars) showed greater divergence from the tutor model across all acoustic measures than the controls (light grey bars). For both average syllable duration and mean entropy, the differences were statistically significant (±SEM; two-tailed Mann-Whitney U test, $^{**}p < 0.001$ for duration and $^{*}p < 0.05$ for entropy; Bonferroni-corrected α-level; shFoxP2 n = 7 animals, ~3 syllables per animal; shControl n = 7 animals, ~4 syllables per animal).[12]

Figure 5 shows the results of an experiment in which the *FoxP2* gene was knocked down in a group of juvenile zebra finches. Both the control group, in which *FoxP2* expression remained intact, and the knockdown birds were all tasked with imitating the vocalizations of an adult tutor. Overall, Zebra Finches with intact *FoxP2* expression produced songs that closely matched the tutor's model across multiple acoustic features. Panel A presents sonograms of syllables produced by both groups. Birds with *FoxP2* knockdown exhibited notable inaccuracies in reproducing syllables, especially A and B, where deviations in pitch and temporal structure compared with the tutor's original pattern are present. In contrast, the control group exhibited greater accuracy and closer resemblance to the tutor's song, highlighting the critical role of *FoxP2* expression in supporting precise vocal imitation and auditory feedback in zebra finches. Panel B quantifies the acoustic differences between the control group (light grey) and the *FoxP2* knockdown group (dark grey). Across key parameters - song duration, entropy, and pitch goodness (PG) - birds with reduced *FoxP2* expression displayed a markedly greater deviation from their tutor's model. The difference in pitch was less pronounced, yet remained detectable, indicating that *FoxP2* influences multiple layers of vocal precision.

These findings underscore *FoxP2*'s central role in enabling zebra finches to produce stable, well-controlled vocalizations through accurate auditory feedback. This stability reflects the ability to map continuous acoustic input onto reproducible motor patterns - a process that mirrors human regulation of speech and pitch. Given the noted homology between the zebra finch auditory pathway and that of humans, *FoxP2* likely serves a similar function in maintaining vocal accuracy in humans. Further, its contribution to pitch regulation suggests a potential link between *FoxP2* activity and auditory abilities, including the precision required for phenomena such as absolute pitch.

Figure 6: Sequence Alignment of Zebra Finch *FoxP2* with other Mammals. The deduced amino acid sequence of zebra finch *FoxP2* cDNA (GenBank accession AY395709) was aligned with three mammalian sequences (human: AF337817, chimpanzee: AF512947, mouse: AF339106). In one region, two residues in the human sequence (N303 and S325) differ from other primates,[13] with the putative zinc finger domain marked by a dotted underscore. Within this domain, the zebra finch shows a conservative change of valine replacing isoleucine at position 350 (I350V, arrow). Four additional substitutions unique to the zebra finch (S42T, S78G, S229N, A243S; data not shown) are located outside currently identified protein domains. Another region includes the Fox domain (solid underscore), which is identical across finch, human, and chimpanzee. An invariant arginine at position 553 in humans, indicated by an asterisk, is notable because mutation of this residue to histidine is linked to a rare speech and language disorder [14,15]

There are still limitations to generalizing results across species due to genetic and anatomical differences. Figure 6 highlights sections of the *FoxP2* amino acid sequence across multiple species. Panel A focuses on a region within the putative zinc finger domain (dotted underscore), revealing subtle but notable differences between zebra finches and humans. In particular, a conservative substitution of valine for isoleucine at position 350 (arrow; I350V) is observed.

While the role of *FoxP2* is well characterised in zebra finches — where altered expression levels clearly disrupt song acquisition and motor sequencing (Figures 2–5) — greater elaboration is needed on the genetic and phenotypic distinctions between humans and other animal models. In humans, *FoxP2* is implicated broadly in speech and language development; however, despite the sequence homology referenced in Figure 6, there is currently no direct evidence that *FoxP2* significantly alters absolute pitch (AP) ability or associated brain morphology. Hence, while song learning in zebra finches provides a valuable model for studying vocal learning circuitry, it does not necessarily translate directly to human absolute pitch perception, which involves fine-grained auditory discrimination rather than vocal imitation alone.

FoxP2 in humans: roles and functions:

Building on insights from *FoxP2* expression and its role in zebra finches, we can examine its role in the human brain, where its functions may help explain structural differences such as the planum temporale observed between musicians with absolute pitch and those without.

FoxP2 is a transcription factor that binds to DNA and regulates the expression of other genes without altering the DNA sequence itself. Among the genes influenced by *FoxP2* are *MET* proto-oncogene receptor tyrosine kinase (*MET*), very low-density lipoprotein receptor (*VLDLR*), and sushi-re-

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peat-containing protein X-linked 2 (SRPX2), all of which are involved in neuronal migration and synapse formation.

MET is expressed in the neocortex during periods of peak dendritic outgrowth and synaptogenesis. It plays roles in dendritic morphogenesis, modulation of spine volume, and excitatory synapse development.[16] Further, *MET*, the tyrosine kinase receptor encoded by the cellular proto-oncogene, and its ligand, hepatocyte growth factor (HGF), are expressed in the nervous system from prenatal development to adult life, where they are involved in neuronal growth and survival.[17] However, *VLDLR* is one of the two main receptors in Reelin, and the major role of *VLDLR* is to suppress neuronal invasion into the marginal zone (MZ) during neocortical development.[18,19] Finally, *SRPX2* plays a critical role in the development and maintenance of neural circuits in the brain, where it functions as a neuronal complement inhibitor, binding to C1q to prevent excessive microglial-mediated synapse elimination, which is essential for proper synaptic connectivity in regions such as the thalamus and the somatosensory cortex.[20] Variants of the *SRPX2* gene have also been linked to neurodevelopmental disorders affecting the Rolandic and Sylvian speech areas, highlighting its importance in cortical development and language-related brain regions.[21] Further, *SRPX2* has been shown to regulate synapse formation in the developing brain and influence vocalization in mice, highlighting its critical role in neural circuit formation relevant to language development.[22] While these genes are not limited to defining the structure of neuropathways in the brain, their abilities to do so provide insight into the existing structural discrepancies observed between absolute pitch musicians and non–absolute pitch individuals. Similarly, since *FoxP2* acts as the modulator or regulatory centre for its downstream genes, its relationship with brain anatomy may also be commented upon.

That said, several independent genes unrelated to *FoxP2* also contribute to neuronal development and cortical organization. For instance, *BDNF* supports synaptic plasticity and dendritic growth, *RELN* regulates neuronal migration, and *CNTNAP2* has been associated with language-related neural connectivity. Hence, while *FoxP2* does contribute to certain aspects of neuronal development, brain development is influenced by a range of different genes, meaning that the link between *FoxP2* and brain structure is present but not absolute.

The Planum Temporale:

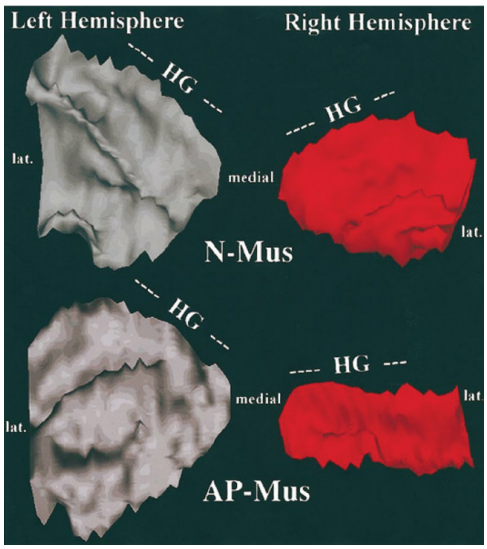

Figure 7: Comparison of Planum Temporale between Non-Musician and AP Musician. Surface reconstructions of the left and right planum temporale are shown for a non-musician and a musician with absolute pitch. The approximate location of the transverse gyrus of Heschl (HG) is marked on each PT reconstruction. Notice the substantial difference in the size of the right PT between the two individuals.[23]

The planum temporale (PT) is a region of the temporal plane that plays an important role in auditory processing and language-related functions. Traditionally, it has been associated with language comprehension, particularly in the left hemisphere, often showing structural asymmetry in most humans. However, recent studies suggest that the PT is not limited to language processing but is also engaged in more basic auditory discriminations, such as distinguishing pitch. In fact, the left PT responds robustly not only to speech but also to tonal stimuli, indicating its broader involvement in acoustic analysis rather than being exclusively language-specific.[24] Structural asymmetry of the PT has also been linked to differences in auditory and musical abilities, including absolute pitch and enhanced pitch discrimination, suggesting that its morphology and function contribute to the precision of auditory perception in individuals.[23,25] Figure 7 illustrates this difference in asymmetry between non-musicians and musicians with absolute pitch, showing a noticeably larger difference between the left and right PT in AP musicians.

Researchers investigated the structure of the planum temporale in absolute pitch musicians using magnetic resonance imaging (MRI). They compared three groups: musicians with absolute pitch, musicians without absolute pitch, and non-musicians.

Absolute pitch ability was confirmed through pitch-naming tests, and surface area measurements of the planum temporale were obtained from the MRI scans. Their results showed that absolute pitch musicians displayed a stronger leftward asymmetry of the planum temporale compared to both control groups. This difference was mainly due to a smaller right planum temporale rather than a larger left side. Since both musical groups began training before the age of seven, the study concluded that early musical training alone does not account

for the structural difference. Instead, the findings suggest that biological factors, possibly established before birth, contribute to the unique brain structure of absolute pitch musicians.[23]

While *FoxP2*'s role in synaptic migration and regulation is well established, numerous other factors - both genetic and environmental - also contribute to these processes within the human neuronal pathway. Further, structural differences observed in musicians may also arise from polygenic influences, experience-dependent neuroplasticity, or gene–environment interactions. What is more, because the study examined the brains of individuals who already possessed absolute pitch, it cannot definitively determine whether the observed structural differences were present from birth. Instead, these anatomical variations could also reflect the long-term effects of musical training on brain structure. Consequently, although *FoxP2* may partially account for the anatomical differences observed, it is unlikely to provide a complete explanation.

Language Influence: Environmental Implications:

Apart from genetic factors, one of the main proposals for the acquisition of absolute pitch links closely to environmental exposure, specifically the exposure to tonal languages, where evidence suggests that AP is more commonly found in East-Asian, rather than Western populations.[26,27]

A more precise definition is useful here. Absolute pitch is not limited to the accurate perception of pitch height. It involves the ability to identify or reproduce a specific pitch and correctly link it with its corresponding categorical label (*e.g.*, identifying a tone as "A♭" or "C♯"). Hence, even if one theoretically does have absolute pitch at birth, they still won't be able to demonstrate this ability without first learning the relevant symbolic system for naming notes. This process of attaching labels to pitch links closely to auditory memory and is very unlikely to be developed innately. Consequently, it is reasonable to suspect a connection between the environment and the development of absolute pitch. Therefore, the higher prevalence of absolute pitch among tonal language speakers can be explained. In tonal languages, even a slight change in pitch can significantly alter the meaning of a word. As a result, individuals exposed to tonal languages from an early age learn to distinguish between subtle pitch variations. Over time, this continuous practice and exposure enhance their sensitivity to pitch changes. This idea is supported by experimental evidence showing that individuals who speak tonal languages demonstrate greater accuracy and faster responses when detecting small pitch shifts compared to non-tonal speakers.

Early experience with a tone language has been shown to improve pitch discrimination.[28] Two groups were tested in a soundproof room while wearing earphones, while their brain activity was recorded using electroencephalography (EEG). In each trial, participants first heard a standard note (C5) and, after 500 ms of silence, a second tone was played, which was either the same or different. Participants then judged whether the second note matched the first. While similar experiments have been conducted, those typically used large pitch shifts of up to 800 cents (100 cents equal 1 semitone), which are much easier to detect. This experiment instead used smaller pitch shifts, providing a more precise measure of pitch sensitivity.

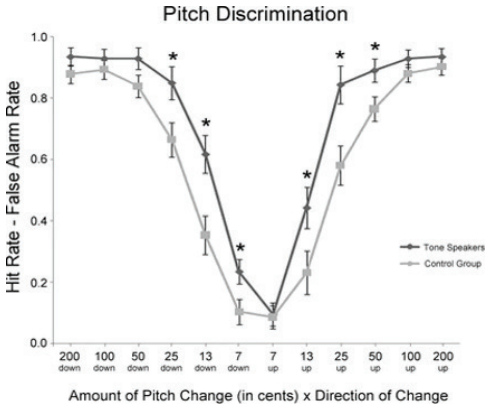

Figure 8: Behavior performance between tonal and non-tonal groups. Behavioral performance (Hit rate – False Alarm rate) for the two groups on the pitch discrimination task. The X-axis represents both the direction and the magnitude of the pitch shift. Significant differences in performance between tonal and non-tonal speakers are indicated with stars. Note that 100 cents equal 1 semitone (e.g., A to A#).[29]

Figure 8 shows the comparison between Mandarin speakers and English speakers (control), specifically those without musical training. Mandarin speakers are exposed to their language for their entire life, whereas English speakers have never been exposed to tonal languages. A clear difference in performance was observed, with tonal speakers outperforming the control group in several conditions, especially when the pitch was shifted 25 cents upwards. Both groups generally performed better at detecting downward pitch changes than upward ones. At larger pitch shifts, the control group's performance was similar to that of the tonal speakers. However, tonal speakers were significantly more accurate at detecting smaller pitch shifts, highlighting their enhanced sensitivity to minor changes in tone.

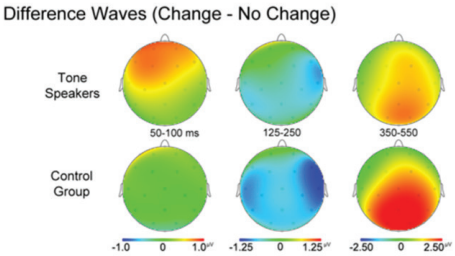

Figure 9: Topographical EEG Maps Across Groups. Topographical maps showing difference waves (change minus no-change trials) in EEG activity for tonal language speakers and a control group across three-time windows. Colours indicate amplitude differences in microvolts (μV), with warmer colours representing more positive differences and cooler colours representing more negative differences.[30]

Figure 9 presents the EEG results capturing participants' brain wave activity throughout the experiment. The first column (50–100 milliseconds) represents early sensory processing, the second column (125–250 ms) represents mid-latency processing, and the third column (350–550 ms) corresponds to later cognitive processing. During the 50–100 ms window, participants in the tonal language group exhibited pronounced brain activity (red and orange), whereas the con-

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trol group showed minimal response (green). In the 125–250 ms timeframe, both groups demonstrated relatively negative differences in brain activity; however, participants with tonal language experience displayed a smaller magnitude of negative feedback, suggesting more efficient processing of tonal stimuli. Finally, the non-tonal group displayed greater positive feedback in the last time frame, indicating a delayed but strong reaction to pitch shifts.

Not only do individuals exposed to tonal languages demonstrate higher accuracy in pitch discrimination, but they also respond more quickly to pitch changes, supporting the connection between speaking a tonal language and enhanced pitch perception—a characteristic feature of musicians with absolute pitch.

Conclusion

In summary, the current evidence provided suggests a mix of both environmental and genetic factors that allow an individual to develop absolute pitch. *FoxP2* plays an important role in the human auditory system, with slight mutations causing significant auditory and speech disorders. Similarly, experiments involving songbirds also display the importance of the *FoxP2* gene in certain species' auditory pathway and feedback. Specifically, its knockdown in young Zebra Finches results in distinct inaccuracies in the imitation of songs and syllables. Due to the homology between the auditory pathway of Zebra Finches and humans, it is reasonable to infer that a similar relationship exists between *FoxP2* and humans' ability to accurately copy and produce sounds, traits that are characteristic of absolute pitch. However, Sequencing of the *FoxP2* gene in zebra finches has revealed small but distinct differences compared to the human *FoxP2* sequence, including a conservative amino acid substitution involving valine. Although such conservative substitutions typically have minimal effects on protein structure or function, these sequence variations suggest that *FoxP2* may have evolved species-specific roles related to vocal communication and learning. To further corroborate the current findings, studies involving different species as subjects could be conducted. In addition, parallel experiments involving human participants would provide critical translational insight, allowing researchers to assess whether the patterns observed in zebra finches generalize to human vocal learning and auditory-motor integration.

Examination of *FoxP2*'s specific functions has also established a possible relationship between this gene and absolute pitch. *FoxP2* is a transcription factor that regulates the expression of other genes, such as *MET*, *SRPX2*, and *VLDLR*, which subsequently regulate the development of neurons, dendrites, and other brain structures, highlighting the link between *FoxP2* and brain structure development. This may partly account for observations that structural differences in the dorsal pallium exist between absolute pitch musicians and non-musicians. Absolute pitch musicians demonstrate a much greater asymmetry between their two dorsal pallia compared to non-musicians. As *FoxP2* contributes to structural growth and development in the brain, it may also play a crucial role in shaping this asymmetry. It is noted that this does not fully support the link between *FoxP2* and absolute pitch, as many other genes and/or environmental factors could also shape the anatomy of the human brain. A further approach to validate the relationship between *FoxP2* and structural variation in the brain is to assess the expression of *FoxP2* within the dorsal pallium, alongside the expression of genes it regulates, including *MET*, *VLDLR*, and *SRPX2*. These genes play key roles in neuronal migration and synapse formation, and their activation in the planum temporale would explain how coordinated genetic regulation shapes the anatomical distinctions observed between musicians with absolute pitch and those without.

Finally, environmental factors are considered, specifically the effect of native experience with tonal languages on pitch detection accuracy. Comparisons between tonal and non-tonal language speakers show significant differences in hit rate and reaction time. On average, tonal speakers identify pitch shifts with greater accuracy and speed than non-tonal speakers. EEG scans further reveal increased speed and strength of brain activity in tonal speakers, while non-tonal speakers display slower but still strong responses to pitch changes. Regardless of potential genetic influences, the evidence suggests that prolonged experience with tonal languages enhances the ability to detect pitch changes both precisely and efficiently.

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