Musical imagery

Sound of silence activates auditory cortex

Auditory imagery occurs when one mentally rehearses telephone numbers or has a song 'on the brain' — it is the subjective experience of hearing in the absence of auditory stimulation, and is useful for investigating aspects of human cognition[1]. Here we use functional magnetic resonance imaging to identify and characterize the neural substrates that support unprompted auditory imagery and find that auditory and visual imagery seem to obey similar basic neural principles.

The few studies that have examined the topic of auditory imagery[2–5] have focused on the neural substrates of directed imagery (for example, "imagine a tone"). What is not known, however, is whether similar principles guide the more pervasive and spontaneous forms of imagery that punctuate everyday life. We used functional magnetic resonance imaging to investigate the recruitment of auditory cortex during spontaneous auditory imagery of excerpts of popular music.

During scanning, subjects passively listened to excerpts of songs with lyrics (for example, *Satisfaction* by the Rolling Stones) and to instrumentals that contained no lyrics (for example, the theme from *The Pink Panther*). Each piece of music was pre-rated by subjects as either familiar or unknown, and a unique soundtrack was created for each individual. Short sections of music (lasting for 2–5 s) were extracted at different points during the soundtrack and replaced with silent gaps. We then monitored the neural activity in subjects that occurred during these gaps. (For details of methods, see supplementary information.)

Brain activity in the primary auditory cortex and in the auditory association cortex (Brodmann's area 22) (Fig. 1a) was compared during gaps of silence in familiar and unknown songs. The results revealed a functional dissociation within the left auditory cortex (region × music-type interaction: $F[1,14] = 48.92$, $P < 0.0001$; Fig. 1b). Silent gaps embedded in familiar songs induced greater activation in auditory association areas than did silent gaps embedded in unknown songs (Fig. 1b); this was true for gaps in songs with lyrics ($F[1,14] = 5.46$, $P < 0.05$; Fig. 1c) and without lyrics ($F[1,14] = 11.56$, $P < 0.005$; Fig. 1d). Moreover, when familiar songs contained no lyrics, cortical activity extended into the left primary auditory cortex ($F[1,14] = 22.55$, $P < 0.0005$; Fig. 1d).

We confirmed that these effects were uniquely attributable to the gaps of silence in the music, rather than simply the result of differences in activation in response to hearing different music categories. By contrast with the gap responses, listening to unknown songs produced greater activity in auditory association areas than did familiar songs (lyrics: $F[1,14] = 11.24$, $P < 0.005$; instrumentals: $F[1,14] = 31.74$, $P < 0.0001$), and activity in the primary auditory cortex did not differ as a function of familiarity (see supplementary information).

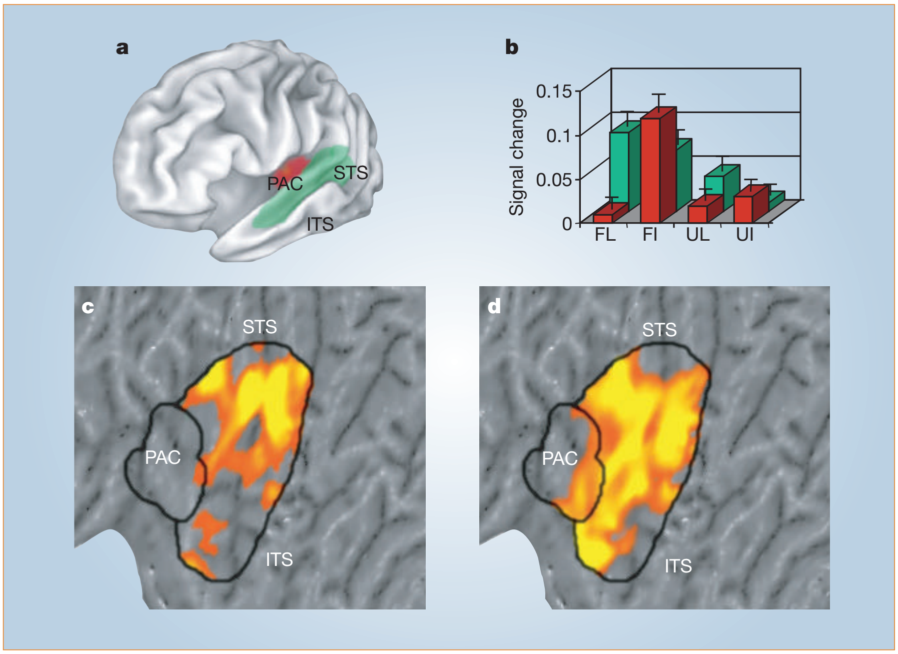

Figure 1 Auditory cortex activation during silent gaps in music. **a,** An inflated rendering of the left hemisphere[9] illustrates primary auditory cortex (PAC; red) and auditory association cortex, also known as Brodmann's area 22 (green). The superior temporal sulcus (STS) and inferior temporal sulcus (ITS) are indicated for reference. **b,** Signal change (arbitrary units) in PAC (red) and Brodmann's area 22 (green) during gaps in familiar songs with lyrics (FL), familiar instrumentals (FI), unknown songs with lyrics (UL) and unknown instrumentals (UI). Error bars denote s.e.m. **c, d,** Difference in activity, which is greater for familiar songs, during silent gaps embedded in songs with (**c**) and without (**d**) lyrics, projected on to flattened views of the left temporal lobe. Dark-grey regions represent sulci; lighter grey regions denote gyri.

Our findings offer a neural basis for the spontaneous and sometimes vexing experience of hearing a familiar melody in one's head. Whereas previous investigations have explicitly directed subjects to imagine a specific auditory experience[2–4], we provided no instruction. Instead, simply muting short gaps of familiar music was sufficient to trigger auditory imagery — a finding that indicates the obligatory nature of this phenomenon. Corroborating this observation, all subjects reported subjectively hearing a continuation of the familiar songs, but not of the unfamiliar songs, during the gaps in the music.

We note also that the extent of neural activity in the primary auditory cortex was determined by the linguistic features of the imagined experience. When semantic knowledge (that is, lyrics) could be used to generate the missing information, reconstruction terminated in auditory association areas. When this meaning-based route to reconstruction was unavailable (as in instrumentals), activity extended to lower-level regions of the auditory cortex, most notably the primary auditory cortex (Fig. 1b, d).

These findings parallel those in the domain of visual imagery. For example, visual imagery elicited when considering names of objects (known as figural imagery) does not rely on the primary visual cortex[6,7]. As these 'low-resolution' images do not demand fine-grained perceptual processing, activity in visual-association areas is sufficient to reconstruct the relevant representation. By contrast, when semantic information is absent or irrelevant (known as depictive imagery), a 'high-resolution' perceptual image is needed to reconstruct a representation, hence activity extends into the primary visual cortex[8]. Our results provide evidence that auditory imagery obeys the same basic neural principles.

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Supplementary information accompanies this communication on *Nature*'s website.

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Supplementary Methods

Subjects

Fifteen subjects between the ages of 23 and 33 (6 male, 9 female, mean age = 27) were recruited from the local Dartmouth community. Subjects reported no significant abnormal neurological history and all had normal or corrected-to-normal visual acuity. Subjects were paid for their participation and gave informed consent in accordance with the guidelines set by the Committee for the Protection of Human Subjects at Dartmouth College.

Materials

Prior to functional scanning, each subject listened to segments of more than 150 songs and rated each one on how familiar the song was to the subject (1-5 scale, 5=familiar). This provided a basis for identifying songs that were 'familiar' (M=4.7) and 'unknown' (M=1.1) on a subject-by-subject basis. Twenty familiar and twenty unknown songs were chosen for each subject. Half of the familiar and unknown songs chosen for each subject contained lyrics; the remaining half were instrumental songs without lyrics. Notably, any song could occur in the familiar category for one subject and the unknown category for another subject, thus controlling for stimulus differences between categories.

Unique soundtracks for each subject were prepared digitally using Audacity 1.2.1 software (http://audacity.sourceforge.net). Soundtracks were comprised of a series of one-minute song segments. Within each song segment, 2-5s snippets of music were extracted and replaced with gaps of silence (Figure S1).

As such, each song segment consisted of 45s of music and 15s of silence. Each soundtrack contained an equal number (10) of familiar songs with lyrics, unknown songs with lyrics, familiar instrumentals, and unknown instrumentals. Soundtracks were presented using an Apple iPod (Apple, Cupertino, CA). Subjects listened to the soundtracks through pneumatic headphones (ER-30, Etymotic Research) at about 90 dB SPL. All subjects reported being able to clearly discern the music from the background scanner noise. Task instructions were to fixate a centrally-presented cross-hair and passively listen to the soundtrack. Subjects were not explicitly told that the study was interested in auditory imagery. To subjects, the audio presentation of the soundtrack appeared to be choppy and cut-out at various, random gaps.

Functional imaging

Anatomical and functional whole-brain imaging was performed on a 1.5 T GE Signa Scanner (General Electric Medical Systems, Milwaukee, WS). Anatomical images were acquired using a high-resolution 3-D spoiled gradient recovery sequence (SPGR; 124 sagittal slices, TE = 6 ms, TR = 25 ms, flip angle = 25°, 1 x 1 x 1.2 mm voxels). Functional images were collected in six functional runs using a gradient spin-echo, echoplanar sequence sensitive to blood-oxygen level-dependent contrast (T2*) (20 slices per whole-brain volume, 3.75-mm in-plane resolution, 5.5-mm thickness, 1-mm skip, TR = 2000 ms, T2* evolution time = 35 ms, flip angle = 90°).

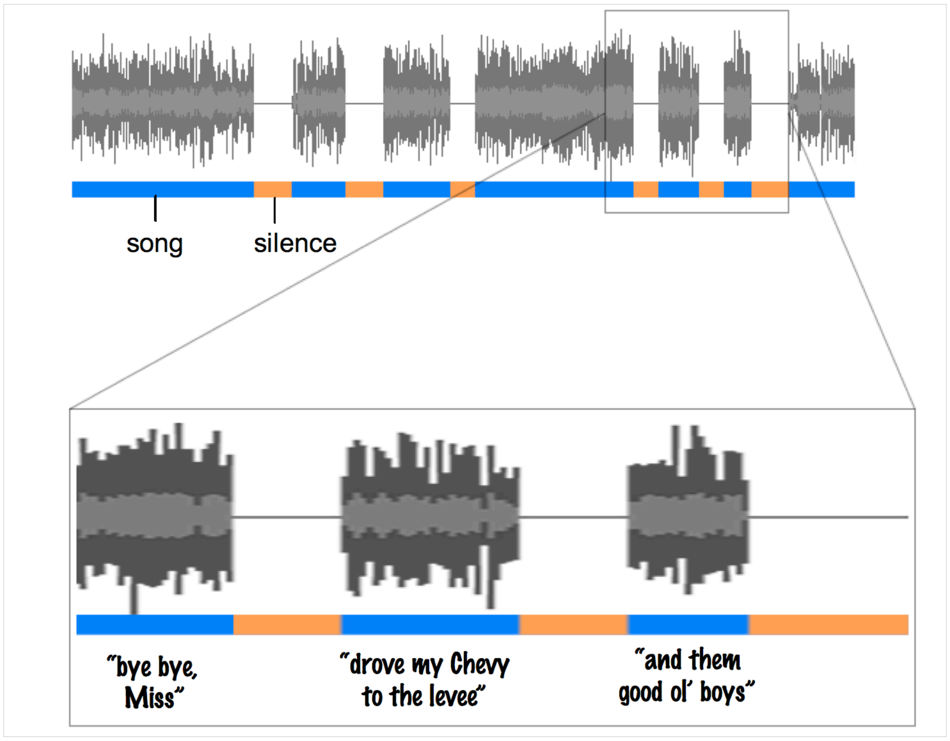

Figure S1. Sample edited segment of song with lyrics ("American Pie" by Don McLean) showing musical portions (blue) and gaps of silence (orange).

Data analysis

fMRI data were analyzed using the general linear model for event-related designs in SPM99 (Wellcome Department of Cognitive Neurology, London, UK). For each functional run, data were preprocessed to remove sources of noise and artifact. Functional data were corrected for differences in acquisition time between slices for each whole-brain volume, realigned within and across runs to correct for head movement, and coregistered with each participant's anatomical data. Functional data were then transformed into a standard anatomical space (2-mm isotropic voxels) based on the ICBM 152 brain template (Montreal Neurological Institute) which approximates Talairach and Tournoux (S1) atlas space. Normalized data were then spatially smoothed (6 mm full-width-at-half-maximum [FWHM]) using a Gaussian kernel. Analyses took place at two levels: formation of statistical images; and regional analysis of hemodynamic responses.

For each participant, a general linear model, incorporating task effects and covariates of no interest (a session mean, a linear trend, and six movement parameters derived from realignment corrections) was used to compute parameter estimates (β) and t-contrast images (containing weighted parameter estimates) for each comparison at each voxel. These individual contrast images were used in a hypothesis-driven region-of-interest analysis focusing on auditory cortex.

To quantify signal change in auditory cortex in an unbiased manner, spherical regions-of-interest (6-mm radius) were defined in primary auditory cortex (PAC) based on (S2) and in auditory association cortex (BA 22) based on (S3). For each participant, parameter estimates of signal change for gaps in familiar instrumentals, unknown instrumentals, familiar songs with lyrics, and unknown songs with lyrics were computed across all voxels within each region-of-interest and examined statistically using repeated measures ANOVA. To ensure that the findings observed during silent moments were not simply related to activation differences that were present when subjects were hearing the different types of music, a separate ANOVA was undertaken. When listening to music, activity in auditory association cortex was greater for unknown than familiar songs. Activity in PAC did not differ as function of whether the song was known or unknown (Fig S2).

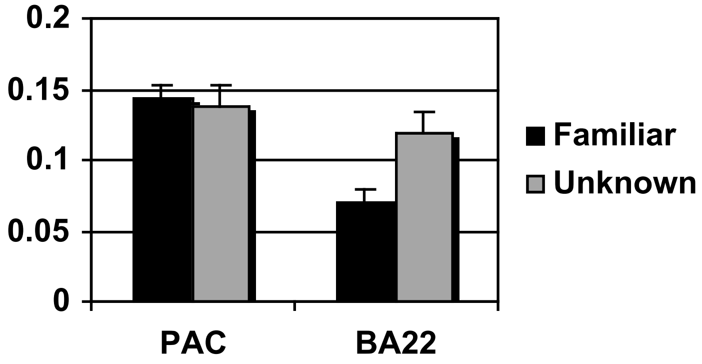

Figure S2. Signal change in PAC and auditory association cortex (BA22) while subjects listened to familiar (black) and unknown songs (gray).

While the current study focused on neural activity in auditory cortex, whole brain imaging was conducted. When gaps in familiar songs were contrasted with gaps in unknown songs, additional activity was observed bilaterally in dorsolateral prefrontal cortex (BA 9) and in the supplementary motor area.

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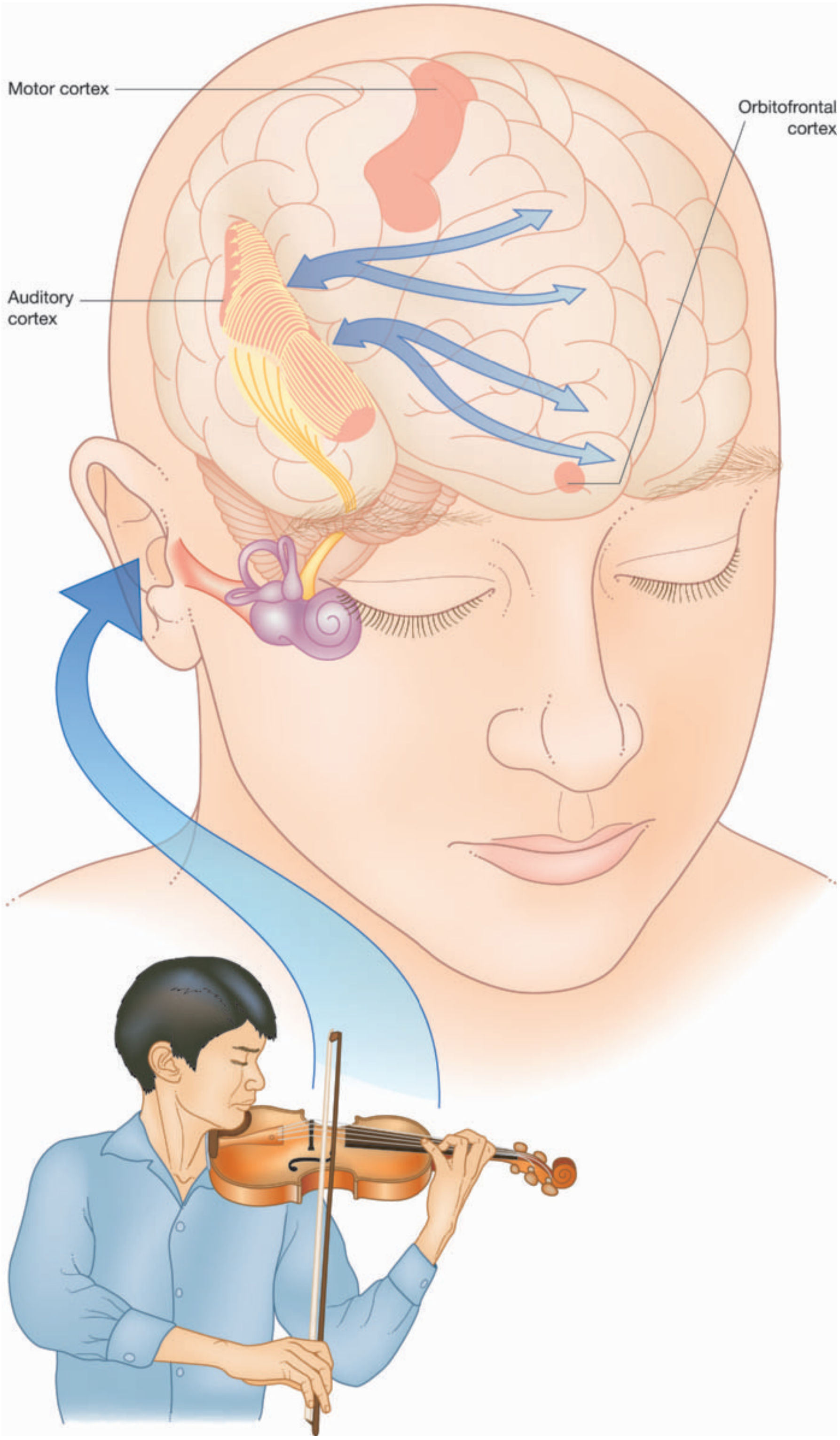

Figure 1 **The processing of sound waves from a musical instrument. After being transduced into neural impulses by the inner ear, information travels through several waystations in the brainstem and midbrain to reach the auditory cortex. The auditory cortex contains distinct subregions that are important for decoding and representing the various aspects of the complex sound. In turn, information from the auditory cortex interacts with many other brain areas, especially the frontal lobe, for memory formation and interpretation. The orbitofrontal region is one of many involved in emotional evaluation. The motor cortex is involved in sensory–motor feedback circuits, and in controlling the movements needed to produce music using an instrument.**

Music, the food of neuroscience?

Playing, listening to and creating music involves practically every cognitive function. Robert Zatorre explains how music can teach us about speech, brain plasticity and even the origins of emotion.

We tend to consider art and culture from a humanistic or historical perspective rather than a biological one. Yet these products of human cognition must have their origin in the function and structure of the human nervous system. As such, they should be able to yield valuable scientific insights. This line of reasoning is nowhere more evident than in the contemporary interest in the neuroscience of music.

Music provides a tool to study numerous aspects of neuroscience, from motor-skill learning to emotion. Indeed, from a psychologist's point of view, listening to and producing music involves a tantalizing mix of practically every human cognitive function. Even a seemingly simple activity, such as humming a familiar tune, necessitates complex auditory pattern-processing mechanisms, attention, memory storage and retrieval, motor programming, sensory–motor integration, and so forth (Fig. 1).

Likewise, the musician does not consider music to be monolithic, but recognizes within it multiple features including melodies, chords, themes, riffs, rhythms and tempos. This complexity — both psychological and musicological — makes music a challenging topic for a scientific research programme. Increasing numbers of investigators are convinced that music can yield valuable information about how the brain works: they believe that the study of the brain and the study of music can be mutually revealing.

How does one go about studying this intricate thing called music? Few scientists would accept that such a complex function could be studied, let alone understood, without first identifying and describing its various components. But this raises the thorny problem of deciding which components of music are pertinent, and how these components are shared or distributed among different cognitive functions. Some cognitive functions, such as figuring out pitch interval ratios, may be unique to music, whereas others, such as memory, may be general systems that are used in many different domains.

The oldest scientific technique for understanding brain functions is to study the consequences of brain lesions. We have long known that severe damage to the auditory cortex — where information coming from the ear is first analysed and interpreted — disturbs the ability to make sense of sounds in general. But occasionally, lesions of certain auditory cortical regions result in an unusual phenomenon: a highly selective problem with perceiving and interpreting music, termed 'amusia'[1].

“Art and culture must have their origins in the function and structure of the human nervous system, and should be able to yield valuable scientific insights.”

People with this type of damage have no problem speaking or understanding speech, or making sense of everyday sounds. But they cannot notice wrong notes inserted into tunes, or recognize even the most familiar melody. Even more surprising is that a minority of otherwise normal individuals appear to be born with the same inability to recognize tunes. In some cases, the deficit seems to run in families, suggesting a genetic component[2].

This extraordinarily selective problem in processing music, whether acquired or inborn, could result from very selective damage or dysfunction in an area of the auditory cortex where fine-grained pitch differences and sound frequency ratios (musical intervals) are processed[3]. Such a specific deficit at one of the earliest steps of music processing could propagate through the perceptual system, resulting in a global disability. The ability to compute pitch relations is critical to music processing, and if the brain is unable to represent pitch, the entire music perception mechanism could easily be destabilized.

The study of people with amusia has shown us that music depends on certain types of neural process. Such people provide living examples of what results when these neural processes are disrupted. And they have shown us that music can indeed lend itself to scientific study.

Music and speech

Scientists would also like to understand why we have evolved a sense for music in the first place, and, in particular, whether musical ability is somehow an extension of speech: many have argued for this on the reasonable grounds that music and speech share several formal similarities. So researchers have tried, using various techniques, to determine the extent to which the processing of music and that of speech share neural resources. The results so far are somewhat conflicting, but also intriguing.

One of the striking things about the neurobiological processing of speech is that it mostly takes place in the left half of the brain. It has therefore been natural to ask whether this asymmetry is mirrored in a right-hemisphere predominance for music. There are also many case reports of individuals who have lost their speech functions after extensive damage to speech regions in the left cerebral hemisphere, yet continue to show intact high-level musical function (for example, the Russian composer Vissarion Shebalin[4]).

These data suggest that music and speech processing do not use completely overlapping neural substrates. But neuroimaging studies indicate that some functions, such as syntax, may require common neural resources for both speech and music[5]. In other words, the ability to organize a set of words into a meaningful sentence and the ability to organize a set of notes into a well-structured melody might engage brain mechanisms in a similar way.

But the data from which we have drawn these conclusions have limitations. On the one hand, many of the case reports were studied in a descriptive, anecdotal manner. On the other hand, neuroimaging can be notoriously difficult to interpret: similar patterns of brain activity do not necessarily mean that similar neural substrates are involved, because many complexities of neural patterning are beyond our present technology's ability to measure.

The key to resolving these questions comes from a more systematic understanding of the different cognitive components involved, and the specific neural circuits associated with them. Fine-grained pitch processing — a highly critical component of music perception — has proven particularly valuable in dissecting the differences between how the brain handles speech and music.

Recent evidence from functional brain activation, magnetic recording and lesion studies, suggests that a particular region of the auditory cortex in the right hemisphere is much more specialized for representing detailed pitch information than its counterpart on the left side of the brain. Tones that are close together in pitch seem to be better resolved by neurons on the right.

Why should this functional segregation have emerged? It could be related to the requirement to sample sound information from the environment in different ways, according to need: either quickly and roughly, or if time allows, accurately[6]. If the sound energy is changing very rapidly, for example, a quick snapshot may be needed. The perceptual system needs to track these changes online, and hence must sacrifice detail to achieve speed. Such may be the case for speech recognition where detailed temporal information is essential to recover the sounds produced by the rapidly moving articulatory muscles of the lips and tongue. Conversely, some aspects of sounds that are important for perceiving music evolve much more slowly, so the nervous system can take a more detailed look at the structure of the sound. This takes more time, of course, but yields a finer-grained internal representation. Naturally occurring periodic sounds (many vibrating objects, voices or animal calls) contain pitch information that is important to process. Pitch is also a good cue to distinguish one sound from another in a noisy environment. So the postulated pitch processing mechanisms need not have evolved for music *per se*, but could be part of a general system for using natural sounds from the environment.

Thus, the different specializations of the auditory cortex on the two sides of the brain can be seen as different parameter settings on what are essentially two parallel systems. This approach shows us that it is perhaps less

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Perfect pitch: children can acquire absolute pitch only if they receive musical training before the age of 12 to 15.

interesting to ask, "on which side of the brain is music processing located?" than to set about systematically studying the various subcomponents that contribute to various aspects of musical function.

Music and development

Another reason music has caught the attention of scientists trying to understand the brain is that the ability to perceive music seems to be present from very early in development. Of course, we learn the specifics of our musical culture from the environment. But the human infant seems to come into the world with a brain already well prepared to figure out its musical world.

Any mother can attest to the way an infant will respond to the pitch and rhythm of her voice. But babies are surprisingly sophisticated mini-musicians: they are able to distinguish different scales and chords, and show preferences for consonant over dissonant combinations, for example[7]. They can recognize tunes played to them over periods of days or weeks, and are capable of remarkable feats of statistical learning, being sensitive to regularities in sounds[8]. In other words, babies' nervous systems seem to be equipped with a capacity to sort out the different musical sounds reaching their ears in order to construct a grammar, or system of rules.

> "Findings of brain plasticity have very general implications for our understanding of the interplay between the environment and the brain."

It could be argued that this is part of a general capacity to make sense of the world — to be able to predict what is coming up next. In some sense this is certainly true. But the notable thing is that this ability endows infants with the capacity expressed later in life to respond to and enjoy music. All this evidence supports the general idea that the ability to perceive and process music is not some recent add-on to our cognition, but that it has been around long enough to be expressed from the earliest stages of our neural development.

Music involves not only listening, but also playing and creating, where individual differences are much more evident. Although nearly everyone seems to have sophisticated neural systems that allow them to perceive music, and to reproduce musical patterns by singing, not everyone is able to play the piano like Vladimir Horowitz.

This leads to two very interesting scientific questions, which are the subject of active research. How can we explain individual differences in 'native' ability? And what effects does training have on brain function and structure? Little progress has been made on the first question, except in the very specific domain of 'absolute pitch', where interactions between genetic and environmental factors are beginning to be unraveled[9]. It is now clear that absolute pitch cannot develop without some musical training, but critically, the exposure must happen during childhood: past the age of 12 to 15, it is essentially impossible to learn it. From this one can conclude that the brain must be particularly sensitive during a certain time in development. But not all children given music lessons develop this skill, so other factors must also be at play. New evidence suggests that genetics has a role[10]. This is a field to watch in the near future.

In contrast, a number of very clear findings are now emerging that help us to understand how the brain is sculpted by musical experience. Most of this work shows that training in music enhances the activity of certain neural systems. For example, areas of the motor cortex corresponding specifically to the fingers of the left hand show an enhanced electrical response among violin players[11]. These changes are directly related to the age at which training is begun: those who began studying music in early childhood show the most extensive modification to brain response, whereas those who waited until after puberty show much less. Similar effects have been described for the auditory cortex's response to sounds produced by specific instruments[11].

Moreover, anatomical changes accompany these enhancements in responsivity. Several studies have reported greater tissue density, or enlargement of motor- and auditory-related structures among musicians, indicating that years of training actually change the underlying structure of the nervous system[12]. These findings should not be taken as evidence that music makes a person's brain bigger and therefore better. The changes are very specific, and it could be that they come at the expense of other functions. But such findings of brain plasticity have very general implications for our understanding of the interplay between the environment and the brain, particularly in the context of development, as the age at which training takes place is so critical.

Music and emotion

One of the questions that most frequently comes up in discussions of music, and yet has received relatively little attention in the neuroscience community, concerns emotion. Indeed, non-scientists are often puzzled that this aspect has been relatively neglected in favour of more esoteric concerns, given that, for most people, music exists solely to express or communicate emotion. There are some sophisticated treatises in the musicological tradition on this question (for example, the classic volume by Leonard Meyer[13]), but only recently has the topic begun to attract serious attention from neuroscientists[14].

One thing we do know is that music can elicit not only psychological mood changes, but also physiological changes in heart rate, respiration and so forth, that mirror the changes in mood. Indeed, music's anxiolytic effect is known not only to the specialist, but to anyone who listens to a favourite piece of music to relax after a trying day.

What brain responses can explain these effects? At the moment we simply don't know. But plausible hypotheses are guiding research. One notion is that music results in physical entrainment of motor and physiological functions: music drives the body. So, loud, rhythmic, fast music tends to make you feel lively — or even want to dance — whereas slow, soft music leads to calmness, and even sadness. A possible explanation is that these effects could be mediated through sensory–motor feedback circuits, which have been much discussed in neurophysiology; that is, through the so-called mirror-neuron system[15]. Although there is no direct evidence for this idea, it is plausible in that this system is thought to mediate imitative behaviour by linking perception directly to action. A similar mechanism might explain some of the effects of music on physical movement, and so mood induction.

But music's emotional undercurrents run deeper than such an analysis might suggest. Studying the very complex and idiosyncratic responses to music is challenging because it depends on so many difficult-to-control factors, not least individual preferences. What is 'music' to one person's ears is often offensive to another's (consider teenagers and their parents as a typical example). So cultural and social factors clearly have important roles in modulating our emotional response to music. Yet there are still likely to be common neural pathways that mediate responses, such as pleasure, to music.

> "Maybe music, and all art in a way, manages to transcend mere perception precisely because it contacts our more primordial neurobiology."

One intriguing and very specific emotional response is the 'chills down the spine' effect. Anyone who has experienced this knows exactly what I refer to: for the minority who haven't, it won't do much good to try to explain it. But we are beginning to understand some of the neural mechanisms that underlie these kinds of response. When listeners experience the chills, neuroimaging shows that the brain areas recruited include regions thought to be involved in mechanisms of reward and motivation. Examples are the basal forebrain and certain brainstem nuclei, along with cortical areas involved in emotional evaluation, such as the orbitofrontal and insular regions[16]. These circuits are similar to those involved in mediating responses to biologically rewarding stimuli, such as food or sexual stimuli.

But why should music, an abstract pattern of sound, have any commonality at all with such survival-related systems? It is a stretch to suggest that music is essential for life or reproduction. However, perhaps this research is beginning to illuminate the complex relation between cognitive–perceptual systems that analyse and represent the outside world, and evolutionarily ancient neural systems involved in assessing the value of a stimulus relative to survival and deciding what action to take. Maybe music, and all art in a way, manages to transcend mere perception precisely because it contacts our more primordial neurobiology.

To caricature the idea, we can think of the neocortex as being able to analyse relations and notice patterns, but then this processed information interacts with the emotion/evaluation system, which in turn leads to pleasure (or sadness, fear, excitement and so forth). The vagueness of these concepts indicates how far we are from having anything like a model of the processes going on — although an optimist might point out that even being able to talk about it, albeit in unclear terms, shows how far we have come. ■

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Nearly everyone can respond to music, but individual differences in native ability are striking.