

- feeding behavior by the Sex Peptide of *Drosophila*. *Curr. Biol.* 16, 692–696.
6. Vargas, M.A., Luo, N., Yamaguchi, A., and Kapahi, P. (2010). A role for S6 kinase and serotonin in postmating dietary switch and balance of nutrients in *D. melanogaster*. *Curr. Biol.* 20, 1006–1011.
 7. Ribeiro, C., and Dickson, B.J. (2010). Sex peptide receptor and neuronal TOR/S6K signalling modulate nutrient balancing in *Drosophila*. *Curr. Biol.* 20, 1000–1005.
 8. Waldbauer, G.P., and Friedman, S. (1991). Self-selection of optimal diets by insects. *Annu. Rev. Entomol.* 36, 43–63.
 9. Wullschlegel, S., Loewith, R., and Hall, M.N. (2006). TOR signaling in growth and metabolism. *Cell* 124, 471–484.
 10. Oldham, S., Montagne, J., Radimerski, T., Thomas, G., and Hafen, E. (2000). Genetic and biochemical characterization of dTOR, the *Drosophila* homolog of the target of rapamycin. *Genes Dev.* 14, 2689–2694.
 11. Yapici, N., Kim, Y.-J., Ribeiro, C., and Dickson, B.J. (2008). A receptor that mediates the post-mating switch in *Drosophila* reproductive behaviour. *Nature* 451, 33–37.
 12. Hässemeyer, M., Yapici, N., Heberlein, U., and Dickson, B.J. (2009). Sensory neurons in the *Drosophila* genital tract regulate female reproductive behavior. *Neuron* 61, 511–518.
 13. Yang, C., Rumpf, S., Xiang, Y., Gordon, M., Song, W., Jan, L.Y., and Jan, Y.-N. (2009). Control of the postmating behavioral switch in *Drosophila* females by internal sensory neurons. *Neuron* 61, 519–526.
 14. Liu, H., and Kubli, E. (2003). Sex-peptide is the molecular basis of the sperm effect in *Drosophila melanogaster*. *Proc. Natl. Acad. Sci. USA* 100, 9929–9933.
 15. Chen, S. (2006). Molecular analysis of structure-function relationships of Sex-Peptide and DUP99B in *D. melanogaster*. Ph D. Thesis, University of Zurich, Zurich, Switzerland.
 16. Isaac, R.E., Li, C., Leedale, A.E., and Shirras, A.D. (2010). *Drosophila* male sex peptide inhibits siesta sleep and promotes locomotor activity in the post-mated female. *Proc. R. Soc. B.* 277, 65–70.
 17. Wigby, S., and Chapman, T. (2005). Sex peptide causes mating costs in female *Drosophila melanogaster*. *Curr. Biol.* 15, 316–321.
 18. Barnes, A.K., Wigby, S., Boone, J.M., Partridge, L., and Chapman, T. (2008). Feeding, fecundity and lifespan in female *Drosophila melanogaster*. *Proc. Biol. Sci.* 275, 1675–1683.
 19. Saudan, P., Hauck, K., Soller, M., Choffat, Y., Ottiger, M., Spörri, M., Ding, Z., Hess, D., Gehrig, P.M., Klauser, S., et al. (2002). Ductus ejaculatorius peptide 99B (DUP99B), a novel *Drosophila melanogaster* sex-peptide pheromone. *Eur. J. Biochem.* 269, 989–997.

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Musical Consonance: The Importance of Harmonicity

A recent study suggests that musical consonance is based on harmonicity, a preference that reflects the central role of harmonicity in auditory perception.

Christopher J. Plack

Musical notes can be played in a sequence to produce melodies, or they can be presented together to produce chords. Certain combinations of notes are *consonant* (sounding pleasant or resolved) while other combinations are *dissonant* (sounding unpleasant or unresolved). The perceptual distinction is exploited by composers to evoke feelings of tension and resolution. Explanations of consonance in terms of the physical characteristics of the sounds, and their physiological and psychological effects, have been debated for hundreds of years without a clear consensus [1]. In a new article, McDermott *et al.* [2] provide compelling evidence that consonance is based on how well the combined frequency components match a single harmonic series.

Harmonicity and Beating

A single note produced by a musical instrument is a *complex tone*, consisting of a series of harmonic frequency components. The frequency of each harmonic is an integer multiple of the fundamental frequency of vibration. For example, the A string on a guitar has a fundamental frequency of

110 Hz, and harmonic components with frequencies of 110 Hz, 220 Hz, 330 Hz, 440 Hz, 550 Hz and so on. When two or more such notes are presented simultaneously, the harmonics are combined. For certain musical intervals the combination can be described as a simple harmonic series with a single fundamental frequency (Figure 1A). These combinations have a pleasant (consonant) sound. For some ratios, however, the harmonics do not match well. For example, a tritone (the notorious “Diabolus in Musica”) corresponds to a ratio of 64:45. For this combination, the harmonics do not form a single series (Figure 1B). Such combinations evoke an unpleasant (dissonant) sound. Hence, our preference for consonance over dissonance may be related to the resemblance of the combination to a single harmonic series [3,4].

Acoustic vibrations are transduced into neural impulses in the cochlea. Running along the length of the cochlear spiral is the basilar membrane. Different places on the basilar membrane are tuned to different frequencies, and in this way the ear separates out the different frequency components of sounds. This allows us to identify sounds on the basis of their spectra, and to segregate sounds from

different sources. However, the frequency resolution is not perfect, and sounds with similar frequencies will produce patterns of excitation that overlap (Figure 1B). Two closely spaced frequency components interact on the basilar membrane to produce a ‘beating’ pattern, characterized by amplitude fluctuations at a rate equal to the frequency difference between the components. This leads to the unpleasant sensation of ‘roughness’. Because dissonant chords often contain harmonics that are closely spaced, it has been suggested that dissonance is related to the degree of beating between the harmonics [5].

The Basis of Consonance

Distinguishing between these two hypotheses is difficult, because inharmonic series tend to produce beats, and combinations of notes that produce beats tend to be inharmonic. The ingenious approach of McDermott *et al.* [2] was to use individual differences in preference ratings for beats and harmonicity using non-musical sounds to determine which factor correlates with the preference for consonance. The authors found that the measure of beating preference did not correlate well with the preference ratings for consonant and dissonant musical chords. In other words, individuals who found beating particularly unpleasant did not show an unusual dislike of dissonant intervals. In contrast, the measures of preference for harmonicity correlated well with the consonance

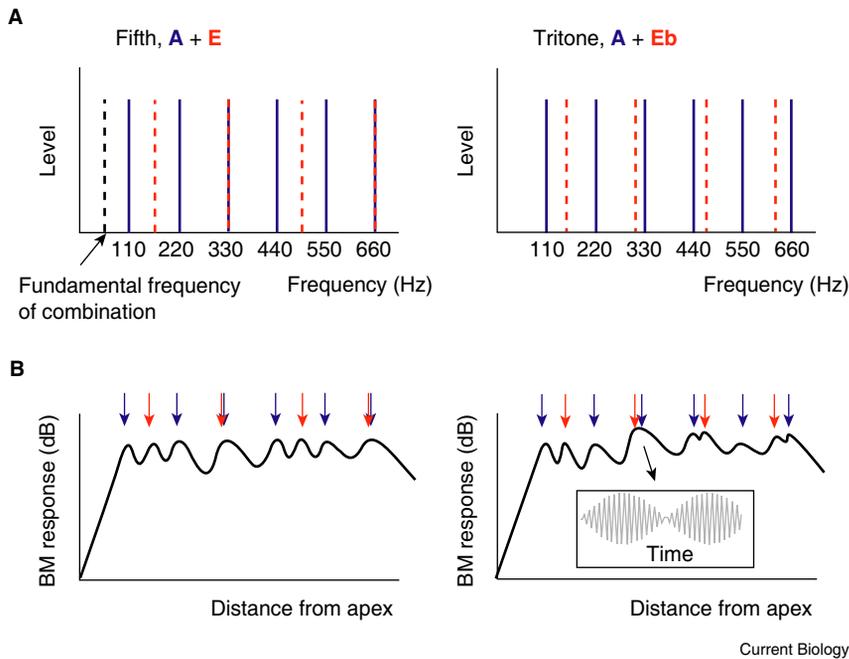


Figure 1. Consonant and dissonant chords and their representations in the cochlea. (A) The spectra of two combinations of tones, in intervals of a fifth and a tritone. The harmonics from the lower tone are shown by blue lines, and from the higher tone by dashed red lines. The dashed black line shows the fundamental frequency of the combined harmonics in the case of the fifth interval. In this case, all the harmonics are integer multiples of this frequency. (B) A highly schematic illustration of the representation of the chords on the basilar membrane (BM) as a function of distance from the apex of the cochlear spiral. When the chord is dissonant, the representations of closely spaced harmonics overlap on the basilar membrane, resulting in a beating pattern of vibration (illustrated in box).

preference. These results suggest that our preference for consonance is driven by our preference for harmonic series. McDermott *et al.* [2] additionally found that preference for harmonicity and for consonance were both correlated with musical experience. This emphasizes the role of prior experience in determining our preference for these acoustic features, although the results do not rule out an innate component.

A possible explanation for why consonance is not linked to beating preference is that beating is unreliable as a cue. The salience of beats will vary greatly depending on the amplitudes, and relative amplitudes, of the interacting harmonics in the chord. The pattern of harmonic amplitudes is different for different instruments, helping to determine their distinct timbres. Hence, the salience of beating for a given musical interval will vary depending on which instrument or instruments are combined in the chord. Harmonicity does not depend on this, and so provides a more general basis for consonance preference.

The Importance of Harmonicity

There are good ecological reasons why harmonicity should have a special role in auditory perception. Many natural sounds are produced by objects that vibrate periodically, producing complex tones with a series of harmonics. The auditory system combines the information from the individual harmonics to identify the fundamental frequencies of sounds such as these, giving rise to the sensation of pitch [6]. Low-numbered harmonics are the most important for pitch. A small perturbation in the frequency of just one of these harmonics can produce a change in the pitch that is heard (Figure 2). Some models of pitch perception suggest that the auditory system contains the equivalent of a harmonic template, that derives pitch by finding the best match of the frequency components of the sound to a known harmonic series [7,8]. Other models are based on the autocorrelation of synchronized neural firing patterns [9]. These models depend on harmonicity to give consistent time intervals between action potentials.

Harmonicity is also one of the most important cues for sound segregation [10]. In most environments several sound sources are present, yet the auditory system can separate out the sounds from different sources from the complex, and seemingly irreducible, mixture of waveforms that enter the ear canal. Frequency components that are harmonically related are likely to come from the same sound source. Since the basilar membrane can separate out the different frequency components of these sounds, the auditory system can group together those components that come from the same harmonic series. In this way, two tones with different fundamental frequencies — for example, speech sounds from a male and female speaker — can be separated out by the ear. The auditory system uses the natural property of harmonicity as a heuristic for sound segregation.

A neat illustration of this is the effect of mistuning, or frequency shifting, a single harmonic in a complex tone (Figure 2). For small mistunings, the pitch of the whole complex is shifted. For mistunings greater than about 8%, the auditory system determines that the harmonic does not come from the same sound source because it is not

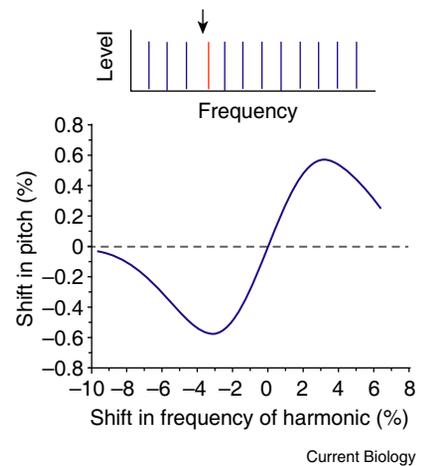


Figure 2. The change in the pitch of a complex tone produced by mistuning the fourth harmonic.

The graph shows the shift in perceived pitch as a function of the percentage shift in the frequency of the harmonic [11]. For small shifts, the pitch of the complex is affected. For large shifts, the harmonic is perceptually segregated from the complex tone and no longer contributes to its pitch. A schematic spectrum for the stimulus with a (positively) shifted fourth harmonic (red) is shown above the graph (the arrow indicates the usual frequency of the fourth harmonic).

part of the same harmonic series. The shifted harmonic is perceptually segregated from the rest of the complex and has little effect on the overall pitch [11].

So although *preference* for harmonicity may be dependent on musical experience, the use of harmonicity in auditory processing is probably not dependent on this specific experience. Instead its use is driven by the adaptation of the auditory system to the acoustic properties of objects in the environment. The preference for consonance reflects the central role of harmonicity in auditory perception, both for the identification of sounds and for the segregation of sounds from different sound sources.

References

1. Burns, E.M. (1999). Intervals, scales, and tuning. In *The Psychology of Music* 2nd edn., D. Deutsch, ed. (San Diego: Academic Press), pp. 215–264.
2. McDermott, J.H., Lehr, A.J., and Oxenham, A.J. (2010). Individual differences reveal the basis of consonance. *Curr. Biol.* 20, 1035–1041.
3. Terhardt, E. (1974). Pitch, consonance, and harmony. *J. Acoust. Soc. Am.* 55, 1061–1069.
4. Ebeling, M. (2008). Neuronal periodicity detection as a basis for the perception of consonance: A mathematical model of tonal fusion. *J. Acoust. Soc. Am.* 124, 2320–2329.
5. Plomp, R., and Levelt, W.J.M. (1965). Tonal consonance and critical bandwidth. *J. Acoust. Soc. Am.* 38, 548–560.
6. Plack, C.J., and Oxenham, A.J. (2005). The psychophysics of pitch. In *Pitch: Neural Coding and Perception*, C.J. Plack, A.J. Oxenham, R.R. Fay, and A.N. Popper, eds. (New York: Springer), pp. 7–55.
7. Goldstein, J.L. (1973). An optimum processor theory for the central formation of the pitch of complex tones. *J. Acoust. Soc. Am.* 54, 1496–1516.
8. Duifhuis, H., Willems, L.F., and Sliyer, R.J. (1982). Measurement of pitch in speech: an implementation of Goldstein's theory of pitch perception. *J. Acoust. Soc. Am.* 71, 1568–1580.
9. Meddis, R., and O'Mard, L. (1997). A unitary model of pitch perception. *J. Acoust. Soc. Am.* 102, 1811–1820.
10. Darwin, C.J. (2005). Pitch and auditory grouping. In *Pitch: Neural Coding and Perception*, C.J. Plack, A.J. Oxenham, R.R. Fay, and A.N. Popper, eds. (New York: Springer), pp. 278–305.
11. Darwin, C.J., and Ciocca, V. (1992). Grouping in pitch perception: Effects of onset asynchrony and ear of presentation of a mistuned component. *J. Acoust. Soc. Am.* 91, 3381–3390.

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Intergroup Empathy: How Does Race Affect Empathic Neural Responses?

How does race affect the human ability to share and respond to the suffering of others? Recent evidence provides novel insight into how and why race alters empathic neural response.

Joan Y. Chiao and Vani A. Mathur

In 1959, John Howard Griffin ingested anti-vitiligo drugs which transformed the color of his skin from white to black, and then travelled through the racially segregated South for the first time from the perspective of a Black man (Figure 1). In his memoir *'Black Like Me'*, Griffin would later remark, "I had no idea what they [Blacks] have to go through. I literally bawled myself to sleep some nights. I learned that when it is night, when it is dark, then the Negro feels safest. Langston Hughes's line, 'Night coming tenderly/ Black like me', has real meaning".

How and why does race affect our ability to understand and share the suffering of others? Race is a potent modulator of neural responses underlying social behavior [1,2]. Prior neuroimaging research has demonstrated that racial majority group members, such as Whites (in the US), show greater fusiform and parahippocampal response when perceiving own-race faces [3], and either heightened [4] or attenuated [5,6] amygdala response to other-race faces, depending on social context

and presence of unconscious racial bias [7–9]. By contrast, members of racial minority groups, such as Blacks, typically demonstrate greater fusiform [3] as well as amygdala activation to own-race faces [4], suggesting that intergroup status moderates the direction and magnitude of neural responses to ingroup and outgroup members [3–6].

Most recently, studies of race and social brain functioning have focused on the neural basis of intergroup empathy [10–12]: in particular, a study reported in this issue of *Current Biology* [10] using transcranial magnetic stimulation (TMS) reveals for the first time greater empathic sensorimotor contagion when observing the physical suffering of subjects of the same race, but not those of other races.

Multiple Routes to Empathy

Empathy is the capacity to understand and share the emotional states of others and serves as a key motivator and the proximate mechanism of altruistic behavior, whereby an individual perceives and shares in the distress of another person, and acts to reduce his or her suffering [13].

Convergent evidence suggests the existence of multiple routes to our ability to understand and share the pain of another, including sensorimotor contagion, affect sharing and cognitive perspective-taking or appraisal [14].

During sensorimotor contagion, seeing a painful sensorimotor experience in another person, such as a needle penetrating another's hand, elicits an isomorphic sensorimotor experience in the observer — for example, muscle-specific freeze within the same region of the observer's hand [15]. By contrast, during affect sharing, seeing the emotional pain of another person, such as a painful facial expression, elicits a shared affective experience, while during cognitive perspective-taking, the capacity to



Figure 1. To understand the experience of racial discrimination, Griffin, a white native from Texas, artificially darkened his skin.