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NEUROSCIENCE

Finding the missing fundamental

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The whole orchestra tunes up to an A note from the oboe — but how do our brains tell that all the different sounds are the same pitch? The discovery of pitch-sensitive neurons provides some clues.

Although Maurice Ravel reportedly came to regret ever having written *Bolero*, it has become a popular staple of the orchestral repertoire. It relies entirely on a single theme, repeated over and over (and over) by different combinations of instruments. Artistic merit aside, the piece raises an interesting question: how do we effortlessly recognize the same melody played by different instruments even though the acoustical structure of the sound reaching our ears varies with the instrument? Bendor and Wang (page 1161 of this issue)[1] have found neurons that figure out what the pitch of a sound is even when they are presented with physically different signals, giving hints to how we come to perceive pitch as a unified entity.

Psychologists are intrigued by the problem of perceptual constancy: essentially, how do we perceive the environment as remaining stable despite huge variability in the inputs reaching our senses? This general question is especially puzzling in the case of pitch, because we have known since the nineteenth century[2] that the pitch of a sound typically corresponds to its fundamental vibrational frequency — even if that frequency is physically absent in the sound reaching our ears. Sounds that have pitch arise from objects that vibrate in a periodic manner, such as columns of air in pipes or the vocal cords (as opposed to aperiodic sounds like wind or rushing water). As Pythagoras knew, if you pluck a string, it will vibrate in its entire extent, as well as in halves, thirds and so on, and each of those vibrational modes will result in a separate harmonic frequency. Yet we usually perceive the pitch as corresponding to the lowest of these, which is the fundamental[3]. For a simple demonstration of the 'missing fundamental' effect, pick up a phone. Most telephone lines cut off the lower frequencies, resulting in a slightly tinny sound, yet the fundamental pitch does not change; a male voice does not sound like Mickey Mouse. The brain seems to figure out the missing pitch.

Bendor and Wang[1] studied the auditory cortex (the region of the brain that enables perception of sound) in the marmoset monkey. They show that there are neurons in this region that respond in essentially the same way to a variety of sounds that all have the same fundamental but do not share any frequencies. For example, a neuron that responds to 200 hertz also responds to the combination of 800, 1,000, and 1,200 hertz because all correspond to the same fundamental. This effect is unusual because neurons usually respond only within their receptive field, which is typically a narrow range of frequencies. The marmoset neurons, however, responded not only to frequencies in their receptive fields, but also when there was no frequency within the receptive field but the other frequencies in the stimulus were harmonically related to the missing one. This property makes psychologists happy, because it provides evidence (if not yet a mechanism) for perceptual constancy. These neurons respond to an abstract property — pitch — derived from, but not identical to, physical sound features. Presumably, therefore, it is thanks to such neurons that we can follow a tune as the instruments change.

One might wonder why marmosets need such a system, given that they don't spend much time listening to iPods. But periodic sounds are important in the natural environment because they are almost exclusively produced by other animals, and so pitch is a good cue to segregate these sounds from background noise[4]. Marmosets are highly vocal creatures, and the development of pitch-sensitive neurons would also be central to communication. From an evolutionary perspective, these abilities could be seen as precursors to human pitch perception, which has led to our unique development of music and is similarly crucial for speech.

The location of the pitch-sensitive cells lateral to the primary auditory cortex, as described by Bendor and Wang, is compatible with studies of the human brain. In human patients, damage to areas analogous to the marmoset pitch-sensitive regions produce specific deficits in perceiving missing fundamental pitch[5]. Moreover, neuroimaging studies in humans demonstrate pitch sensitivity in roughly the same location[6,7]. The human studies typically show specialization for pitch in the right auditory cortex, however. Bendor and Wang do not address this issue, as only a single hemisphere was probed in each of three monkeys. It will be of interest to determine whether lateralization is present in other species (as others suggest[8]), and is therefore related to basic properties of sound processing, or whether it is uniquely human and thus might be a consequence of the development of language.

Now that we know that there are pitch-sensitive neural units, we have to discover how they work. Sound undergoes many transformations before it gets to the auditory cortex, resulting from the biophysical properties of the cochlea and the many neuronal junctions between cochlea and cortex. We do not yet know precisely how periodic, temporal information available in a stimulus is integrated with the spectral information (or individual harmonics) that is also extracted by the system. We also do not know much about the inputs to the neurons described by Bendor and Wang. Do they come in a hierarchical arrangement from other simpler cells in the auditory cortex? Or do they also receive inputs from subcortical structures such as the thalamus? Perhaps top-down influences from centres associated with complex functions in frontal or parietal lobes are also significant. This last point is relevant, because one technical advantage of this work is that the animals tested were awake rather than anaesthetized, meaning that attentional and other cognitive factors could have a role. The animals were not trained or behaving, however, so it is difficult to know the significance of the stimuli for them. Understanding the interaction between basic perceptual systems and their modulation by higher-order mechanisms will require more attention to these factors. Another interesting question is whether these neuronal properties are somehow hard-wired, or whether they are a consequence of the animals' environmental experience with periodic sounds, which contain harmonically related frequencies.

Ian Whitfield[9] noted that the problem of perception is not to determine that two events are different, which is actually fairly trivial, but rather that events that might seem to be different are actually the same. It is the job of the cortex, he argued, to perform the computations needed to extract invariances despite the different inputs that the environment may provide. The present study[1], and those that will no doubt follow, will lead to a more profound understanding of this fundamental problem. ■

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