

receptor, and cytoskeletal components (actin microfilaments and a nonmuscle myosin, together called actomyosin). In response to Wnt5a, all of these proteins become polarized in overlapping bands within the trailing edge of migrating cells (see the figure). Polarized bands of actomyosin contract to lift the trailing edge and, together with cell process extensions at the leading edge, promote migration toward a chemokine source. Multiple pulses of these transient polarizations occur within single cells over time.

In exploring the signaling pathway that mediates this Wnt5a response, Witze *et al.* discovered that actin microfilaments and the cell adhesion protein depend on each other for polarized localization and that both are required for myosin polarization. Like some other noncanonical Wnt pathways, the cytosolic proteins Dishevelled and Protein Kinase C are required. But in contrast to noncanonical pathways that influence actin through the small guanosine triphosphatase (GTPase) RhoA, Wnt5a acts through RhoB, which controls the movement of intracellular vesicles called endosomes. Furthermore, the authors observed an enrichment of multivesicular bodies at the polarized cell edge, and polarization required both the GTPase Rab4 (known to regulate multivesicular body formation) and dynamin (known to control the formation of endosomes at the cell surface). Witze *et al.* also found that polarization of the cell adhesion protein occurs by its transit through the Golgi. The authors conclude that Wnt5a polarizes cells by promoting the recycling of membrane

components to specific surface sites. The concurrent or subsequent recruitment of actomyosin and other factors to these sites defines the trailing edge of the cell and thus the direction of migration.

This admirably integrated view of both cell surface and actomyosin polarization raises important questions. For instance, it's not clear how polarization of the membrane and cytoplasm are coupled, or how different proteins are targeted to the same sites. Also, how does Wnt5a signaling interface with the graded chemokine to ensure that polarization occurs at cell surfaces distal to the chemokine source? Intriguingly, Witze *et al.* observed that some responding melanoma cells polarized in the opposite (proximal) direction. Both distal and proximal polarizations require Wnt5a, with a preponderance of distal events promoting migration toward the chemokine source. Thus, the chemokine and Wnt5a are more tightly coupled to the same axis than they are to the same direction along that axis.

It is interesting to compare Wnt5a to other noncanonical Wnt signals that polarize single cells. One common theme is a requirement for actin. Actin microfilaments and myosin are required for planar cell polarity in *Drosophila* (3), and microfilaments are required in four-cell-stage *C. elegans* embryos for the Wnt-mediated induction of an asymmetric cell division that segregates endoderm from mesoderm (6). However, planar cell polarity acts through RhoA (8), whereas Wnt5a acts through RhoB. Furthermore, the *C. elegans*

Wnt signal that segregates endoderm from mesoderm acts instructively and requires a permissive signal (a tyrosine kinase) (12), in contrast to the permissive action of Wnt5a in the presence of an instructive chemokine signal. Once again, noncanonical Wnt pathways present a bewildering mix of similarities and differences. Appropriately, the Wnt field is evolving toward the use of individual pathway names based on key molecules and properties, and away from the historical distinction between canonical and noncanonical. Presumably, as we learn to speak more clearly about different Wnt pathways, we also will come to better understand their different molecular mechanisms of action.

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#### MUSIC THEORY

## Geometrical Music Theory

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Music theorists normally use discrete mathematics, such as set and finite group theory, to describe musical relations; they also invoke geometry in modeling musical objects such as chords, rhythms, and scales. However, no unified geometric perspective has hitherto emerged. On page 346 of this issue, Callender *et al.* (1) demonstrate that many musical terms can be understood as expressing symmetries of  $n$ -dimensional space, where each dimension represents a voice in the score. Identifying—gluing together—points related by these symmetries

produces exotic mathematical spaces (orbifolds) that subsume a large number of geometric models previously proposed.

The use of mathematics to describe, analyze, and create music goes back millennia. Mathematical questions have previously emerged in music theory that are appealing, nontrivial, and, in several cases, connected to other scientific fields, such as physics, dynamical systems, and crystallography (2–4). Math inspired composers such as Schoenberg, Messiaen, and Xenakis; musical investigations have even motivated mathematical discoveries (5).

However, the geometrical music theory proposed by Callender *et al.* stands out both for the breadth of its musical implica-

Musical operations, such as transpositions, can be expressed as symmetries of  $n$ -dimensional space.

tions and the depth of its mathematical content. It suggests a wealth of new techniques for studying music theoretical topics, including chord similarity and melodic contour, and provides attractive visualizations of harmonic relationships. Although the authors' use of contemporary geometry departs from the discrete mathematics normally used to describe music, they make a convincing argument for the validity of their models.

Although most musicians are not mathematicians, both groups think in degrees of abstraction. Music theorists invoke the mathematical concept of equivalence class—a set of objects that are “the same” if we ignore certain information—to describe these musical struc-

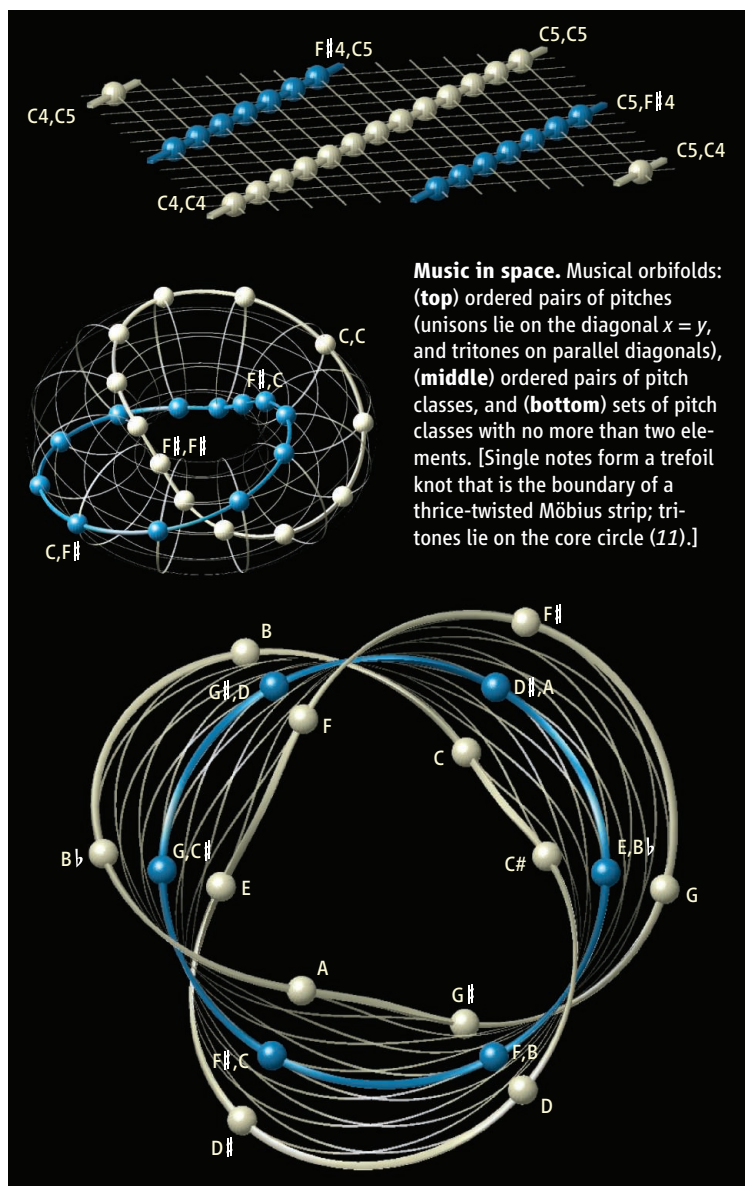
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tures. For example, middle C is a particular pitch (frequency measured on a logarithmic scale), and the letter name (or pitch class) “C” refers to any pitch that is a whole number of octaves away from it. Any collection of C, E, and G notes is a C major chord.

Callender *et al.* (1) show that many musical terms describe equivalence classes under combinations of five basic OPTIC relations: octave shifts, permutation (reordering), transposition (the relation between pitches sharing the same succession of intervals, regardless of their starting note), inversion (turning a sequence upside down), and cardinality equivalence (ignoring repetitions). The authors go beyond traditional music theory by showing that there are two distinct ways in which these symmetries can apply to chord progressions: uniformly, where the same symmetry applies to each chord, and individually, where distinct symmetry operations apply to the harmonies in a progression. This distinction allows Callender *et al.* to formalize the relations among a large number of musical terms as in table S1 of their paper (1).

Following Tymoczko’s previous work (6), they develop geometrical models of these relations. Pitches correspond to real numbers; each point in Euclidean  $n$ -dimensional space (that is, a space with no underlying curvature) represents a sequence of  $n$  pitches. Points near each other differ by microtones (for example, a C major chord played out of tune lies near an in-tune version) and are in this sense similar.

With the exception of cardinality equivalence, each of the OPTIC relations corresponds to a symmetry group. For example, permuting the first two entries in a sequence is equivalent to reflection in a plane of  $n - 1$  dimensions (a hyperplane), and transposing a sequence is equivalent to a translation. Gluing together points in  $n$ -dimensional space on the basis of their memberships in equivalence classes creates families of quotient spaces, or orbifolds. Many of these mathematical spaces are geometrically and



topologically complex; they may be non-Euclidean, meaning that there may be more than one line connecting two points (see the figure). These features have musical ramifications. Callender *et al.* provide a comprehensive catalog of their geometrical spaces in table S2 (1).

Distance and movement within these spaces have natural meanings. A musical score represents pitch vertically and time horizontally. Each vertical harmonic state (the notes played at one time) corresponds to a pitch sequence, ordered by instrumental voice; a score for  $n$  voices becomes a succession of points in  $n$ -dimensional space, where each coordinate tracks the melody sounded by an individual voice. Voice leadings—mappings between adjacent chords in a score—correspond to directed line segments connecting harmonic states. The size of a voice leading

depends on the amount of vocal movement between states. Composers typically try to minimize this movement—a problem equivalent to finding the shortest path between two points.

Although the design of efficient voice leadings is central to traditional compositional practice, the systematic study of voice leading is comparatively recent (7–10). Geometrical music theory essentially represents a voice leading by a vector that connects a source chord to a target chord. The authors show the musical distinction between individual and uniform applications of symmetries corresponds to the geometrical notion of a bundle, which allows them to define analogs of voice leadings between abstract musical objects such as major chords and minor chords.

Geometrical music theory suggests new directions for research in traditional music theoretical topics, such as chord and voice leading similarity, and new tools for teaching and conceptualizing music, and will perhaps inspire composers. Moreover, one can envision practical applications of geometrical music theory, such as in the design of music visualization tools, interactive musical toys, or even new

musical instruments.

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## Geometrical Music Theory

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