

Evolution of Music by Public Choice

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Music evolves as composers, performers and consumers favour some musical variants over others. To investigate the role of consumer selection we constructed a Darwinian music engine consisting of a population of short audio loops that sexually reproduce and mutate. This population evolved for 2,513 generations under the sole selective influence of 6,931 consumers who rated the loops' aesthetic qualities. We found that the loops quickly evolved into music due, in part, to the evolution of aesthetically pleasing chords and rhythms. Later, however, evolution slowed. Applying the Price equation, a general description of evolutionary processes, we found that this stasis was mostly due to a decrease in the fidelity of transmission. Our experiment shows how cultural dynamics are explicable in terms of competing evolutionary forces.

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The music made by the world's cultures is immensely diverse[1, 2]. Since music is transmitted from one musician to another, and frequently modified in transmission, this diversity must arise from descent by modification rather than the diversity of living things, languages and other cultural artifacts[3]. What drives this process? It is often supposed that the music we listen to is primarily the product of aesthetic decisions made by “producers”—composers and performers[4]. Early Greek texts speak of specialist composers/performers, and the rudiments of formal musical theory, at least 2500 years ago[5]; and specialist composer/performers are found in many other societies as well[6]. Yet the reproduction, spread and persistence of particular songs must also depend on the preferences of “consumers”—the people who listen to them[7]. These preferences are also clearly a selective process and, like any selective process, can have a creative role[8]. Disentangling the roles of composers, producers and consumers in shaping musical diversity is difficult in existing musical cultures. For this reason, inspired by studies of experimental evolution in microbes[9, 10], digital organisms[11, 12, 13, 14, 15, 16] and previous work on evolutionary music and art[17, 18, 19], we developed an artificial system for studying musical evolution called “DarwinTunes”. Using it we ask: is it possible to make music without a composer? If so, what kind of music is made? And what limits the evolution of music?

DarwinTunes: a musical variation-selection engine

In brief, DarwinTunes works as follows: an algorithm maintains a population of digital genomes, each of which encodes a short polyphonic sound sequence—a loop. While the tempo, meter and tuning system are fixed for all loops, note placement, instrumentation and performance parameters are specified by the genome. No human-derived sounds, rhythms or melodies are provided as input to the algorithm (for details, see SI A). During the experiments, loops periodically replicate to produce new loops. The daughter loops are not, however, identical to their parents for two reasons: First, in a process analogous to recombination, the genome of each daughter loop is formed from the random combination of its two parents' genomes. Second, in a process analogous to mutation, each daughter also contains new, random, genetic material.

These two processes mimic the fusion of existing, and invention of new, musical motifs, rhythms and harmonies that can be heard in musical evolution[6]. The only selective pressure in DarwinTunes comes from a population of consumers who listen to samples of the loops via a web interface and rate them for their appeal. These ratings are then the basis of a fitness function which determines which loops in a given generation will be allowed to mate and reproduce. We therefore expect that the frequency of musical traits will evolve under the influence of this selective process rather than trait frequencies in organisms do under the influence of natural selection.

The processes underlying a single DarwinTunes population are shown in Figure 1A. At any given time, a DarwinTunes population has 100 loops, each of which is eight seconds long. Consumers rate them on a five-point scale (“I can't stand it” to “I love it”) as they are streamed in random order. When 20 loops have been rated, truncation selection is applied whereby the best ten loops are paired, recombine, and have two daughters each. These daughters replace their parents that die. In our first experiment, designated Experimental Population 1 (EP1), we began with 100 loops that had been generated from two random founders and that were then allowed to evolve for 100 generations without selection to maximise the stock of standing variation in the starting population. Public consumers were then recruited to rate the loops. Since consumers did not know each other's ratings, there is no possibility of social influence on rating[7]. In all, 6,931 consumers made 85,533 ratings over the course of 2,513 generations of evolution during which 50,480 loops were born. We recorded the ratings, number and identity of offspring, and genome of each loop. Thus we can describe the evolutionary dynamics of these populations in detail.

Results

Selection rapidly evolves music from noise, but then stops.

As EP1 evolved it seemed to us that the loops were becoming more pleasing to listen to; that we were, in fact, evolving music from noise (examples can be heard at <http://soundcloud.com/uncoolbob/sets/darwintunes/>). To test this objectively we carried out a new experiment. We randomly sampled 2,000 of the 50,480 loops produced at any time during EP1's evolution and, via a web-interface, asked public consumers to rate them as before. Since in this experiment consumers heard and rated loops sampled from the entire evolutionary trajectory, their ratings can be used to

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estimate the mean absolute musical appeal, M , of the population at any time. This is analogous to bacterial experiments in which the fitness of an evolved strain is compared directly to that of its ancestor[10]. Figure 1B shows that M increased rapidly for the first 500-600 generations but then came to an equilibrium. Thus, in our system, musical quality evolves but it seems that it does not do so indefinitely.

What makes the loops of later generations so much more pleasing? The aesthetic value of a given piece of music depends on many different features, such as consonance, rhythm and melody[20]. In recent years, music information retrieval technology (MIR) has permitted the automatic detection of some of these features[21, 22, 23]. Reasoning that our raters listen to, and like, Western popular music, we measured the phenotypes of our loops using two MIR algorithms designed to detect features in this music. The first, Chordino, detects the presence of chords commonly used in the Western repertoire[24]. The fit of a loop to Chordino’s canonical chord models is given by a log-likelihood value C_L and is an estimate of the clarity of the chordal structure. The second, Rhythm Patterns[25], extracts a rhythmic signature, from which we derive a complexity measure, R (SI, Materials and Methods). To validate these algorithms, we tested them on a standardised test set of specifically generated loops (SI, Materials and Methods).

To examine the evolution of musical qualities in EP1, we measured C_L and R for every loop. We found that, like musical appeal, these traits increased rapidly over the first 500-600 generations but then appear to fluctuate around a long-term mean (Figure 2 A,B). Given these dynamics, and because C_L and R are measured without error, we are able to model their evolution using a discrete version of the Ornstein-Uhlenbeck (O-U) process, according to which the change in the mean of a character from one generation to the next is anticorrelated to how far it is from a long-term mean:

$$\Delta\bar{z} = a(u - \bar{z}) + \varepsilon,$$

where $\Delta\bar{z}$ is the difference between the means of each offspring and parental generation, $\bar{z}_o - \bar{z}_p$, a is a constant such that $a > 0$, u is the long-term mean, and ε is a normally distributed random variable with mean 0. For both C_L and R , the confidence limits on the long-term mean do not include the initial values ($p = 1.0 \times 10^{-6}$ and 2.0×10^{-7} respectively), confirming the visual impression that C_L and R increased significantly over the course of the experiment (Figures 2 A,B & Table S6).

Since musical appeal and its components all increase it is likely that they are under selection. However the trajectory of a DarwinTunes population, like that of any evolving population, depends not only on selection but also stochastic sampling, the analogue of genetic drift. To show that the evolution of chords is due to selection rather than drift we undertook additional experiments and analyses. In experimental evolution, replicable responses are a signature of selection[26, 10], so we repeated the experiment in a more controlled setting. To do this, we cloned additional populations from the same base population that EP1 started with, and asked undergraduates to rate them. These populations, designated EP2 and EP3, were allowed to evolve independently for about 400 generations and received an average of 10,683 ratings. We found that C_L and R increased rapidly in these populations too (Figure S5), strongly suggesting that these traits are under positive selection; these populations could also be described by an O-U process (SI, Supporting Text “Describing the evolutionary responses”). As controls we generated 1000 additional populations with the same origin as the experimental populations and subject to the same variational processes and demogra-

phy for 400 generations, but differing from them in that ratings were assigned randomly rather than by consumers. We found that mean C_L and R of the selected populations were significantly higher than those of the unselected control populations by generation 100 (Figure 2 C, D; SI, Supporting Text “Comparing selected and unselected control populations by generation”). We also used the control populations to examine whether C_L and R are intrinsically related to each other and found that they are weakly correlated, $r = 0.26(\pm 0.016)$, (mean \pm 95%CI) (SI, Supporting Text “Correlation between C_L and R ”). Thus, although selection on one of these features may influence the evolution of the other, they are largely independent. We cannot, however, preclude the possibility that either feature is highly correlated with unmeasured traits that are more direct targets of selection.

The adaptive and variational landscape of DarwinTunes populations. The increase in C_L and R implies that selection is directional. So why do our populations stop evolving? Remarkably, it is not merely that these traits cease to evolve: musical appeal itself does too. This pattern of fast-slow evolution or even stasis is often seen in biological populations, whether in the laboratory, wild or fossil record. Stasis can result from several different population genetic forces, however it has often been difficult to distinguish among them[10, 27, 28, 29]. Since we know the complete histories of the DarwinTunes populations we can study the forces driving their evolutionary dynamics in detail. We first considered the possibility that DarwinTunes populations have arrived at an adaptive peak so that selection, which was previously directional, now stabilises the population means. To investigate this we estimated selective surfaces using multivariate cubic-spline regression[30] and plotted adaptive walks on them. Figure 3A shows that EP1 has a single adaptive peak near high R and C_L and that although it walks erratically up the slope towards the peak, it does not reach it. Very rhythmic loops (very high R) may be less fit than slightly less rhythmic ones; even so it is clear that EP1 has stopped evolving at least one standard deviation in each dimension away from its adaptive peak, thus stasis is not due to an absence of selection. Interestingly, the topology of the EP1 adaptive landscape suggests that R and C_L have a synergistic effect on fitness: high C_L loops are especially fit when they have a high R as well; a model with $C_L \times R$ interaction explains significantly more of the variation than one without. A similar interaction is found in EP2 but not EP3 (SI, Supporting Text “Adaptive surfaces for EP2 and EP3”).

We next considered the possibility that the populations have simply run out of selectable variation and that they have become fixed for all beneficial variants. Figure 3 B, C show the frequency distributions of C_L and R over the evolution of EP1. The rapid progress of the population before generation 1000 is associated with a decrease in frequency of loops with the lowest chordal clarity and rhythmic complexity, likely due to selection. However, as the population continues to evolve new low- C_L and R loops are reintroduced by mutation and recombination, and throughout the evolution of the populations many loops have higher C_L and R values than the long-term O-U mean. Thus the lack of progressive evolution after about generation 500 is not due to fixation of high C_L and R variants and complete exhaustion of selectable variation. This is also true for EP2 and EP3 (Figure S8).

Using the Price equation to unravel the causes of stasis. This lack of directional selection pressure or selectable variation does not suffice to explain stasis. Alternatively, stasis could be due to an increase in the negative genetic pressures of mutation and/or recombination. To understand the

forces acting on these populations, we made use of the Price equation[31, 32, 33, 34]. The Price equation, a general description of all evolutionary processes, decomposes the mean response to selection in a given generation, $\Delta\bar{z}$, into a covariance term which describes the effect of selection, and a transmission term which describes the effect of inheritance:

$$\begin{aligned}\Delta\bar{z} &= \text{covariance term} + \text{transmission term} \\ &= \text{cov}(w/\bar{w}, z) + E((w/\bar{w})\Delta z)\end{aligned}$$

where z is the phenotype of an individual, \bar{z} is the mean phenotype of the population, w is the fitness of an individual (how many offspring it has), \bar{w} is the mean fitness of the population, $\Delta z = z_o - z_p$, where z_p is the phenotype of an individual and z_o is the mean phenotype of its offspring, and $\Delta\bar{z}$ has been defined previously. The covariance term in any generation is the product of the population variance, $\text{var}(z)$ and the strength of directional selection which, in turn, can be estimated as the slope of a linear regression of the fitness of parents on a phenotype, $\beta(w, z)$. The transmission term is based on the phenotypic similarity of parents to their offspring and so estimates the fidelity of transmission: when it is zero inheritance is perfect; when it is negative then offspring have a lower phenotype than their parents, when it is positive, a greater one.

At evolutionary equilibrium, $\Delta\bar{z} = 0$, the covariance and transmission terms must be equal in magnitude but opposite in sign. Given that our populations appear to be at equilibrium one or both of these terms must have changed during their evolution. But which? As noted above, in an O-U process the expected change from one generation to the next is a linear function of the current value with a negative slope (i.e., changes are expected to be positive when the current value is below the long-term mean, and negative when it is above). We now decompose $\Delta\bar{z}$ into covariance and transmission terms and test whether either changes as a function of the mean, \bar{z} . Considering only the first 400 generations, before C_L and R approach equilibrium, then in all cases the change in trait value due to selection (i.e., the covariance term) is independent of the current value, but the amount by which offspring differ from their parents (i.e., the transmission term) becomes increasingly negative as the current value increases (Figure 3 D, (SI, Supporting Text “Price equation parameters”). This indicates the fidelity of transmission becomes an increasing impediment to progress as adaptation proceeds. It is this factor that causes evolution to slow down as C_L and R increase over the first 400 generations.

Transmission fidelity and the limits to evolution. In organisms, a decrease in the fidelity of transmission could be due to an increase in environmental variance, recombination pressure, or mutation pressure. Since the genome for any Darwin-Tunes loop produces an identical sound file on all computers, there is no environmental variance; a decrease in the fidelity of transmission must therefore be due to either an increase in recombination or mutation pressure or both. Since the genomic rates of recombination and mutation were constant throughout the experiment, this increase cannot be due to an increase in the frequency of recombination or mutation, but must be due to increasingly deleterious phenotypic effects. Recombination could have increasingly deleterious effects if, as the population evolves, high fitness comes to depend on particular genomic configurations that can be broken up by sex, in other words, fitness epistasis increases[35]. As noted above, there is some evidence for synergistic fitness epistasis between R and C_L . Perhaps loops with pleasing combinations of R and C_L are selected, but then quickly broken up by recombination. If so, this would imply that these traits are controlled by different regions of the loops’ genomes, but we do not know this, and rhythm and chordal clarity may themselves be influ-

enced by multiple interacting loci. Alternatively, mutations may become increasingly deleterious as the populations become more adapted for the same reasons that R. A. Fisher inferred they do in organisms: the increasing vulnerability of complex, fine-tuned, structures to change[36, 37]. We cannot distinguish between these explanations for decrease in transmission fidelity in our populations, but further experiments may do so.

Curiously, if we consider all 2,513 generations of EP1, we get a different picture in which the transmission term is no longer significant for C_L , and the covariance terms for both C_L and R show a significant decline (Figure 3D). To investigate this further we decomposed the covariance term into the strength of selection, $\beta(w, z)$, and the variance of the trait, $\text{var}(z)$. The slopes $\beta(w, C_L)$ and $\beta(w, R)$ are in all cases significantly positive, showing directly that both C_L and R were under directional selection (SI, Supporting Text “Price equation parameters”). As the population mean increases, $\beta(w, C_L)$ remains constant, while $\beta(w, R)$ increases significantly, thus, consistent with our impression from the adaptive landscapes, the long-term stasis of neither trait is due to a decline in the strength of directional selection. By contrast, both $\text{var}(C_L)$ and $\text{var}(R)$ decline as the population mean increases, implying that the long-term stasis of this population is at least partly due to a decrease in the amount of phenotypic variance present (SI, Supporting Text “Price equation parameters”). Thus while recombination or mutation pressure limit adaptive evolution in the short term, in the longer term even a subtle decline in the amount of selectable variation can do so as well.

Since C_L and R have increased due to selection, they must be contributing to the overall increase in musical appeal (M) (Fig. 1). But music has many dimensions and we only measured two. We used single and multiple linear regression to estimate how much of the overall increase in M is due to the features we measured. We find that C_L alone is responsible for 3.0% of the increase in M , R alone is responsible for 2.8%, while together they account for 4.2%, leaving 95.8% unexplained (SI, Supporting Text “Explaining variance in musical appeal, M ”); thus other features must also contribute to the evolution of appealing music in these populations. In the future, we will be able to examine these with an expanded MIR toolkit.

Discussion and Conclusions

We have shown that a simple Darwinian can produce music. In recent years, inspired by cultural transmission theory[38, 39], the evolution of simple material artifacts such as stone tools has also been analysed in terms of selection-variation processes[40, 41, 42]. Our results suggest that the evolution of music can be viewed in the same way. Although our system is an artificial one it may shed light on the evolution of real musical cultures. In our system musical appeal increased rapidly but then stopped, and this stasis is mostly due to a decrease in the fidelity of transmission. Analogously, musical styles in pre-modern societies appear to be very conservative; some may be thousands of years old[6, 43, 3]. Given that many such societies lacked symbolic or mechanical means of transmitting their music, we speculate that the cause of stasis is the same: low transmission fidelity that, in such musical cultures, arises from the errors introduced as musicians teach and learn complex musical themes. Our results are also relevant to the evolutionary equilibria commonly observed in the evolution of genetic algorithms, digital organisms and real organisms[11, 10, 27, 28, 29]. Although convergence of evolving populations to an equilibrium is often interpreted as ar-

rival at an adaptive optimum or else exhaustion of selectable variation, it may be that a decrease in transmission fidelity as more complex, or at least more finely adapted, structures evolve is a very general cause of evolutionary stasis.

In focusing on the role of consumer selection, our system and analysis captures the creative role of one of the processes responsible for the music we listen to. However, the evolution of music in human societies is certainly more complex than this. Humans do compose music before releasing it for public consumption[6]; and consumers do not choose the music they like entirely on the basis on aesthetic quality, but are also influenced by the preferences of others[7]. Thus musical evolution is the result of selection at multiple levels: within individuals (producers), among individuals (consumers), and among groups (social networks of consumers). The theoretical framework we have used here can be extended to accommodate these forces since the Price equation is particularly suited to partitioning the effects of selection at different levels[32, 34, 44]. The DarwinTunes system can, similarly, be extended to accommodate these additional selective forces by allowing individual consumers to select among variants (i.e.,

compose) before releasing them into the population or by allowing consumers to see each other's preferences. The relative importance of selection at these different levels—producer, consumer, consumer-group—in shaping the evolution of the world's music is unknown and may vary among societies. Western societies have long had specialist guilds of composers and performers, but in other cultures participation is more widespread (e.g., early 20th C. Andaman Islanders[45]). The ability to download, manipulate, and distribute music via social-networking sites (e.g., ccMixer: <http://ccmixter.org>; soundcloud: <http://soundcloud.com>) has democratised the production of music and may change the balance of these forces again. In partitioning these selective forces, then, our analysis points the way to a future evolutionary dynamics of digital culture[46].

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