Graduate Research Plan Statement

Title: Energy-information trade-off in vocal development

Background: Vocal development is the result of interactions among several biomechanical and physiological processes, all of which are constrained by energy. Our attempts to understand how all these mechanistic pieces are coordinated over postnatal life is thus a formidable challenge. While the importance of energetic costs in development is obvious, we must also consider that these costs must be traded-off with information transmission: human infants and other animals use vocalizations (e.g., cries, contact calls) to solicit care from conspecifics. How these costs are traded-off during development has not been considered, yet it could provide a common, high-level framework across species within which low-level mechanistic findings may be interpreted. I propose to investigate whether a model that considers energy and information trade-offs best predicts the shape of vocal developmental trajectories in mammals; I will then test the model's predictions with empirical data.

Three different models could potentially explain the trajectory of vocal development, and each can be characterized mathematically using a cost function. The first model is through a constant and progressive change (Fig. 1a,d). The second model relies on a strong initial change followed by slow adaptation (Fig 1b,e). Both models can account for associative learning. The second model can also account for bodily growth in at least 60 species[3]. The third model considers development as stepwise (Fig 1c,f). Using data from three different mammalian species—marmoset monkeys[1,2], bats[5] and humans[6,7], all of which exhibit vocal learning—I extracted four standard acoustic features (call duration, dominant frequency, amplitude modulation frequency, and Wiener entropy) and calculated their principal component to generate one single acoustic measure. Using that measure, I found that the best model is the stepwise model. The adjusted R^2 for the linear, gradual and stepwise model are shown in Fig. 2. The stepwise model is also the only one able to accurately predict the day of transition between immature and mature-sounding vocalizations. It will therefore serve as the model for investigating the constraints that shape vocal development.

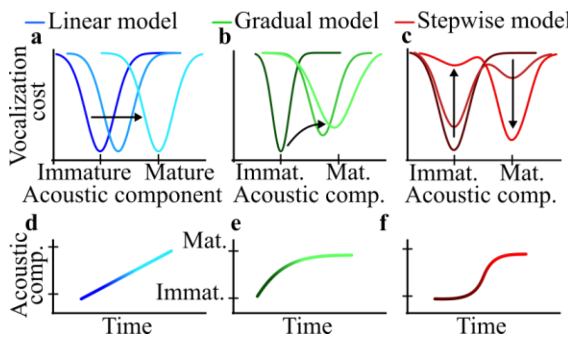

Figure 1. Model schematics. (a) First model: linear shift of the cost. (b) Second model: cost modeled through recurrence equation[4]. (c) Third model: two fixed costs balance each other. (d) Linear change. (e) Gradual change. (f) Stepwise change.

Hypothesis: The stepwise transition of vocal output is predicted to be shaped by physiological (energetic) and social (informational) constraints. These can be manipulated independently to determine how each might influence development. **Aim 1:** Test whether energy changes the transition timing in marmoset monkeys. One factor influencing the energy required to vocalize is respiratory power, thus lighter air should reduce its energetic cost. I will fit the stepwise model with vocal data collected while infants were in a helium-oxygen (lighter air) during brief daily sessions over 2 months and compare it to data outside the helium-oxygen chamber (regular air). **Aim 2:** Test whether the in-

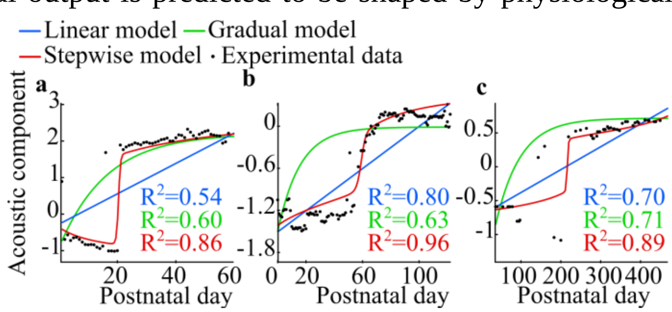

Figure 2. Model fitting. (a) Marmoset monkey. (b) Egyptian fruit bat. (c) Human.

formation transmission changes the transition timing in marmoset monkeys. Efficient information transmission is characterized by how well the infant's vocalization can be used to predict the parent's vocalizations. I will fit the stepwise model with infant vocal data recorded in sessions with high versus low levels of parental feedback over 2 months[2].

Methods: To achieve aim 1, I will study energetic manipulations using vocalizations recorded in a heliox chamber[8]. Heliox (20% O_2 and 80% He) has a lighter mass than regular air, so the energy required to pump the air out of the lungs is lower. Marmoset infants are placed for 20 min in a chamber that holds 45 L of air, and their vocalizations are recorded. To achieve aim 2, I will use vocalizations from infants placed in a 20-min playback condition, in which infants receive auditory feedback from a closed-loop playback system[11]. The infants receive either the father's or the mother's mature calls. With the closed-loop system, we can control the amount of contingent playback they will receive, thus manipulating the rate at which infants can change the informational content of their vocalizations.

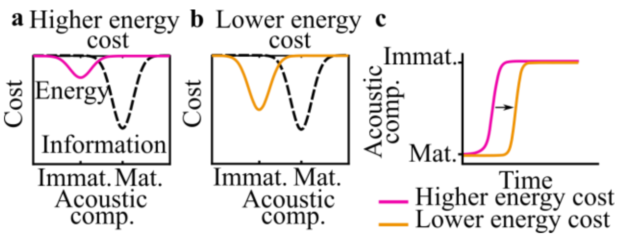

Figure 3. Schematics of energy cost manipulation. (a) Higher and (b) lower cost. (c) Simulation using costs from (a) and (b).

Results Evaluation: I can use the stepwise model to predict the change in the transition day when either the energy or information cost is manipulated (Fig. 3). That change will be compared with the change obtained in the experiments. In aim 1, by decreasing the energy cost in the heliox chamber, the transition day should happen later. By decreasing the information cost in aim 2, the transition should happen sooner. If the predictions do not hold, then either the constraints of the model are not energy and information, or the way they constrain development is not the one proposed by the model. In the first case, I can investigate other possible constraints, for example, how differences in the environment affect development. In the second case, I can check if variations of the model (such as a different cost shape) can better explain the data.

Intellectual Merit: The project has the potential to explain how vocal learning can happen in marmoset monkeys and likely other species, including humans and other vocal learners. It incorporates different factors important for vocal development into one framework, highlighting the importance of the body and the environment into behavior. The stepwise model is also generalizable to other behavioral systems (e.g., locomotion), and thus potentially useful to describe the transitions we see when categorizing any behavior into different stages.

Broader Impacts: Low socioeconomic status populations have a higher incidence of speech-language impairments, such as reduced vocabulary and phonological awareness[9]. A better understanding of vocal development can meaningfully inform intervention programs. For example, it can be used to measure how diet (energy) versus social interaction (information) lead to healthy vocal development. The computational nature of my project allows me to involve undergraduate students early on in my research. This will be facilitated by the ReMatch program at Princeton, that encourages first and second-year undergraduates to do research. The subject is engaging due to the natural curiosity around how humans and other animals communicate. Moreover, I will disseminate my findings in scientific meetings as well as in forums accessible to the public (including video lectures).

References: [1]Takahashi et al., 2015. [2]Takahashi et al., 2017. [3]Renner-Martin et al., 2018. [4]Fehér et al., 2009. [5]Prat et al., 2017. [6]Cruz-Ferreira, 2003. [7]Brent et al., 2001. [8]Zhang and Ghazanfar, 2018. [9]Perkins et al., 2013.