

FOXP2 MEDIATES OPERANT SELF-LEARNING NECESSARY FOR LANGUAGE DEVELOPMENT

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FOXP2 is a transcription factor involved in gene regulation and neural plasticity. It is of particular interest as it was discovered as the first gene to have a relationship with the development of language. At Evolang IX, FOXP was shown to affect operant learning in *Drosophila*. This finding suggests that the development of language is a form of operant learning through vocal and auditory systems. I hypothesize that functional auditory and vocal systems, integrated via FOXP2, are required for a species to be able to access complex vocal language.

1. *Language is operant learning.*

Acquisition of speech, and other non-reflexive sound production, is a form of operant learning. As I have previously shown, for children to acquire spoken language non-referent, reflexive vocalizations are controlled and conditioned into novel vocalizations (i.e. babbling) and further conditioned into complex speech (Green et al., 2012). I hypothesize that the ability to receive feedback and make appropriate modifications in this context is predicated upon functional vocal and auditory systems and therefore if either system functions incorrectly, speech and all other operant sound production will be affected. For example, post-lingually deafened adults experience deterioration in speech over time (Cowie et al., 1982). Similarly, songbirds show degradation in song after surgical deafening (Woolley et al., 1997). I further hypothesize that FOXP2 is the coordinator of the interactions between hearing and speech development.

2. *FOXP2.*

Forkhead-box protein P2 (FOXP2) is a transcription factor encoded by the FOXP2 gene. FOXP2 is comprised of a forkhead-box DNA-binding domain, polyglutamine tracts, a zinc finger, and a leucine zipper. These are common

motifs by which a transcription factor binds to DNA to regulate other genes. FOXP2 is known to regulate CNTNAP2, a gene associated with specific language impairment, among dozens of other genes (Vernes et al., 2008).

3. *Mutations in FOXP2 result in failure to develop language.*

FOXP2 was the first gene discovered to have a relationship with the development of language. A family with mutations in the FOXP2 gene, without cognitive or motor limitations, had marked communicative disabilities (Vernes et al., 1998). Vernes et al. showed that individuals with FOXP2 mutations have difficulty achieving the oral coordination necessary for speech (in addition to their other linguistic deficits).

4. *FOXP2 in non-human primates.*

FOXP2 is one of few genes that vary between humans and other primates. Enard et al. have shown two amino-acid changes in the FOXP2 gene are present in human lineage after diverging from chimpanzees. In contrast, one synonymous amino-acid change is present in orangutan lineage, but no other primates present any variants from chimpanzees (Enard et al., 2002). This human variant is fundamental and proposed as a sine qua non of primate language.

Diller and Cann point out that these amino-acid changes may not be an immediate precursor to language development, a position consistent with this theory (Diller et al., 2009). I hypothesize that FOXP2 is necessary for the development of all complex vocal communication including protolanguage. Improved vocal control then increases the selective advantage of further speech-related developments such as the vocal tract and ear ossicle optimization seen in both Neanderthals and humans.

4.1. *Neanderthal language.*

Neanderthals have a vocal tract that is adequate for phonation as summarized by Johansson (2012). A Neanderthal hyoid bone was found (Arensburg et al., 1989) in addition to two hyoid bones of likely ancestors of Neanderthals (Martinez et al., 2008) which closely resemble the hyoid of the modern human. These findings suggest a vocal tract adequate for speech.

As summarized by Johansson (2012), increased perception of sounds in the 2-4 kHz range has occurred during human evolution. Minor changes in the ear ossicles account for this increased sensitivity (Martínez et al., 2004). This

change is not present in ape ears. However, Neanderthals likely possessed this increased sensitivity as ear ossicles found have no significant differences from those of the modern human (Quam & Rak, 2008).

Neanderthals were found to possess the modern FOXP2 (Krause, 2007). Benitez-Burraco et al. (2012) discussed the gene's possible involvement in language as involvement in oral coordination related to language (White, 2010) or as a regulator of the language network/s. In contradistinction, I propose that FOXP2 is involved in oral coordination related to language **and** as a regulator of the language network/s.

With adequate speech and hearing organs as well as modern FOXP2, Neanderthals possessed all the necessary requirements for language development. FOXP2 allows for fine motor control of the speech organs while the advanced sound perception allows for focused feedback. FOXP2 mediates this relationship allowing for the Neanderthal to make minute changes in vocalization to create distinct syllables and furthermore complex speech.

5. *Operant learning in Drosophila.*

The relation between FOXP2 and language is likely related to operant learning. *Drosophila*, for example, show complete absence of self-corrective operant learning with an RNAi-mediated knockdown of the FOXP gene (Mendoza et al., 2012).

6. *FOXP2 in songbirds.*

Bird song is relevant to human speech as it is composed of rhythmic, stressed structures with varied intonation and is produced by conditioned and controlled vocalizations (Asano, 2012). During the song-learning period, the zebra finch, an age-limited song-learner, has higher levels of FOXP2 in Area X. Interestingly, canaries, seasonal song-learners, have seasonal increases of FOXP2 in Area X (Haesler et al., 2004). As shown by Haesler et al. (2007), knockdown of FOXP2 in the zebra finch causes a variable and inaccurate song. This finding suggests that FOXP2 allows for the production of stable, accurate song. I hypothesize that FOXP2 mediates operant self-learning in this context, allowing the bird to regulate song and detect differences from its song and the tutor song more accurately.

According to a study by Schulz et al., knockdown of FOXP2 in Area X of the zebra finch causes a decrease in the spine density of newly generated spiny

neurons: where FOXP2 is expressed (Schulz et al., 2010). This decrease reduces the number of synaptic pathways in Area X, reducing the plasticity and the bird's song learning ability.

A study by Teramitsu et al. (2012) has shown that deafened zebra finches do not have a deficit in basal FOXP2 levels; however, a correlation between singing and FOXP2 levels was only present in hearing birds (Teramitsu et al., 2010). This finding suggests that FOXP2 and hearing are directly related. Hearing allows for auditory feedback of song production and FOXP2 mediates the relationship between this feedback and song production. I hypothesize that the basal levels of FOXP2 do not increase in deaf birds due to the absence of feedback necessary for the operant self-learning acquired through FOXP2.

7. Discussion.

Hominid FOXP2 allows for fine coordination of the speech organs. Increased auditory perception in the 2-4 kHz range has given early humans the ability to detect slight differences between vocalizations (Johansson, 2012). FOXP has been shown to affect operant self-learning in *Drosophila* (Mendoza et al., 2012). This finding suggests that the modern FOXP2 mediates the relationship between the greater control of the speech organs and the increased auditory perception of early humans by allowing them the ability to self-correct vocalizations.

I hypothesize that FOXP2 increases oral coordination by the operant self-learning it allows. The advanced auditory perception of modern humans allows for distinction between vocalizations with only minute differences. Through operant self-learning FOXP2 allows humans to vocalize and analyze the sound produced, then to use this analysis to produce a slightly different sound. If the desired sound is not achieved, then another slightly different sound can be produced. I hypothesize that FOXP2 allows for humans to understand the effects of different motions vocally and achieve the greater coordination through conditioning as seen in the previously aphonic reconstructed children that I discussed (Green et al., 2012).

I propose that the increased ability for speech production and perception mediated by self-correction via FOXP2 is the necessary prerequisite for complex spoken language.

8. *Future Directions.*

To further understand the relation between vocal and auditory systems and FOXP2, a series of experiments could help to delineate the feedback loops. Songbirds, as previously mentioned, are an ideal model for study due to the similarity of bird song to human speech. Separating out hearing from song can be accomplished by a surgical deafening of the birds (Teramitsu et al., 2012; Wooley et al., 1997). More complex techniques are required to separate song from hearing.

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