Evidence for a causal inverse model in an avian song learning circuit.

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To allow for learning by imitation such as in speech, sensory targets must be able to instruct the brain's motor codes. The computational principles underlying this instruction remain largely unknown. In a vocal learner we explore the closed sensory-motor loop or inverse-model hypothesis according to which auditory signals feed into vocal motor areas by inverting the causal mappings from motor commands to sounds to auditory signals. Causal inverse models are appealing because they constitute the simplest known neural mechanism capable of explaining motor feats such as single-trial imitation. Causal inverse models predict that sensory inputs to motor areas follow motor responses with a temporal offset given by the total loop delay, i.e., the sum of auditory and motor response latencies. We test for existence of such models in adult male zebra finches by chronically recording from the cortical output area of a basal- ganglia pathway. At many single and multi-unit sites, sensory responses tend to mirror motor-related activity with a temporal offset of about 40 ms, in accordance with minimal loop delays estimated using electrical and auditory stimulation. We show that vocal-auditory mirroring agrees with a simple eligibility-weighted Hebbian learning rule that constitutes a generative mechanism for inverse models and that can explain puzzling aspects of auditory sensitivity in motor areas, including selectivity for the birds own song, lack of sensitivity to distortions of auditory feedback, and dependence of mirroring offsets on firing variability. Namely, variable motor sequences as in the cortical area we study (the lateral magnocellular nucleus of the anterior nidopallium, LMAN) give rise to large mirroring offsets and to causal inverse models (that map sensation to action), whereas stereotyped motor sequences as found elsewhere (HVC) give rise to zero mirroring offsets and to less powerful predictive inverse models (that map sensation to future action).