Na^+ Currents Promote Ultra-fast Spiking in Projection Neurons

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EDITORIAL

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Speed and accuracy of muscle control and coordination depend on the spiking activity of upper motor neurons. In mammals, a subclass of layer 5 pyramidal neurons (L5PNs) project from the motor cortex to various targets in the brainstem and spinal cord. These cells are involved in specific aspects of fine motor control and they produce narrow half-width action potentials (APs). Changes to their intrinsic properties have been implicated in facilitating the learning of complex motor skills in some species. Notably, primates and cats possess varying numbers of very large L5PNs with wide-caliber militated axons, fast AP conduction velocities, and ultra-narrow AP spikes. These specialized Betz-type cells, first discovered in the human motor cortex, send projections that often terminate directly onto lower motor neurons and are thought to be involved in highly refined aspects of motor control.

Birds display a diverse array of complex behaviours and cognitive skills ranging from elaborate nest building and tool usage to episodic memory and vocal mimicry. Remarkably, birds accomplish this without a typical six-layered neo cortex, which underpins the capacity for complex motor skills in mammals. Nonetheless, avian pallial nuclei form microcircuits that appear analogous to those in the mammalian neo cortex. In songbirds, the robust nucleus of the arco pallium (RA) plays a key role in singing and provides direct descending projections to brainstem motor neurons that innervate the avian vocal organ (syrinx; and respiratory muscles. RA projection neurons (RAPNs) can thus be considered analogous to L5PNs in the motor cortex Indeed, these cells share important features, like wide-caliber militated axons and multiple spine-studded basal dendrites, although RAPNs lack the large, multilayer-spanning apical tufted dendrites that are a hallmark of L5PNs. However, detailed knowledge of the ion channel composition, biophysical properties, and firing patterns of RAPNs is limited. Therefore, it is still unclear to what extent they function in an analogous manner to L5PNs.

Zebra finch RAPNs face considerable spiking demands during singing, which requires superfast, temporally precise coordination of syringeal and respiratory musculature. As the adult male sings, RAPNs exhibit remarkably precise spike timing (variance ~0.23 ms). RAPNs also exhibit increased burstiness during the developmental song learning period, their instantaneous firing rates changing from 100 to 200 Hz when they produce immature vocalizations (subsong) to 300–600 Hz when a song becomes mature (crystallized). Average overall spike rates of RAPNs increase from 36 Hz at subsong to 71 Hz in adults. Song maturation thus correlates with reduced variability in the timing of increasingly high-frequency bursts with a refinement of single spike firing precision. Importantly, nerve firing rates of >75 Hz are required for force summation in the superfast syrinx muscles. This high spike frequency in RAPNs during song production is energetically demanding as indicated by increased staining for cytochrome C in maturing males, but not female zebra finches.

Songbird RAPNs thus seem to share with Betz-type L5PNs similar evolutionary pressure for fast and precise signaling, a constraint that can lead to neurons in unrelated species sharing similar expression patterns for a specific repertoire of ion channels. A good example is electric fish species from different continents, which have convergently evolved electrocytes exhibiting similar physiology and molecular features. Indeed, high-frequency firing electrocytes with extremely narrow AP spikes co-express fast activating voltage-gated Na^+ (Nav) and K^+ (Kv) channels.