CHAPTER 6

MOTOR CORRELATES OF VOCAL DIVERSITY IN SONGBIRDS

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1. INTRODUCTION

Oscine songbirds invest a substantial amount of time producing song, which has important roles in male–male competition and in attracting and stimulating a mate (Howard, 1920), as well as in species (Becker, 1982) and individual (Falls, 1982) recognition. Their diverse and often elaborate songs have placed them at the interface of neurobiology, behavior, and ecology as excellent subjects in which to study vocal communication. Toward this end, neurobiologists have made important advances in understanding the neural basis of vocal learning (e.g., Doupe, 1993; Arnold, 1992) and the central control of song production (e.g., Yu and Margoliash, 1996; Vu *et al.*, 1994) and behavioral ecologists have gained new insights into the perceptual significance and communicative functions of song (e.g., Searcy and Yasukawa, 1996).

Between the brain mechanisms for song production, on the one hand, and vocal communication, on the other, lie the syrinx and vocal tract, which link the brain to acoustic behavior by converting the pat-

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terns of neural activity generated in the song control system of the brain into the acoustic signals that transmit information about the singer throughout the environment. The peripheral vocal system thus forms the interface between the brain and acoustic behavior—the final common path, as it were, that translates internal neural communication into external vocal communication and behavior.

The peripheral vocal system of songbirds is not simply a passive conduit through which neural signals generate sound. It is instead an equal partner with the brain and behavior in shaping vocal communication. Together with the respiratory system, the vocal periphery actively determines the limits of vocal performance and can modulate the properties of vocal signals. A knowledge of its function, limitations, and capabilities is important, both in order to decipher its neural control and to better interpret vocal behavior (Suthers, 1997, 1998). Here we summarize some of the recent advances in understanding the different motor strategies various songbirds use to produce their distinctive songs and relate these findings to the behavioral ecology of vocal communication.

2. SONG PRODUCTION: BASIC MECHANISMS

2.1. Structure for Phonation

The energy required for song production is supplied by the activity of abdominal and thoracic respiratory muscles which move air through the syrinx. These muscles are innervated by branches of various cervical, thoracic, and lumbar spinal nerves. A number of muscles participate in respiratory ventilation, but four abdominal muscles, aided by several thoracic muscles, play a major role in expiration; other thoracic muscles are responsible for inspiration (Fedde, 1987). Together, respiratory muscles ventilate the small, inelastic lungs by alternately compressing and expanding the air sacs in a bellows-like action. Most adult birds possess several air sacs, some of which are laterally paired, whereas others, such as the clavicular (=interclavicular) air sac, are fused across the midline to provide a pathway by which air can flow between air sacs on opposite sides of the body. Anatomical details, including the connections between paired air sacs, vary with the species (McLelland, 1989). There are no known anatomical valves below the syrinx (A. S. King and Payne, 1960). Because all air sacs are interconnected, only very small pressure differences are present between them during normal respiration (Scheid and Piiper, 1989; Brackenbury