C H A P T E R

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Neurobiology of Speech Production

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59.1 INTRODUCTION

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p0010 Speech is one of the most distinguishing human traits. It represents a model neural system for studying a range of human characteristics from sensorimotor control to cognition. It uses a complex control system optimized for sequential output and is used for both self-expressive and interactive communication. The production of speech reflects a complex and dynamic process dependent on the interaction among multiple cortical and subcortical regions for the fine control of more than 100 muscles located in the oral cavity, neck, and abdomen (see Figure 59.1 for an overview). In the following, we identify the set of processes involved in speech production as well as their neural substrate.

59.2 NEUROBIOLOGY OF SPEECH MOTOR CONTROL

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59.2.1 Speech Representations

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p0015 From a linguistic perspective, a number of potential candidate constructs may be represented in the neural processes associated with the production of speech. One view in the psycholinguistic literature is that grammatical encoding, or the creation of lexical items within a syntactic frame, and phonological encoding, including the specification of prosodic structure, are the two fundamental processes that create the phonetic plan (Garrett, 1993; Levelt, 1992, 1993). The phonetic plan interfaces seamlessly with speech motor processes that generate the sequence of sounds specified in the plan.

p0020 One approach to associate these broad psycholinguistic processes with their neural substrates comes from studies using speech errors. Speech errors can provide valuable insights regarding the linguistic principles that are involved in the production of speech because these errors are generally consistent with language-specific phonological rules (Goldrick & Daland, 2009). Based on speech error analyses, some researchers have postulated that the units of speech planning are individual phonological features (Mowrey & MacKay, 1990), whereas others propose that these units are bigger [e.g., phonemes (Roelofs, 1997, 1999; Stemberger, 1982), syllables (Levelt, 1999), or words]. Recently, Peeva and colleagues (2010) used functional magnetic resonance imaging (fMRI) and a repetition–suppression (RS) paradigm (Grill-Spector, Henson, & Martin, 2006; Grill-Spector & Malach, 2001) to study speech representations. Capitalizing on the RS phenomenon in which the repetition of a stimulus leads to reduced neural activity (Henson & Rugg, 2003), the authors varied the repetition rate of phonemes, syllables, and pseudowords expecting that areas sensitive to the processing of a specific type of phonological unit would show specific RS effects. Sensitivity to phonemic information was found in the supplementary motor area (SMA), the left palladium (in the basal ganglia or BG), the left posterior superior temporal gyrus (STG), and the left superior posterior lateral cerebellum. Sensitivity to syllable level information was found in the ventral premotor cortex (vPMC), which was also sensitive to phonemic information. Finally, sensitivity to supra-syllabic information was found in the right superior posterior lateral cerebellum. These results suggest that multiple levels of representations, including phonemic and syllabic, are involved in the production of speech sounds.
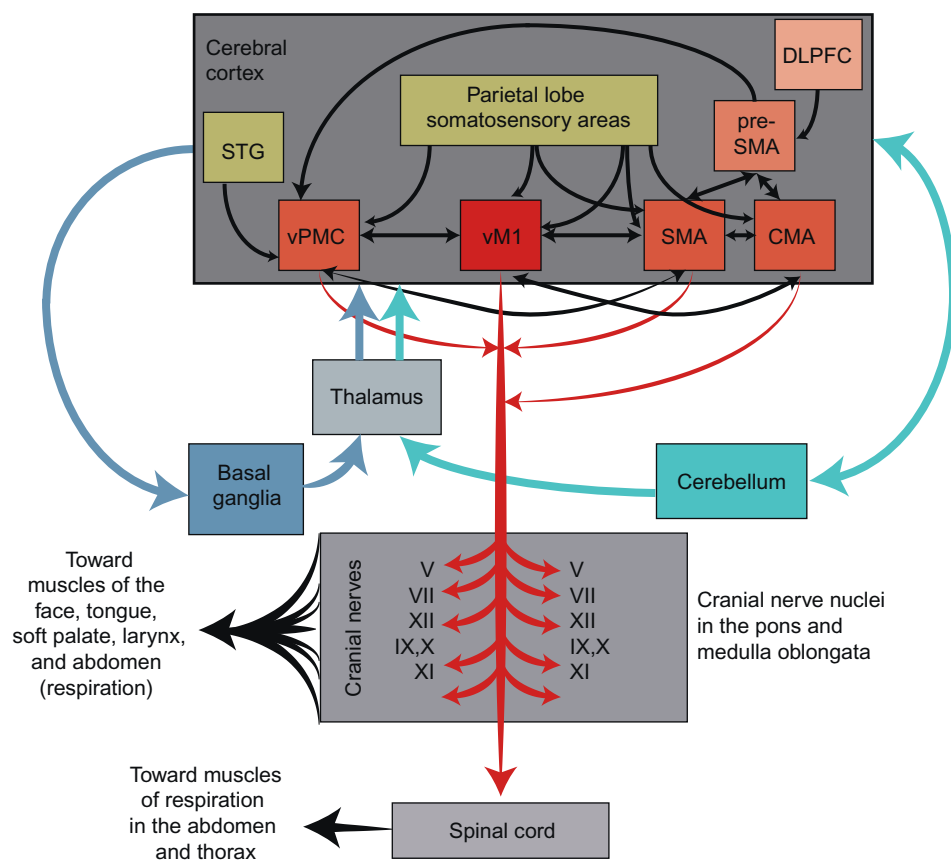
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FIGURE 59.1 Simplified illustration of the motor speech system including main cortical components and their connectivity, subcortical loops (cortico-striatal-thalamic loops and cortico-cerebellar-thalamic loops), as well as peripheral components (cranial and spinal nerve innervations to speech-related structures in the face, oral cavity, neck, and abdomen). f0010

59.2.2 Speech Motor Planning and Programming

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During speech production, phonological encoding is the retrieval of the phonological code that consists of segmental (phonemes, syllables) and suprasegmental information (such as stress). This information is used to build a representation of the syllabified word form. The syllabified word form provides the framework for the planning of a motor act. Although models of speech production converge on the notion that the output of phonological encoding is a phonological word in which metrical, syllabic, and segmental properties are fully specified, models of speech production differ with regard to whether the retrieval of the phonological code is presyllabified. For some, the syllabification is computed online depending on the context (Levelt, Roelofs, & Meyer, 1999), whereas for others the phonological code is presyllabified (Dell, 1988). Regardless of the theoretical perspective, phonological encoding is associated with the process of speech motor preparation, which involves the activation and translation of phonological representations into multiple domain-general mechanisms, including response selection, response sequencing, and movement initiation. These important mechanisms, often referred to as "supra-motor functions" or "motor cognition" (Freund, Jeannerod, Hallett, & Leiguarda, 2005), are not specific to speech production but instead are part of the planning of all voluntary actions. Speech production builds on common action control mechanisms consistent with the notion that the speech system is an overlaid functional system that "[. . .] *gets what service it can out of organs and functions, nervous and muscular, that have come into being and are maintained for very different ends than its own*" (Sapir, 1921).

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59.2.2.1 Response Selection

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Response selection in spoken language production is the process by which a set of lexical units forming a message is transformed into motor programs, that is, stored motor routines. Several neuroimaging studies have examined the process of selecting nonspeech motor responses (such as finger and hand movements) and revealed activation in the presupplementary motor area (pre-SMA) (Brodmann's medial area 6) in which the increase in activation is commensurate with demands on response selection. For instance, activation in pre-SMA is enhanced when participants are free to choose a motor response from among several alternatives compared with when they are required to execute a specific,

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stimulus-driven, motor response (Deiber, Ibanez, Sadato, & Hallett, 1996; Lau, Rogers, & Passingham, 2006; Weeks, Honda, Catalan, & Hallett, 2001). Consistent with the nonspeech literature, several fMRI studies have shown that manipulating response selection during single word production modulates distributed brain networks including the pre-SMA, but also the adjacent cingulate motor area (CMA) and the vPMC (Crosson et al., 2001; Nagel, Schumacher, Goebel, & D'Esposito, 2008; Tremblay & Gracco, 2006; Tremblay & Small, 2011). Importantly, the pre-SMA is involved in selecting single words (Alario, Chainay, Lehericy, & Cohen, 2006; Tremblay & Gracco, 2006) but also noncommunicative oral motor gestures (Braun, Guillemin, Hosey, & Varga, 2001; Tremblay & Gracco, 2010), revealing a domain-general selection mechanisms. Moreover, transcranial magnetic stimulation (TMS) to the pre-SMA leads to impaired voluntary selection of actions, including words and noncommunicative oral motor gestures (Tremblay & Gracco, 2009), supporting the notion of a domain-general selection process. Taken together, these results suggest that the pre-SMA plays a central role in selecting motor responses for speech production. The pre-SMA has a connectivity pattern that is ideal for linking higher-level cognitive (including linguistic) and motor processes, a *sine qua non* for the implementation of response selection, with important projections from the prefrontal cortex, particularly the dorsolateral prefrontal cortex or DLPFC (Lu, Preston, & Strick, 1994; Luppino, Matelli, Camarda, & Rizzolatti, 1993), and connections with several nonprimary motor areas, such as the SMA-proper and the PMC (Luppino & Rizzolatti, 2000), for controlling motor output. Recent fMRI evidence suggests a role for the caudate nucleus in response selection for speech production (Argyropoulos, Tremblay, & Small, 2013), consistent with evidence on the anatomical connectivity of the caudate, which connects with the prefrontal as well as the SMA/pre-SMA (Di Martino et al., 2008; Lehericy et al., 2004), suggesting that response selection is implemented through cortico-striatal connections between the pre-SMA and the caudate nucleus.

59.2.2.2 Response Sequencing

In his classic article on serial order, Lashley described the problem of organizing component parts of an action into movement sequences as the *action syntax problem* (Lashley, 1951). The manifestation of action syntax can be seen in a multitude of behaviors ranging from human thought (Marsden, 1984) to grooming behavior in rats (Aldridge, Berridge, & Rosen, 2004). For speech, action sequences can be organized around multiple components (phonemes, syllables, words, phrases, etc.); without appropriate timing, in terms of either initiating the action or sequencing the action units, communication would be difficult. fMRI studies have shown that motor sequencing is implemented in a network of regions organized around nonprimary motor areas (SMA-proper, PM), the cerebellum, and the BG (Bengtsson, Ehrsson, Forssberg, & Ullen, 2005; Gerloff, Corwell, Chen, Hallett, & Cohen, 1997; Macar et al., 2002). Repetitive TMS of the SMA-proper results in sequential timing disruptions in a complex finger movement task (Gerloff et al., 1997); SMA-proper activation accompanies tasks requiring the processing of temporal patterns (Macar et al., 2002). Using fMRI, Bohland and Guenther (2006) showed a bilateral network including the SMA, the anterior insula, and the superior cerebellum that was more strongly recruited for the production of complex sequences of syllables (ka-ru-ti) compared with the production of simpler sequences, which consisted of repeating the same sound three times (ta-ta-ta), consistent with the non-speech literature. Although there remains a number of issues regarding the implementation of selection and sequencing mechanisms for speech, the available empirical evidence, though limited, suggests that speech production relies on common action control mechanisms centered on the pre-SMA, SMA, and vPMC.

59.2.2.3 Motor Programming

Preparing speech production also involves fine-tuning of the planned motor routines, including adjustments of velocity, muscle tone, movement range, and direction. Motor programming is necessary because even though a closed set of syllables is available in each language and probably stored as set of motor routines, syllables and words are never produced identically, they are co-articulated and modulated as a function of the linguistic, environmental, emotional, and social contexts. Motor programming is usually believed to involve both online feedback-based and feedforward control systems. According to Van der Merwe (2009), regions involved in programming include the cerebellum, SMA-proper, M1, and the BG, but experimental evidence is lacking. The issue of feedback-based motor control is discussed in Section 59.3.

59.2.2.4 Movement Initiation

The initiation and termination of an action is fundamental to all voluntary motor behaviors. For speech production, starting and stopping speech movements are associated with a diverse range of communicative actions such as turn-taking, producing a list of words, and the insertion of pauses for emphasis. The SMA-proper has been previously identified as contributing to speech timing (Brendel et al., 2010; Gracco, 1997) and, more generally, has been associated with sequence timing as well as the perception of time. Recently, using functional connectivity analysis, and evaluating the temporal dynamics of the BOLD signal, two separately organized networks for speech

production have been proposed (Brendel et al., 2010; Riecker et al., 2005) with the SMA and the insula identified as network components contributing to motor timing. For example, TMS to the SMA results in sequential timing disruptions (Gerloff et al., 1997), varying rate of stimulus presentation during reading results in modulation of SMA-proper activity (Price, Moore, Humphreys, Frackowiak, & Friston, 1996), and SMA activity accompanies tasks requiring the processing of temporal patterns (Bengtsson et al., 2005; Macar et al., 2002). Similarly, damage to the insula results in speech initiation impairments (Shuren, 1993) and apraxia of speech (Dronkers, 1996), a disorder of temporal sequencing, although there is controversy surrounding the role of insula in motor sequencing (Hillis et al., 2004). One possibility is that the SMA-proper and insula may be working to coordinate and time sequential actions, possibly through priming and then triggering motor cortex output. Speech and oral movements are localized around the central sulcus of the insula in an area that does not have direct projections onto lower motor neurons but does connect to frontal regions, including the DLPFC as well as the SMA and the sensorimotor portions of the striatum (Augustine, 1996). The DLPFC on the right hemisphere is known to modulate lower level systems (Shallice, 2004) and activity in the right DLPFC may be contributing to speech timing and/or temporal processing of action sequences (Coull, Frackowiak, & Frith, 1998; Vallesi, Shallice, & Walsh, 2007). It appears that the insula and SMA-proper form an integrated network component, operating in concert with peripheral feedback systems, to time sequential speech motor output. When there is a need for explicit timing control, prefrontal cortex participation is recruited.

p0050   Another way to study movement initiation is to compare the manner in which movements are triggered, whether externally by sensory events or at will. Movements initiated by external stimuli produce reliable activity in SMA-proper (Lee, Chang, & Roh, 1999; Thickbroom et al., 2000; Wiese et al., 2004) as well as in the left dorsal PMC (Krams, Rushworth, Deiber, Frackowiak, & Passingham, 1998; Lepage et al., 1999; Weeks et al., 2001), suggesting that these areas are involved in initiating actions based on external sensory triggers. In humans, TMS to the left PMC results in a response delay and a disruption in the early stage of reaching and grasping (before movement execution), suggesting a role in the onset of movement (Schluter, Rushworth, Passingham, & Mills, 1998). Importantly, the contrast of self-initiated and externally triggered movements reveals activation in the pre-SMA (Deiber et al., 1996; Jenkins, Jahanshahi, Jueptner, Passingham, & Brooks, 2000; Tsujimoto, Ogawa, Tsukada, Kakiuchi, & Sasaki, 1998), suggesting a role for this region in the

generation of an internal trigger to move, which supports a role for the SMA/pre-SMA in the timing and initiation of actions. Another potentially important region for the timing of actions and the generation of a movement trigger is the BG. In patients with Parkinson's disease (PD), a disorder of BG, there is a clear decline in the ability to initiate movements at will without a concomitant reduction or slowing of externally triggered actions (Cunnington, Iansek, & Bradshaw, 1999; Freeman, Cody, & Schady, 1993; Praamstra, Stegeman, Cools, Meyer, & Horstink, 1998). Other BG dysfunctions lead to difficulty starting, stopping, or sustaining movements including speech (Speedie, Wertman, Ta'ir, & Heilman, 1993), as well as abnormal rate, regularity, and temporal ordering of speech movements (Ludlow, Connor, & Bassich, 1987; Skodda, 2011; Skodda & Schlegel, 2008; Volkmann, Hefter, Lange, & Freund, 1992), demonstrating the importance of BG for the timing of speech actions.

59.3 SPEECH MOVEMENT EXECUTION   s0050

p0055   The final output for speech comes mainly from the ventral part of the primary motor cortex (vM1), which contains the neurons controlling the vocal tract (Penfield & Boldrey, 1937). It has been estimated that approximately 100 striated and visceral muscles, distributed across the abdomen, neck, larynx, pharynx, and oral cavity, are involved in the production of speech, reflecting the immense complexity of this functional system, which, in mature speakers, may produce as many as 14 phonemes per second (i.e., between six and nine syllables per second) (Kent, 2000).

p0060   The pyramidal system, which includes the corticospinal and corticobulbar tracts, is one of the most important efferent pathways for the control of voluntary muscle contractions. It connects neurons in the cortex (upper motor neurons, UMN) to alpha (lower) motor neurons (LMN) located in the brainstem and spinal cord. LMN innervate the muscle fibers located in the face, neck, and abdomen. M1 is the cortical area that contains the largest number of pyramidal fibers (Kuypers, 1973; Murray & Coulter, 1981; Ralston & Ralston, 1985), particularly the giant Betz cells located in cortical layer V. However, anatomical studies have shown that M1 is connected through long and short association fibers to multiple nonprimary motor areas, including the SMA (Dum & Strick, 1991, 1996; Muakkassa & Strick, 1979) the CMA located just beneath the SMA on the dorsal and ventral banks of the cingulate sulcus (Dum & Strick, 1991; Muakkassa & Strick, 1979) and the dorsal and ventral PMC (Barbas & Pandya, 1987; Dum & Strick, 1991; He, Dum, & Strick, 1993). Importantly, these nonprimary motor areas

contain a high density of corticospinal and corticobulbar neurons, directly projecting to the spinal cord through the pyramidal tract (for a review of the connectivity of nonprimary motor areas, see Picard & Strick, 1996, 2001), and thus each has the potential to influence the generation and control of movement independently of M1 (Dum & Strick, 1991). Electrical stimulation of the SMA (Fried et al., 1991; Morris, Dinner, Luders, Wyllie, & Kramer, 1988; Penfield & Welch, 1951; Talairach & Bancaud, 1966) and CMA (von Cramon & Jurgens, 1983) induce vocalization and speech arrests in humans, suggesting a role in the control of phonation and articulation for these regions.

p0065 The corticospinal tracts innervate motor nuclei located in the spinal cord, whereas corticobulbar fibers innervate motor nuclei located in the brainstem. Because the motor nuclei involved in the control of respiration (mainly expiration), phonation, and articulation are located in the pons, down to the lumbar portion of the spinal cord, the production of speech depends on the integrity of both the corticospinal tract, for the innervations of the muscles of respiration in the abdomen, neck, and shoulder, and the corticobulbar tract, for the sensorimotor innervations of laryngeal and supralaryngeal muscles (for reviews, see Jurgens, 2002, 2009) through six pairs of cranial nerves (CN V: trigeminal; CN VII: facial; CN IX: glossopharyngeal; CN X: vagus; CN XI: accessory; CN XII: hypoglossal).

p0070 All cortical axons (originating from M1, SMA, CMA, and PMC) forming the corticobulbar and corticospinal tracts converge into the internal capsule, located between the thalamus and BG, with fibers originating from ventral areas located rostrally to those originating from more dorsal areas (Beevor & Horsley, 1890; Dejerine, 1901). Most pyramidal fibers cross from one side to the other before entering the spinal cord at the level of the medulla oblongata (i.e., the pyramidal decussation); corticobulbar fibers cross at the level of the brainstem, although there are substantial bilateral innervations of the CN motor nuclei. The exceptions include contralateral innervations of ventral cell groups of the motor nucleus of the facial nerve (CN VII), which supply muscles of the lower quadrants of the face (e.g., the orbicularis oris muscle), and the hypoglossal nucleus (CN XII), which supplies the intrinsic and extrinsic muscles of the tongue.

p0075 It has been suggested that vocalizations are controlled through two distinct cortical-subcortical pathways, one involving a circuit formed by the CMA, the periaqueductal gray matter (PAG), and the reticular formation for the control of innate vocal patterns (e.g., crying, laughing, and moaning), and another connecting M1 to the phonatory motoneurons through the reticular formation for the control of patterned speech and singing (Hsieh, Petrosyan, Goncalves, Hickok, & Saberi, 2011; Jurgens,

2002). This second circuit involves the cortico-striatal motor loop. Thus, M1 is connected not only to multiple nonprimary motor areas in the frontal lobe but also to the BG and cerebellum through the thalamus, and also to the reticular formation in the brainstem, controlling multiple aspects of speech production including respiration, vocalization, and articulation.

59.4 FEEDBACK PROCESSING AND SENSORY-MOTOR INTEGRATION s0055

p0080 Early in the developmental process, the functional connection between speech perception and speech production is established and the ability to modify this coupling reflects the neural plasticity that continues throughout the life span. The resultant sensorimotor learning is the substrate on which developmental stages of speech and language develop, and one in which sensory feedback plays a crucial role (Mowrer, 1952). Somatosensory information from the lips and jaw have real-time access to modulate the spatial (Abbs & Gracco, 1983; Abbs, Gracco, & Cole, 1984; Gracco & Abbs, 1985; Shaiman & Gracco, 2002) and temporal aspects of speech sequences (Gracco & Abbs, 1989; Saltzman, Lofqvist, Kay, Kinsella-Shaw, & Rubin, 1998). Similar kinds of results are obtained from unanticipated alteration of auditory feedback for pitch (Burnett, Freedland, Larson, & Hain, 1998; Jones & Munhall, 2000) and formants (Purcell & Munhall, 2006a, 2006b). The overarching conclusion is that sensory and motor systems for speech are in a constant state of interaction and integration and, most importantly, the sensorimotor integration forms the basis for successful and efficient speech production (Gracco, 1991).

p0085 From a control perspective, speech production can be conceptualized as representing a hybrid control scheme consisting of feedforward and feedback-like neural processes (Abbs et al., 1984; Guenther, Ghosh, & Tourville, 2006; Hickok, 2012; Houde & Nagarajan, 2011; Tourville, Reilly, & Guenther, 2008). Feedforward control is used to compute, before movement onset, the necessary motor commands that will achieve generally a desired movement goal given the system's current state. That is, the feedforward controller assembles a basic motor plan prior to movement onset and sends the commands to the appropriate musculature for execution. In contrast, feedback processes are used to adjust and correct motor commands that are planned or executed by the feedforward controller. However, if such adjustments would depend solely on afferent input signals, there would be an unavoidable delay that may be too long for movements as fast as those involved in many skilled actions, including speech production. Feedback control processes can also be used to

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predict the sensory consequences of movements by making use of a copy of the prepared motor commands (efference copy or corollary discharge) (Sperry, 1950; Von Holst & Mittelstaedt, 1973). As such, information from somatosensory and auditory systems contributes in multiple ways. First, as part of the feedforward process, the sensory systems provide information about the initial conditions such that the motor commands for a desired outcome can be successfully achieved given the state of the vocal tract. Second, as part of the predictive process, they interact with the control signals to estimate the consequences of the planned action. Finally, as part of the feedback process, they modulate, in real time, adjustments to the motor commands based on re-afferent input during movement execution as well as signaling the achievement of the desired action.

p0090 The neural substrate associated with the sensorimotor aspects of speech production involves a mostly bilateral network of brain regions, including vM1 and sensory areas (somatosensory cortex, STG), nonprimary motor areas (vPMC, SMA-proper, CMA, and the insula), and subcortical regions associated with sensorimotor control (putamen, cerebellum, thalamus) (Ackermann & Riecker, 2004; Argyropoulos et al., 2013; Grabski, Tremblay, Gracco, Girin, & Sato, 2013; Riecker et al., 2004, 2005; Riecker, Wildgruber, Dogil, Grodd, & Ackermann, 2002; Tremblay, Deschamps, & Gracco, 2013; Tremblay & Gracco, 2006, 2009; Wise, Greene, Büchel, & Scott, 1999), areas that are known to receive afferent input from auditory and somatosensory areas. For example, in the macaque, the vPMC receives projection from sensory areas, including associative somatosensory area SII (Matelli, Camarda, Glickstein, & Rizzolatti, 1986) and the posterior STG (Chavis & Pandya, 1976; Schmahmann et al., 2007), whereas the SMA-proper receives important projection from the superior parietal lobule (area PEci, in the cingulate sulcus), which contains a complete somatosensory map of the body (Pandya & Seltzer, 1982) as well as from areas SII and SI (Luppino et al., 1993; McGuire, Bates, & Goldman-Rakic, 1991a, 1991b). Projections to the putamen have been reported from regions within the supratemporal plane and the STG (Yeterian & Pandya, 1998). The rostral and medial parts of STG project to rostroventral and caudoventral portions of the putamen, whereas the caudal portion of STG projects to caudal putamen. Recently, using resting state functional connectivity in humans, the dorsal portion of the putamen has been shown to connect with regions of the temporal cortex (Di Martino et al., 2008). As such, reafference may be an important source of information to assist in both the spatial and timing adjustments for the dynamic modulation of speech motor output as well as signaling successful achievement of speech motor goals (Gracco & Abbs, 1989).

p0095 For the cerebellum, bilateral posterior lobe activation in the vicinity of hemisphere lobule VI (Schmahmann et al., 1999) has been consistently reported during speech production (Ackermann, Mathiak, & Riecker, 2007; Riecker et al., 2002; Wise et al., 1999), most likely reflecting cortico-ponto-cerebellar projections from and to M1 (Kelly & Strick, 2003), possibly as part of an efference copy signal. A second area of activation on the inferior portion of the cerebellar hemisphere lobule VIIIA has been associated with auditory (Tourville et al., 2008) and somatosensory (Golfinopoulos et al., 2011) perturbations, as well as with rhythmic orofacial movements (Corfield et al., 1999) and sequencing nonmeaningful syllables (Bohland & Guenther, 2006; Riecker, Kassubek, Groschel, Grodd, & Ackermann, 2006). The posterior lobe of the cerebellum receives sensory input from the trigeminal nerve (which provides sensorimotor innervations of the muscles of mastication) as well as the auditory system (Huerta, Frankfurter, & Harting, 1983; Ikeda & Matsushita, 1992; Pastor et al., 2002), and this area of the cerebellum may be implicated in multisensory rather than motor processing (Stoodley & Schmahmann, 2009; Thickbroom, Byrnes, & Mastaglia, 2003). Hence, sensory information from the dynamics of speech articulation has access to multiple brain regions through cortico-cortico, cortico-striatal, and cortico-cerebellar control loops.

59.5 CONCLUSION s0060

p0100 In this chapter, we have shown that the neural system that controls speech production is immensely complex at all levels of the nervous system, involving multiple sensorimotor regions for motor planning and execution including M1, SMA, pre-SMA, CMA, the insula, and the supratemporal and inferior parietal cortices. Loops of internal control involving the BG, thalamus, and cerebellum are also involved in several aspects of speech movement preparation, including sequencing and temporal ordering. These regions work in concert to assemble complex, temporally ordered, and co-articulated sequences of speech movements; motor commands are sent through corticospinal and corticobulbar tracts involving seven cranial nerves, multiple spinal nerves, and more than 100 striatal and visceral nerves. Despite this remarkable complexity, the chain of events that leads to the production of speech occurs within several hundreds of milliseconds.

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J. SPEAKING

NON-PRINT ITEM

Abstract

Speaking is a dynamic process in which neural representations associated with language and the constantly changing vocal tract configurations used to produce speech are seamlessly integrated to communicate. This integrative process requires a stable repertoire of motor routines and associated flexible sensorimotor and cognitive processes for speech preparation, execution, and monitoring. The development of neurobiologically plausible models of speech production requires an understanding of the role and contribution of both central and peripheral factors in the acquisition, maintenance, and reorganization of the brain-behavior patterns underlying speech production. Recent advances in brain imaging and neuromodulation methods, signal processing, and data analysis techniques have provided new insights into the organization of the brain networks and brain-behavior relations, leading to more comprehensive and more realistic models of speech production. In this chapter we identify the set of processes that are involved in producing speech and their neural substrate.