

Motor system evolution and the emergence of high cognitive functions



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ABSTRACT

In human and nonhuman primates, the cortical motor system comprises a collection of brain areas primarily related to motor control. Existing evidence suggests that no other mammalian group has the number, extension, and complexity of motor-related areas observed in the frontal lobe of primates. Such diversity is probably related to the wide behavioral flexibility that primates display. Indeed, recent comparative anatomical, psychophysical, and neurophysiological studies suggest that the evolution of the motor cortical areas closely correlates with the emergence of high cognitive abilities. Advances in understanding the cortical motor system have shown that these areas are also related to functions previously linked to higher-order associative areas. In addition, experimental observations have shown that the classical distinction between perceptual and motor functions is not strictly followed across cortical areas. In this paper, we review evidence suggesting that evolution of the motor system had a role in the shaping of different cognitive functions in primates. We argue that the increase in the complexity of the motor system has contributed to the emergence of new abilities observed in human and nonhuman primates, including the recognition and imitation of the actions of others, speech perception and production, and the execution and appreciation of the rhythmic structure of music.

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Abbreviations: 9, dorsolateral prefrontal area 9; 9d, dorsolateral prefrontal area 9d; 12l, ventrolateral prefrontal area 12l; 46, dorsolateral prefrontal area 46; 46d, dorsolateral prefrontal area 46d; AIP, anterior intraparietal area; AS, arcuate sulcus; A1, primary auditory area; ASAP, action simulation for auditory prediction hypothesis; CS, central sulcus; CN, caudate nucleus; DLPFC, dorsolateral prefrontal cortex; DTI, diffusion tensor imaging; fMRI, functional magnetic resonance imaging; GPe, globus pallidus externus; GPi, globus pallidus internus; IPL, inferior parietal lobe; IPS, intraparietal sulcus; ITC, inferior temporal cortex; LIP, lateral intraparietal area; LS, lateral sulcus; LuS, lunate sulcus; M1, primary motor area; M2, secondary motor cortex; mCBGT, motor cortico-basal ganglia-thalamo-cortical circuit; MD, nucleus medialis dorsalis; MIP, middle intraparietal area; MPC, medial premotor cortex; mt, time of movement; PE, parietal area PE; PEc, parietal area PEc; PF, part of rostral inferior parietal convexity; PFG, part of rostral inferior parietal convexity, caudal to PF; PFC, prefrontal cortex; PG, part of caudal inferior parietal convexity, caudal to PFG; PMd, dorsal premotor cortex; PMdc, caudal dorsal premotor area; PMdr, rostral dorsal premotor area; PMv, ventral premotor cortex; PMvc, caudal ventral premotor area; PMvr, rostral ventral premotor area; PrCS, precentral sulcus; pre-SMA, presupplementary motor area; PS, principal sulcus; SCT, synchronization–continuation tapping task; SMA, supplementary motor area; SNr, substantia nigra pars reticulata; SPL, superior parietal lobe; STG, superior temporal gyrus; STN, subthalamic nucleus; STS, superior temporal sulcus; S1, primary somatosensory cortex; st, time of stimulus presentation; VApC, nucleus ventralis anterioris pars parvocellularis; VIP, ventral intraparietal area; VLPFC, ventrolateral prefrontal cortex; V1, primary visual area; V2, secondary visual area.

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preparation and execution of different goal-directed actions and the processing of the corresponding sensory information. M1, PMdc, SMA, PMvc, and PMvr have main reciprocal connections with specific regions in the parietal cortex and are considered to be parieto-dependent motor areas (Battaglia-Mayer et al., 2003; Dum and Strick, 1991; He et al., 1993). Additionally, all of these areas send direct projections to the spinal cord (Dum and Strick, 1991; He et al., 1993). In contrast, the pre-SMA and PMdr receive major connections from the prefrontal cortex (granular-prefronto-dependent areas, including the frontal eye fields, the dorsolateral and the orbitofrontal cortex; Bates and Goldman-Rakic, 1993; Luppino et al., 2003; Wang et al., 2005), and instead of projecting to the spinal cord, they project to the motor nuclei of the brainstem (Dum and Strick, 1991). Based on this pattern of connectivity, different researchers have suggested that prefrontal inputs enter into the motor system mainly through the pre-SMA and PMdr areas (Rizzolatti et al., 1998).

The predominant connections between motor and parietal subdivisions support the existence of parallel circuits specialized in the use of sensory information for motor control and cognition (Fig. 1, Andersen and Buneo, 2002; Bisley and Goldberg, 2003; Caminiti et al., 1996; Colby and Goldberg, 1999; Colby and Duhamel, 1991; Middlebrook and Sommer, 2012; Murata et al., 1996; Powell and Goldberg, 2000; Purcell et al., 2012; Quian Quiroga et al., 2006; Rizzolatti et al., 1998; Sakata et al., 1995; Shikata et al., 1996; Snyder et al., 1997; So and Stuphorn, 2012). Such parieto-frontal circuits participate in several sensory-motor functions, including, but not limited to:

- (1) VIP-PMvc. The representation of the peripersonal space and the transformation of object locations into reaching movements toward them (Colby and Goldberg, 1999). The representation of movement in near extrapersonal space for the guidance of movements in dense space (Bremmer et al., 2013; Chen et al., 2011, 2013a,b) and the control of defensive movements in response to objects approaching the head (Cooke et al., 2003).
- (2) AIP-PMvr. The performance of visuomotor transformations for grasping movements (Murata et al., 1996; Sakata et al., 1995; Shikata et al., 1996).
- (3) PF-PMvr. The recognition of observed actions (Nelissen et al., 2011; Rizzolatti and Sinigaglia, 2010).
- (4) The use of somatosensory (PEip/PEc-PMdc) or somatosensory and visual information (MIP-cPMd) to control reaching and leg

movements (Caminiti et al., 1996; Colby and Duhamel, 1991; Ferraina et al., 1997; Lacquaniti et al., 1995).

- (5) Supplementary eye fields/PMdr-LIP. The cognitive processing of information associated with the oculomotor system (Andersen and Buneo, 2002; Bisley and Goldberg, 2003; Colby and Goldberg, 1999; Middlebrook and Sommer, 2012; Powell and Goldberg, 2000; Purcell et al., 2012; Quian Quiroga et al., 2006; So and Stuphorn, 2012; Snyder et al., 1997).

In accordance with these proposed parieto-frontal circuits, it has been shown that intracortical microstimulation in the anterior half of posterior parietal cortex (PPC) produces the following evoked behaviors: stimulation of dorsal PPC caused contralateral forelimb movements, including defensive, hand-to-mouth, and reaching movements; whereas stimulation of the most medial PPC sites evoked complex movements of forelimbs and hindlimbs (Stepniewska et al., 2005, 2009). Remarkably, such parieto-frontal circuits have been found in prosimian primates, new world monkey, as well as in macaque monkeys (Kaas et al., 2011).

2. The evolution of the motor system

Primates are classified into two main lines: Strepsirrhines, which include lemurs and lorises, and Haplorhines, which comprise tarsiers and anthropoids (Cartmill, 2010; Williams et al., 2010). Extant anthropoids are classified, in turn, as Platyrrhini constituted by the New World Monkeys, and Catarrhini, which contains Old World Monkeys (Cercopithecoidea), apes, and humans (Fig. 2, Hominoidea, Cartmill, 2010; Kay et al., 1997; Williams et al., 2010). New World monkeys are characterized by some dentition traits and molecular markers (Cartmill, 2010), and they have evolved unique characteristics among primates, such as the prehensile tail observed in some species of the families Atelidae and Cebidae (Wildman et al., 2009). In the past, it was thought that New World monkeys had poor brain folding in comparison with Old World Monkeys (Connolly, 1950). Nevertheless, when controlling for brain size, all anthropoids show an equivalent extent of cortical folding (Zilles et al., 1989).

Apes are traditionally divided further into the lesser apes that include all the species of gibbons and the great apes that comprise chimpanzees, gorillas, orangutans, and bonobos (Dixson, 1981). Great apes and humans share adaptations thought to be related to an arm-swinging form of locomotion, including long forearms with

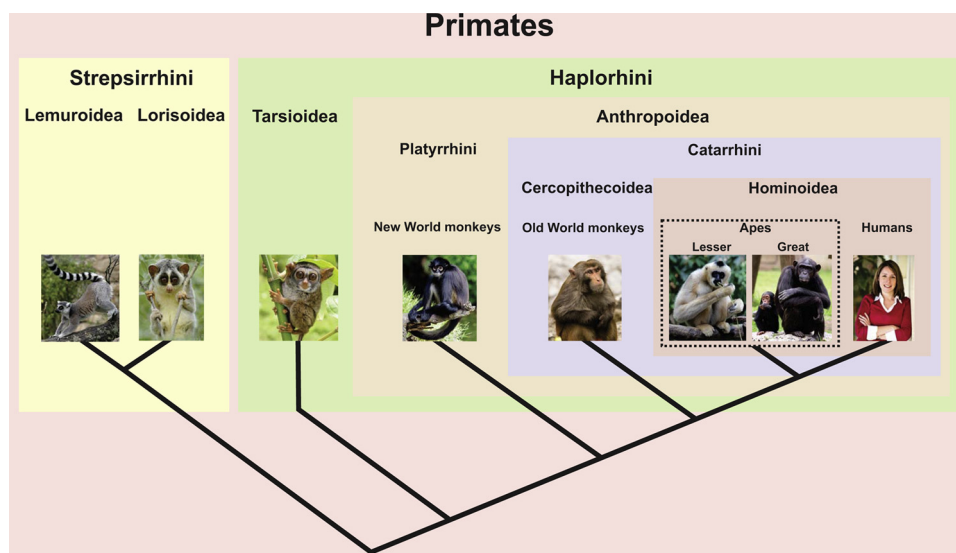


Fig. 2. Classification of extant primates.

articulations modified for greater flexibility, elongated clavicles, a transversely broadened thorax, and a reduction of the lumbar section of the vertebral column (Cartmill, 2010). Characteristic of apes are also the lack of a tail, longer gestation, and later time of first reproduction than Old World monkeys (Kaas, 2005).

The study of the fossil record and the comparison of common features observed across the major branches of the mammalian radiation have facilitated the inference of changes experienced by the motor system from the appearance of mammals to the evolution

of modern primates. The evidence obtained with these methodologies suggests that the original motor system was modest. The first mammals had simple sensory and motor systems, with few cortical areas associated with each system (Kaas, 2010). Indeed, some authors consider that a well-differentiated M1 was not present in such extinct groups. In that case, the motor cortical neurons could have overlapped with somatosensory cortical neurons, as observed in extant marsupials (Fig. 3a, Frost et al., 2000; Kaas, 2004, 2008, 2011; Walsh and Ebner, 1973).

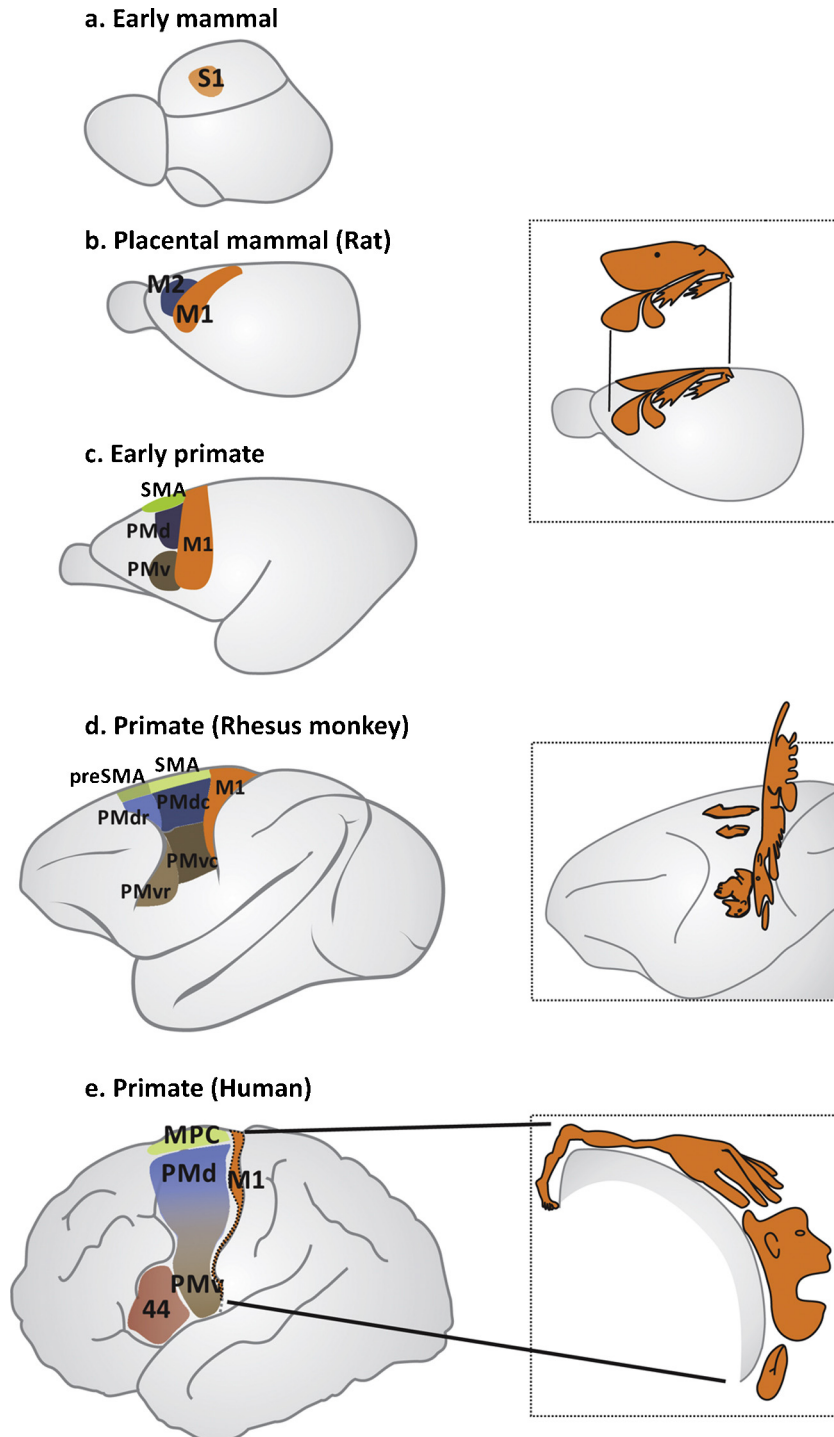


Fig. 3. Comparison of the segmentation and somatotopy of the motor system across several mammalian groups. Note that early mammals are thought to lack a differentiated M1 area (see main text). M1: primary motor cortex, M2: secondary motor cortex, PMd/PMv: dorsal/ventral premotor cortex, PMdr/PMdc: rostral/caudal dorsal premotor areas, PMvr/PMvc: rostral/caudal ventral premotor areas, S1: primary somatosensory cortex, SMA/pre-SMA: supplementary/presupplementary motor areas. Area 44 in (e) corresponds to part of Broca's area. The drawings are not to scale. (a) Modified from Kaas (2011); (b) adapted from Brecht (2011) and Kaas (2004); (c) modified from Kaas (2004); (d) adapted from Rizzolatti and Luppino (2001); (e) adapted from Picard and Strick (2001) and Schott (1993).

A well-differentiated M1 likely emerged in placental mammals (Kaas, 2004, 2010). In this group, the major source of inputs to M1 comes from the somatosensory cortex (Kaas, 2004). A secondary motor area has also been described in some placental mammals. In the rat, for example, there is a second forelimb representation with a pattern of connections that resembles those of premotor and supplementary motor areas of primates (Fig. 3b, Kaas, 2010). Tree shrews (Scandentia), one of the closest living relatives to primates, also have a second motor representation (M2) and a cingulate-like motor area in the medial part of the cerebral hemisphere (Kaas, 2010). On the other hand, direct cortico-motoneuronal connections are thought to be present only in some anthropoids, as they are absent in cats, rats, raccoons mice, tree shrews, lemurs, and marmoset monkeys (Lemon, 2008).

In contrast to the relatively few motor areas present in nonprimate placental mammals, early primates (the hypothetical ancestors of extant primates based on comparative anatomy) showed an increment in the number of frontal motor area. Primate ancestors likely had a well differentiated M1 with large representations of forelimb trunk, leg, and face movements. In addition, these animals probably had dorsal and ventral premotor areas, SMA and pre-SMA, and two or more cingulate motor areas (Fig. 3c, Kaas, 2004, 2010). Both motor and premotor cortices received projections from rostral regions of the posterior parietal cortex (Kaas, 2004); premotor areas also received inputs from the prefrontal cortex (Kaas, 2008). Early primates had a frontal eye field where electrical stimulation evoked eye movements (Kaas, 2004). Nevertheless, the control of individual digit movements was limited (Kaas, 2004).

A subsequent refinement of the motor system was observed in anthropoid primates (monkeys, apes, and humans, Kay et al., 1997; Schmitt, 2010). M1 of anthropoids shows an increase of the area devoted to hand and individual digit movements, and it is segmented into rostral and caudal portions with different physiology, connectivity, and architecture (Kaas, 2004). In addition, the cortico-motoneuronal connections are well developed in Old World monkeys and some New World monkeys, and they are more numerous in apes (Lemon, 2008). Anthropoids also have PMvr, PMvc, and two or three divisions of the dorsal premotor cortex, including the PMdr and PMdc (Fig. 3d, e). In addition, an important characteristic of anthropoids is a foveate retina with a cone-rich central region, an enlarged brain, and a higher complexity of the visual centers (Cartmill, 2010). Remarkably, the appearance of the foveate retina and a higher degree of individual digit control suggest improved manual motor activities guided by visual information in monkeys, apes, and humans.

A final increase in brain size occurred in humans that have the largest brain of primates (Creely and Khaitovich, 2006). Interestingly, the proportion of cortex dedicated to the frontal lobe is similar in humans and great apes, but is smaller in lesser apes and monkeys (Semendeferi et al., 2002). Similarly, some regions of the inferior parietal lobe of humans are enlarged in comparison with macaques and strong connections between this region and the frontal cortex are observed in humans but not macaques (Mars et al., 2011). Studies of parcellation of the dorsal frontal cortex on the basis of functional and anatomical connectivity suggest that the organization of human and monkey frontal regions is similar with respect to the number of cortical areas (Sallet et al., 2013). In spite of these similarities between the brain of humans, apes and monkeys, the frontal lobe of humans has undergone major structural changes compared with nonhuman primates (Aldridge, 2011) and additional functional modifications have been described. Humans show a more graded representation of digit movements in the primary motor cortex (Schieber and Santello, 2004) and a higher number of corticospinal fibers (Courtine et al., 2007) which, in addition to biomechanical (Schieber and Santello,

2004; Serlin and Schieber, 1993) and motor-unit differences, explain in part the greater degree of independence in digit movements in humans, as compared to nonhuman primates (Häger-Ross and Schieber, 2000; Schieber, 1991). Like other primates, humans show the major divisions of the medial premotor cortex (MPC): pre-SMA and SMA (Picard and Strick, 2001). As in the monkey, the human pre-SMA appears to be involved in more abstract aspects of motor preparation, the control of sequences of movements, and the control of self-initiated movements (Picard and Strick, 2001). In addition, areas equivalent to the monkey's PMdr and PMdc are also present in humans (Picard and Strick, 2001). One of the main modifications of the human motor system is the emergence of Broca's area, probably a modification of the left ventral premotor cortex for speech (Fig. 3e, Kaas, 2004). Interestingly, different levels of asymmetry are also observed in the homolog equivalent of Broca's area in great apes (Cantalupo and Hopkins, 2001; Hopkins et al., 2007).

In summary, a motor system with a well-differentiated M1 area (dissociated from the primary somatosensory cortex) probably emerged with placental mammals. After that, a major expansion of premotor areas occurred in early primates. A later refinement of the motor regions devoted to the control of fingers, and further regionalization of premotor areas accompanied by the appearance of a foveate retina, were observed in anthropoid primates. Finally, a major specialization of the left ventral premotor cortex occurred in humans, associated with the development of speech. These processes were accompanied by a notable increase of the total brain size. There is, for example, a fivefold difference between primates and insectivores in neocortical volume relative to the rest of the brain (Barton and Harvey, 2000). Consequently, the most evident changes in the primate brain evolution are the greater total size of the brain, the larger relative size of the neocortex, and the number of cortical fields. These modifications arguably increased the complexity of cortical processing, which in turn permitted the emergence of new abilities. However, other important, but less obvious modifications could have taken place during the evolution of the primate brain, including the changes in the functional organization and connectivity between and within cortical fields (Krubitzer, 2007) and between subcortical structures such as the basal ganglia and the cerebellum.

3. Cortical motor areas and their role in some high-order cognitive functions

3.1. The control of movement and beyond: perception and decision-making

The functional study of the motor cortex started with the observation by Fritsch and Hitzig that the application of electric current in regions of the dog's brain elicited body movements (Taylor and Gross, 2003). This study was also the first to demonstrate the topographical representation of the body (somatotopy), which is an important anatomical property of the motor areas (Taylor and Gross, 2003). Later, the advent of the recordings of extracellular neural activity in the behaving monkey increased our comprehension of the cortical neurophysiology of movement (Evarts, 1968a). Classic studies required the training of monkeys to perform repetitive stereotyped movements and the recording of neurons in the motor/premotor cortex (Evarts, 1968b; Georgopoulos et al., 1982; Hanes and Schall, 1996; Schall, 1991a,b; Tanji and Evarts, 1976), but more recent studies have employed spontaneous non-restricted movements (Aflalo and Graziano, 2006, 2007). It has been shown that the activity of neuronal populations in premotor and motor areas is associated with the encoding of important parameters of such as the reaching movement force, direction, speed, and final postures (Aflalo and

Graziano, 2006, 2007; Ashe and Georgopoulos, 1994; Evarts, 1968b; Georgopoulos et al., 1982, 1988, 1992, 2007; Naselaris et al., 2006a,b; Reina et al., 2001). Additional studies showed that motor and premotor cortex participates not only in motor execution but also in the preparation of movement (Churchland et al., 2010; Hanes and Schall, 1996; Kaufman et al., 2014; Romo et al., 1997; Romo and Schultz, 1987, 1992; Schall, 1991a,b; Tanji and Evarts, 1976; Tanji and Kurata, 1982, 1985; Weinrich and Wise, 1982).

As the experimental paradigms and goals became more complex, it was clear that motor cortex actively participates in a vast set of cognitive aspects such as spatial cognition, motor learning, sensory-motor transformation, preparation and execution of sequences of movements, as well as perception, and decision making (de Lafuente and Romo, 2005, 2006; Georgopoulos et al., 1989b; Hernández et al., 2002; Lee and Quessy, 2003; Mountcastle et al., 1992; Nakamura et al., 1998, 1999; Pellizzer et al., 1995; Romo et al., 1993, 1997, 2004; Schwartz et al., 2004; Shima and Tanji, 2000).

An interesting discovery was that neurons in the motor and premotor regions commonly respond to the presentation of sensory visual, somatosensory, or auditory stimuli (Graziano et al., 1994; Merchant et al., 2001, 2004a,b, 2015a; Rizzolatti et al., 1981; Romo and Schultz, 1992; Schall, 1991a,b). For example, motor cortical cells respond to expanding optic flow stimuli, suggesting that visual directional approach information is available to the motor cortex for potential, but not obligatory, use in preparing a motor response (Merchant et al., 2001; Merchant and Georgopoulos, 2006). In some premotor regions responses are observed when the sensory stimulus is important for the monkey's behavior, for example, when the stimulus indicates to the monkeys the nature of a subsequent movement it had to perform in order to get a reward (Tanji and Evarts, 1976; Kurata and Tanji, 1985; Tanji and Kurata, 1982). When the same stimulus is presented in a passive context, the associated sensory responses in the premotor regions are not observed (Kurata and Tanji, 1985; Tanji and Kurata, 1982). Consequently, this kind of sensory responses are important for sensory-motor transformations, e.g. the selection of appropriate motor patterns in response to sensory stimulus (Kurata and Tanji, 1985; Romo and Schultz, 1987; Tanji and Kurata, 1982).

In 1992, Mountcastle and coworkers proposed that some neurons in the primary motor cortex show activity related to the perceptual judgment of rhesus monkeys working in a discrimination task. In this task, the monkeys had to discriminate the frequency of two subsequent vibratory stimuli delivered to the glabrous skin of the hand (Mountcastle et al., 1992). Subsequent studies by Romo et al. (1993, 1997) showed that perceptual decision signals are already present in the premotor system. In one study, rhesus monkeys were trained to categorize the speed of a probe moving through the glabrous skin of one restrained hand as high or low on the basis of learned categories. Speeds from 12 to 30 mm/s at steps of 2 mm/s were employed. In order to communicate its perceptual decision, the monkeys pressed one of two switches with the unrestrained hand. It was observed that the activity pattern of some MPC neurons reflected the categorical report of the monkeys. Such neurons presented categorization-related activity during the stimulus presentation or, most commonly, during reaction time period (Romo et al., 1993, 1997). These observations contradicted the previous notion that considered the motor system as a system exclusively dedicated to the preparation and control of movement (Romo et al., 1995; Merchant et al., 1997; Zainos et al., 1997).

Other experiments showed that premotor areas and the primary motor cortex are also implicated to motor and perceptual memory processes (Ashe et al., 1993; Hernández et al., 2002;

reviewed in Romo and de Lafuente, 2013 and Romo and Salinas, 2001, 2003; Smyrnis et al., 1992). Georgopoulos and colleagues, for example, showed that during the delay period of a memorized reaching task, the neuronal population vector represented the direction of the future movement, suggesting that the motor cortex is involved in both encoding and holding in memory directional information about reaching movements (Smyrnis et al., 1992; Ashe et al., 1993). Remarkably, other studies have shown that premotor neurons show activity related to maintaining in memory sensory information that is relevant for the behavior. Hernández et al. (2002) employed a vibrotactile discrimination task in which monkeys had to indicate, with two different movements, whether the frequency of a comparison stimulus (f_2) was lower or higher than the frequency of a previously presented base stimulus (f_1). Importantly, stimulus were separated in time by a constant interval. Consequently, to solve the task, monkeys need to store in memory f_1 and later compare it with f_2 . Recordings showed that activity of MPC neurons correlated with different aspects of the discrimination process (Hernández et al., 2002). Some MPC neurons represent the actual or the memorized frequency of the base stimulus or the actual frequency of the comparison stimulus. Interestingly, some neurons switched from the representation of the stimuli (base or comparison) to the representation of the comparison process (whether f_1 was higher than f_2 or f_2 was higher than f_1 , Hernández et al., 2002). Surprisingly, when monkeys were forced to postpone their reports by the introduction of a delay before the motor response, activity encoding the previously presented stimuli (f_1 and f_2) and activity related to the perceptual decision were both observed during the delay in MPC (Lemus et al., 2007). Lemus et al. (2007) suggested that maintaining the sensory information in memory allows for the continuous updating of the perceptual decision. Further recordings in other cortical areas showed that PMv and in lesser amount PMd have neurons with similar patterns of activity to that observed in MPC: neurons with activity related to the base stimulus frequency, currently or previously presented, the comparison process and the motor execution (Hernández et al., 2010; Romo et al., 2004). Moreover, similar neural responses were observed in the PMv of monkeys working in auditory discrimination tasks indicating that premotor regions participate in perceptual and mnemonic processes irrespective of the sensory modality (Lemus et al., 2009).

Additional studies of Romo and coworkers showed that the motor system and specially the MPC form part of the cortical regions that participate in the transformation of sensory signals into perceptual decisions (de Lafuente and Romo, 2005, 2006). For example, de Lafuente and Romo trained monkeys to indicate through two different movements the presence or absence of a vibratory stimulus in the glabrous skin of a finger, and recorded the activity of somatosensory and MPC neurons. Recordings in S1 showed that the activity of S1 neurons was related to the stimulus intensity. In contrast, neurons in MPC represented the perceptual judgment about the presence or absence of the vibratory stimulus (de Lafuente and Romo, 2005). Importantly, the microstimulation of MPC during the detection task triggered perceptual reports. Monkeys tended to report the presence of stimulus more often when it was accompanied by electrical stimulation of MPC. Moreover, the replacement of the sensory stimulus by electrical stimulation of MPC resulted in similar psychophysical performance (de Lafuente and Romo, 2005). A subsequent study using simultaneous recordings in several brain areas found a gradual transformation between the stimulus-related activity observed in primary and secondary somatosensory areas and the activity more related to the perceptual judgment present in frontal regions and especially in the MPC (de Lafuente and Romo, 2006). Overall, these studies show that the activity of motor and premotor neurons are not only related to the planning and execution of the motor act. In

fact, perception and decision making appear to occur within an extensive reciprocally connected network that include motor and premotor areas as important components (reviewed in Romo and de Lafuente, 2013).

3.2. The motor system and action imitation

Primates have the ability to imitate, explain, and predict the behavior of others in different degrees (Savaki, 2010). Imitation, broadly defined as copying the actions of another (Whiten et al., 2009), allows the rapid mastering of complex motor tasks (Iacoboni and Dapretto, 2006), the inheritance of behavioral traits beyond genetic restrictions, and the development of culture (Fitch et al., 2010). In order to understand the evolution of this cognitive function, several studies have compared the imitation abilities and the corresponding neural substrates across primate groups. Interestingly, the evidence suggests that action understanding and imitation depend strongly on the same system that controls action execution. Thus, in contrast to classic ideas, the current hypothesis postulates that the motor system is important not only for motor control but also for the perception of actions (Cisek and Kalaska, 2004; Dushanova and Donoghue, 2010; Evangelidou et al., 2009; Ferrari et al., 2009; Fogassi et al., 2005; Mukamel et al., 2010; Raos et al., 2004, 2007; Savaki, 2010; Suminski et al., 2009; Tkach et al., 2007).

There is evidence that the abilities for action imitation differ among primate species. Monkeys, for example, can reproduce to some degree the movements of a demonstrator in order to get rewards from foraging boxes with or without the use of tools [pig-tailed macaques (Custance et al., 2006), marmosets (Voelkl and Huber, 2007), capuchins (Fredman and Whiten, 2008)]. In these experiments, the animals had to imitate transitive actions (actions directed to an object: foraging boxes or 'artificial fruits'). Nevertheless, other studies show that monkeys are not as good at reproducing actions that are not directed to objects (intransitive actions). For example, one study compared the ability of capuchins to imitate familiar or novel actions directed to an object, to a substrate, or to their own body. In these circumstances the monkeys' behavior only approximated familiar actions directed to objects and did not match familiar gestures that were not related to object manipulation, especially those directed to their own body (Fragaszy et al., 2011). Hence, it was proposed that capuchins are better at imitating transitive than intransitive actions (Fragaszy and Visalberghi, 2004). Nevertheless, monkeys show the ability of facial expression imitation, including movements of the mouth and tongue, which is then their only intransitive imitation behavior (neonatal rhesus monkeys: Ferrari et al., 2006, juvenile and adult geladas: Mancini et al., 2013).

On the other hand, it is known that chimpanzees can imitate a method to obtain food from feeding devices and transmit this information to other individuals with high fidelity (Horner et al., 2006; Whiten et al., 2005). In contrast to monkeys, chimpanzees, and orangutans are more proficient at imitating body postures, as was demonstrated in *do as I do* paradigms where the apes reproduced some gestures such as touching specific body parts or clapping hands (Call et al., 2005; Custance et al., 1995). Nevertheless, the imitation of body postures by chimpanzees has not always been observed (Tennie et al., 2012), suggesting that body-posture imitation is not well developed in apes. Finally, neonatal chimpanzees are also able to imitate facial expressions including tongue and mouth movements (Bard, 2007).

The limited capacity of nonhuman primates for action imitation contrasts with that of humans' (Custance et al., 2006; Ferrari et al., 2006; Whiten et al., 2009). Since childhood, humans learn a large amount of sensorimotor and social skills through action imitation. However, there is evidence that the human ability to imitate may

be over-developed at the expense of efficiency (Whiten et al., 2009). In studies where humans and apes had to reproduce a previously demonstrated, purposeful action, adult and young human subjects accurately copied the components of the behavior (Call et al., 2005; Horner and Whiten, 2005), including those that were causally irrelevant (Horner and Whiten, 2005). Apes, on the contrary, failed to copy the fine details of the behavior, but they tended to achieve the demonstrated goal with their own motor repertory (Call et al., 2005; Horner and Whiten, 2005; reviewed in Whiten et al., 2009). It was proposed that for human children, who commonly need to learn complex motor patterns with no clear causality, it is more advantageous to copy the movements with fidelity using a 'copy-all, refine/correct-later' strategy (Whiten et al., 2009). These observations suggest that humans can extract or attend better to the details of the movement of other actors, which is not the case in nonhuman primates (especially monkeys) that commonly neglect such information. A precaution note is in place here, since action imitation studies have not been carried out systematically across species, with a strong diversity in behavioral tasks, training periods, and analytical methods among papers. Therefore, cross-species behavioral studies are urgently needed, not only for action imitation, but also for speech and rhythmic entrainment behaviors (described in the sections below).

An important step toward the comprehension of action understanding and imitation was the discovery in 1992 by Giacomo Rizzolatti and coworkers of the mirror neurons in area PMv of the monkey (di Pellegrino et al., 1992). These cells are active when monkeys perform an action, such as grasping for a piece of food, and also when they observe another subject performing the same or a similar action. Hence, these results support the notion that perception and action are not necessarily segregated in the brain. Crucially, these neurons do not discharge when the monkey observes similar biological movements mimicked in absence of a target (reviewed in Ferrari et al., 2009). Consistent with this, some mirror neurons are activated when monkeys observe a reaching movement toward an object, even when the final part of the action is hidden behind a screen. On the contrary, when the monkeys know that the action is mimicked and that there is not an object behind the screen the neurons do not respond (Ferrari et al., 2009). Furthermore, neurons in PMv also show mirror responses for ingestive and communicative mouth gestures such as lip smacking (Ferrari et al., 2003). Nevertheless, posterior studies found PMv mirror neurons that are active for intransitive actions. Importantly, the proportion of neurons that showed intransitive responses is quite lower than for neurons responding to transitive actions (Kraskov et al., 2009, 2014). Therefore, these findings coincide with the ability of monkeys to imitate mainly object-directed actions (Fragaszy et al., 2011) and facial expressions (Ferrari et al., 2006; Mancini et al., 2013). From the neurophysiological point of view, these studies are based on the phenomenological characterization of cell responses in mirror neurons, and a quantitative assessment of their encoding properties is still lacking.

Subsequent neurophysiological studies found mirror-like neurons in the inferior parietal lobe of the monkey (Fogassi et al., 2005) and in other motor and non-motor areas of humans and rhesus monkeys; including M1, PMd, SMA, and the hippocampus (Cisek and Kalaska, 2004; Dushanova and Donoghue, 2010; Mukamel et al., 2010; Suminski et al., 2009; Tkach et al., 2007). The main property of these cells is their increase in activity both during the execution of a specific action and while observing others performing the same action. In addition, fMRI studies performed in humans have shown the existence of several brain areas with relatively high BOLD activation during action imitation/execution/observation, including the pars opercularis of the inferior frontal gyrus, the posterior parietal cortex, the superior temporal sulcus,

the primary visual cortex, S1, M1, SMA, and the neostriatum (Aziz-Zadeh et al., 2006). However, only the pars opercularis, the posterior parietal cortex, and the superior temporal sulcus are commonly considered as part of the core human mirror system (Aziz-Zadeh et al., 2006; Iacoboni and Dapretto, 2006). It is claimed that such regions are the only ones with a proper mirror pattern of activity, namely, they show the highest activation during action imitation, lower activation during the view of static images and intermediate levels of activity during the observation or execution of actions (Aziz-Zadeh et al., 2006; Iacoboni and Dapretto, 2006). Consequently, the idea that the mirror system is constituted by few cortical regions is clearly at odds with the findings in monkeys and humans which show the participation of a more complex cortical network (Cisek and Kalaska, 2004; Dushanova and Donoghue, 2010; Mukamel et al., 2010; Suminski et al., 2009; Tkach et al., 2007). Hence, these opposite views should be resolved by additional neurophysiological and imaging studies in humans.

It is commonly assumed that mirror neurons are a necessary component of action understanding. Nevertheless, the available information suggests that not all action categories constitute the focus of the mirror system. In support of this, an fMRI study that employed unsmoothed, single-subject data found that the activity of the human mirror system is associated with the observation/execution of transitive but not intransitive actions (Agnew et al., 2012). Consequently, a wider brain network would be needed to explain the primate's abilities for action understanding and imitation. Savaki and coworkers have shown that a large sensory-motor network is activated in a similar fashion during action and action observation in macaques (Evangelidou et al., 2009; Raos et al., 2004, 2007; Savaki, 2010). Employing high-resolution techniques to measure glucose consumption in the whole brain of monkeys, this group found that both the execution and the observation of the same motor act are accompanied by the activation of similar sensory-motor circuits (Evangelidou et al., 2009; Raos et al., 2004, 2007). The activated regions included areas of the parietal and occipito-temporal association cortices, in addition to the primary and supplementary sensory and motor regions (Evangelidou et al., 2009; Raos et al., 2004, 2007). Based on such findings, Savaki (2010) proposed that the observation-comprehension of intelligent acts depends not only on the activity of some mirror neurons in a few premotor or parietal areas, but also on the activation of a more extended sensory-motor circuit. Specifically, she proposed that the neural circuits that allow for the control of actions also participate in the comprehension of such acts (Savaki, 2010). This proposal is in accord with the *simulation theory* which states that action comprehension is the result of our ability to use our own mental processes to simulate the mental states of the others (Gordon, 1986; Savaki, 2010).

Recent comparative diffusion tensor imaging (DTI) studies in humans, chimpanzees, and macaques found differences in the connectivity of the supposed mirror system that appear to correspond to the contrasting abilities of the three species for action imitation (Hecht et al., 2013a). In humans, chimpanzees, and monkeys the regions of the posterior parietal cortex, the superior temporal sulcus, and frontal lobe (BA 44 and homologous regions) that participate in the recognition/execution of actions are connected between them by several pathways, including the middle/inferior longitudinal fasciculus and the third branch of the superior longitudinal fasciculus, traveling dorsally and by the extreme/external capsule in the ventral aspect of the brain (Fig. 4, Hecht et al., 2013a). Indeed, the superior longitudinal fasciculus seem to have grown gradually from monkeys to chimpanzees to humans, since is the tract connecting mirror areas of the parietal and frontal lobe that has the largest development in the *Homo sapiens*. In macaques, the ventral connections linking areas related to biological motion processing and object/tool recognition in the

temporal cortex with frontal regions that process goals are more profuse than the dorsal connections. In chimpanzees, both pathways are comparable, but in humans, the ventral pathway is relatively small. Additionally, connections of the parietal mirror region with the inferior temporal cortex, a region related to recognizing objects and tools, are weak in macaques, stronger in chimpanzees, and strongest in humans. Finally, in humans, but not in chimpanzees and macaques, the pathway between frontal and parietal mirror regions showed important projections to the superior parietal cortex, a region related to spatial attention (Fig. 4, Hecht et al., 2013a). Interestingly, fMRI studies show additional functional differences in the putative mirror system of monkeys, chimpanzees and humans. A cortical network which is similar to the one observed in humans and monkeys is active in the chimpanzee brain during the execution and observation of object directed actions. Interestingly, activation elicited by mimicked actions (actions not directed to objects) was also observed in chimpanzees and humans but not in monkeys (Hecht et al., 2013b).

In conclusion, a complexity gradient is observed in the action understanding/imitation system of primates, at the behavioral and neural levels. Monkeys show the ability to imitate transitive actions but lack the capacity to imitate intransitive actions. This contrasts with the great capacity of humans to imitate transitive and intransitive actions. Intermediate abilities are found in apes. These behavioral observations correlate with the known structure and function of the neural networks related with action understanding/imitation of monkeys, apes and humans, and with neurophysiological studies of single neuron activity in monkeys. In addition, action imitation is a cognitive function that largely depends on the integration of perceptual and motor information about the actions of others and self. Interestingly, the evidence shows that the motor system is able to represent such abstract information. In this respect, the parieto-premotor mirror system proposed to exist in monkeys and humans could be an important component for action recognition (Ferrari et al., 2009; Fogassi et al., 2005). In addition, the qualitative and quantitative differences in the tracts that connect frontal, parietal, and temporal areas likely explain some of the differences in the action-imitation abilities of primate groups. Nevertheless, additional evidence suggests that a wider network in the brain of primates, including motor and premotor cortices and several association areas, also supports the high ability for action comprehension and imitation observed especially in humans (Cisek and Kalaska, 2004; Dushanova and Donoghue, 2010; Evangelidou et al., 2009; Mukamel et al., 2010; Raos et al., 2004, 2007; Savaki, 2010; Suminski et al., 2009; Tkach et al., 2007).

3.3. The motor system and speech production and comprehension

Language can be considered a system that permits the expression of thoughts as signals and the reverse, the interpretation of such signals as thoughts (Fitch et al., 2010). It is a capacity unique to our species and allows the interchange and accumulation of information. Two important characteristics of human language are the following. First, it depends on the learned ability to produce complex rhythmic motor sequences and vocalizations (Jürgens, 2002, 2009; Patel, 2003) and second, it relies upon the ability to arbitrarily assign abstract information to an auditory stimulus (Cappa, 2012; Jürgens, 2002). As expected, our closest relatives, the nonhuman primates, have only limited abilities for both functions. It is well known that nonhuman primates show low variability within call types (Roian-Egnor and Hauser, 2004), little vocal learning (Hammerschmidt et al., 2000; Owen et al., 1993; Roian-Egnor and Hauser, 2004), and a limited ability to precisely associate different calls or call sequences with meanings (Arnold and Zuberbühler, 2006; Ouattara et al., 2009). In addition, other

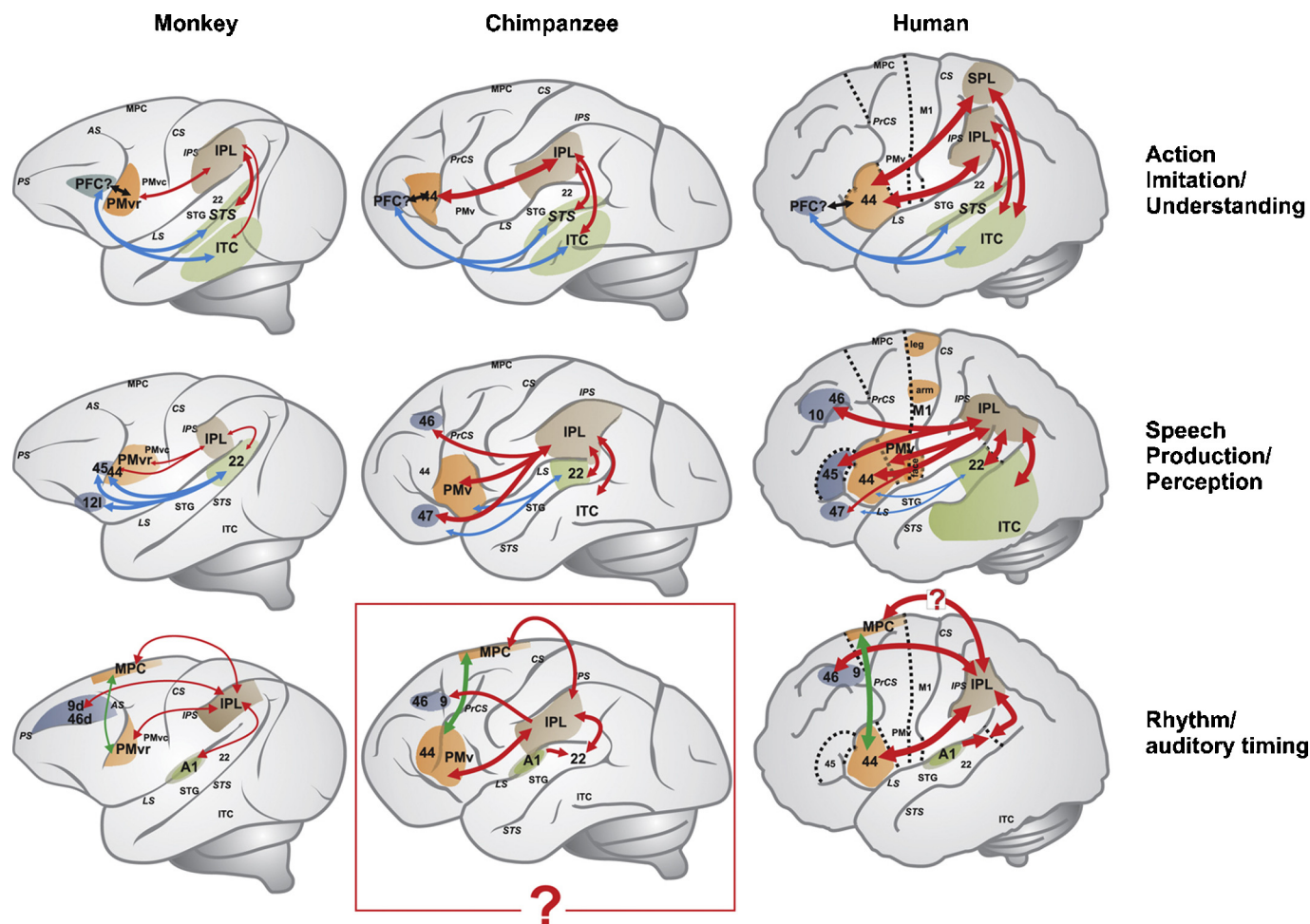


Fig. 4. Schematic representation of the neural circuits for action imitation/understanding, language, and rhythmic processing in three closely related primates. Ventral (blue) and dorsal (red) main connections of temporal (green) and parietal (brown) areas with motor/premotor (orange) and prefrontal (gray) areas are depicted. A prediction for the rhythm/auditory timing system of chimpanzees is shown. In addition, we posit that connections between human IPL and MPC must be strongest in comparisons to other primates. For details, see main text. 9: dorsolateral prefrontal area 9, 9d: dorsolateral prefrontal area 9d, 12l: ventrolateral prefrontal area 12l, 46: dorsolateral prefrontal area 46, 46d: dorsolateral prefrontal area 46d, AS: arcuate sulcus, CS: central sulcus, DLPCF/VLPFC: dorsolateral/ventrolateral prefrontal cortex, IPL: inferior parietal lobe, IPS: intraparietal sulcus, ITC: inferior temporal cortex, LS: lateral sulcus, M1: primary motor cortex, MPC: medial premotor cortex, PFC: prefrontal cortex, PMvr: rostral ventral premotor cortex, PrCS: precentral sulcus, PS: principal sulcus, SPL: superior parietal lobe, STG: superior temporal gyrus, STS: superior temporal sulcus. Upper, middle and lower panels adapted from Hecht et al. (2013a), Rilling et al. (2008) and Merchant and Honing (2014), respectively.

studies suggest that the auditory systems of non-human primates lack the fine perceptual capacities that make possible the human language. For example, monkeys are worse than chimpanzees and chimpanzees are not as good as humans in tone discrimination tasks (Kojima, 2003). In detection tasks, chimpanzees and monkeys, but not humans, show reduced sensitivity to tones in the range of 4–8 kHz which are close to the frequencies commonly present in human speech (Kojima, 2003). Furthermore, the long-term memory abilities for auditory stimuli appear to be less developed in nonhuman primates in comparison to that of visual or somatosensory stimuli (Fritz et al., 2005). Consequently, several comparative behavioral and neurophysiological studies in human and nonhuman primates have been done in order to identify the neural particularities that made human language possible.

The classical view of the neurobiology of language was based on the study of the behavioral consequences of cortical lesions in stroke patients, electroencephalographic measurements during surgical interventions, and other relatively crude sources of information such as the Wada test for language lateralization in human patients (Geschwind, 1970). This model includes Broca's area in the inferior frontal gyrus (BA 44/45) that participates in language production and the temporoparietal junction (where Wernicke's area is thought to be located) that participates in

language perception, and suggests that these two regions are connected by the arcuate fasciculus fiber bundle (Geschwind, 1970). The recent use of imaging techniques has transformed the classical model. First, it is now known that the auditory processing of language is carried out by two main processing streams: the ventral stream associated with lexical recognition and lexical combinations, and the dorsal stream involved in sensorimotor transformations for language production (Fig. 4, Hickok and Poeppel, 2004; Rauschecker, 2012). Second, it has been shown recently that Broca's area is composed of many subregions that support different functions, such as language production and comprehension, working memory, action perception, and the execution and perception of music (Amunts et al., 2010; Poeppel et al., 2012). Finally, new data suggest that motor regions different from Broca's area also participate in perceptual aspects of language (Hauk et al., 2004; Pulvermüller et al., 2006). For example, employing fMRI techniques, Hauk et al. (2004) showed that the passive reading of action words related to specific effectors involves the activation of effector-specific regions in the motor and premotor cortex. Thus, words referring to face, arm, or leg movements elicited the activation of motor and/or premotor areas adjacent to or overlapping with areas activated for the movement of the tongue, fingers, or feet, respectively (Hauk et al.,

2004). Furthermore, it has been shown that during speech perception, the phonetic features of speech sounds appear to activate motor representations related with the production of those sounds, with a somatotopic pattern of activation of motor regions when subjects listened to lip- versus tongue-related sounds (Pulvermüller et al., 2006).

These observations suggest that the human motor system participates not only in the production of language, but also in language perception at two different levels: (1) evoking the motor pattern that produces specific vocal sounds; and (2) evoking the motor patterns associated with action words/concepts. The first function was proposed as a mechanism for improving speech perception in demanding conditions (by example, noisy environments, D'Ausilio et al., 2012; Meister et al., 2007; Sato et al., 2009). This idea is supported by studies that showed language discrimination impairment resulting from transcranial magnetic stimulation on motor and premotor areas (D'Ausilio et al., 2012; Meister et al., 2007; Sato et al., 2009). In addition, it could also be important during normal language acquisition (Tschida and Mooney, 2012). Indeed, it has been suggested that an audio-motor mapping could serve as long-term memory storage for language and other pronounceable sounds (Schulze et al., 2012). The second function is probably related with giving meaning to words (Hauk et al., 2004). Accordingly, motor neuron disease is associated more often with deficits in the comprehension of action verbs than of nouns (Baka and Hodgesa, 2004). Arguably, these capacities were coincident in human evolution and promoted the emergence of our complex communication system. In fact, there is evidence that a system for matching vocalization sounds and the corresponding vocal motor patterns has evolved several times among vertebrates, as neurons that activate for song perception/production are also present in birds (Mooney, 2009; Prather et al., 2008).

Overall, the current notion regarding the role of motor, premotor, and Broca's areas in human language not only includes the production of language, but also various important aspects of language perception. Some of the neural specializations associated with the human capacity for language appear to be present in non-human primates. Analogs of Broca's area, for example, have been described in several primate species. In humans there is a left-hemispheric dominance of area 44/45 for language-related functions and anatomical asymmetries have been described (Nishitani et al., 2004). Furthermore, some studies have found asymmetries in the homolog of the human inferior frontal gyrus of great apes (Cantalupo and Hopkins, 2001; Spocter et al., 2010) as well as a tendency to be right handed (Lonsdorf and Hopkins, 2005). In chimpanzees (*Pan troglodytes*), the homologs of Broca's and Wernicke's areas show asymmetries related to handedness in tool use. Right-handed chimpanzees had a greater hemispheric asymmetry compared with non-right-handed ones (Hopkins et al., 2007). Additionally, Hopkins et al. (2012) found a correlation between communicative capacity and the white-to-gray matter ratio in the homolog of Broca's area of chimpanzees. Finally, one study in marmoset monkeys showed an association between the degree of hand preference and the ability to perform foraging and predator detection simultaneously (Piddington and Rogers, 2013), suggesting an additional evolutionary advantage for the emergence of lateralization. However, other studies have not found evidence of asymmetries in the ape homolog of Broca's area, which has generated some controversy (Schenker et al., 2010).

Anatomical, cytoarchitectonic, and functional evidence supports the existence of an homologue of human area 44 in the monkey's brain. Several investigators favor the notion that PMvr is such homolog region (Coudé et al., 2011; Croxson et al., 2005; Gil-da-Costa et al., 2006; Glenberg and Gallese, 2011). In support of

this proposition it has been shown that human area 44 and PMvr show similar patterns of connectivity with parietal regions (Croxson et al., 2005). Additionally, neurons in the PMvr of the pig-tailed macaque (*Macaca nemestrina*) respond to the production of "coo" calls in a conditioned-vocalization task. The electrical stimulation of some of these neurons elicited coordinated movements of the jaw, lips, tongue, and larynx (Coudé et al., 2011). On the other hand, Gil-da-Costa et al. (2006) showed that the PMv of monkeys is activated in response to species-specific vocalizations and not in response to control, non-biological sounds matched in frequency, rate, scale, and duration. Considering the well-known function of the premotor cortex in selecting the adequate motor patterns in response to a sensory stimulus and context, it was proposed that premotor cortex activation during vocalization listening could be related to the association of the stimulus with its pragmatic consequences (Gil-da-Costa et al., 2006). In spite of this evidence, the exact location of the Broca's homologues in the brain of monkeys is still debated. Petrides et al. (2005) and Petrides and Pandya (2009) consider that the monkey homologue of human area 44 is located in the fundus of the lower branch of the arcuate sulcus, immediately anterior to and differentiated from PMvr.

A recent DTI study compared the connectivity between temporal, parietal, and frontal brain regions related to language processing in humans and the analog structures in nonhuman primates. Similar to the findings described previously about the connections involved in imitation, compared to chimpanzees and monkeys, the human dorsal pathway (arcuate and superior longitudinal fasciculus) is more prominent than the ventral pathway (extreme capsule). Additionally, the human dorsal projections reach more posterior regions in the middle and inferior temporal gyrus and have stronger connections with the prefrontal cortex and both divisions of Broca's area. In contrast, the extreme capsule was the most important pathway connecting temporal and anterior structures in monkeys, and a pattern intermediate between humans and monkeys was found in chimpanzees (Fig. 4, Rilling et al., 2008). Therefore, the huge differences found in motor and cognitive capacity for vocal communication between human and nonhuman primates could be related, to an unknown degree, to the different patterns/strengths of connectivity.

The evidence reviewed so far points to a major role of the motor system, not only in speech production but also in language perception and comprehension. It is possible that the capacity of humans to arbitrarily encode the abstract meaning of words is related to their ability to evoke wide sensory-motor activity in response to particular words. Some of the motor system innovations necessary for speech processing appear to be present in nonhuman primates. Nevertheless, additional traits appear to be present only in humans, including a unique pattern of connectivity between the temporal, parietal, and frontal cortical areas. Interestingly, in addition to the well-known speech-related function of Broca's area, some imaging studies in humans have related it to other, apparently discordant functions, including the estimation of time intervals and the reproduction of rhythms (Nishitani et al., 2004). In the next section, we review how time processing is another important cognitive function where the primate motor system is deeply involved. The proposed existence of a dorsal stream dedicated to audio-motor mapping (Hickok and Poeppel, 2004) predicts auditory-related functions for the inferior parietal lobe that have not been shown in the brain of monkeys, as most of the neurophysiological studies in this region have focused on the processing of spatial information in the visual modality (Andersen and Buneo, 2002; Battaglia-Mayer et al., 2006; Colby and Goldberg, 1999; Johnson et al., 1996; Merchant et al., 2001, 2003a, 2004a,b, 2011a, 2014).

3.4. Timing and rhythm entrainment in the motor system

Rhythmic entrainment refers to the ability to align motor actions with an auditory beat, where a beat corresponds to the perceived pulse that marks equally spaced points in music or a sequence of auditory stimuli (Honing, 2012; Large and Palmer, 2002). In humans, rhythmic entrainment is a common and widespread behavior that involves timed movements of different body parts (such as finger, foot taps, or body sway). Human listeners can synchronize at rates which are integer multiples or fractions of the basic beat (Large and Jones, 1999). This indicates that the human mind has access to several distinct levels of periodicity, one of which can be selected at any given time as the beat (Drake et al., 2000; Phillips-Silver and Trainor, 2007). In addition, rhythmic behaviors in humans also can emerge without the presence of a cueing sensory stimulus, as occurs when a musician plays alone. In this case, an internal representation of rhythm must exist. Therefore, rhythmic entrainment in human subjects is a complex cognitive phenomenon that seems to depend on a dynamic interaction between the auditory and the motor systems in the brain (Merchant and Honing, 2014; Patel, 2014).

The timed movements of humans during rhythmic entrainment match the musical beat in both period and phase (Merchant and Honing, 2014, Fig. 5). Period matching means that the period of movement equals that of the musical beat. Phase matching means that rhythmic movements occur near the onset times of musical beats. The difference between the time of a movement and the time of the corresponding beat is called asynchrony (Fig. 5). In humans, asynchronies normally show negative values, which implies that the movement precedes the musical beat, and suggests that rhythmic synchronization in humans is based on temporal anticipation (Repp, 2005, Fig. 5). Thus, humans show a remarkable ability to adjust, in both period and phase, their rhythmic action to a wide range of tempi and to complex musical signals with a changing tempo (Large and Jones, 1999). In addition, rhythmic behaviors in humans are biased toward the auditory modality. The temporal performance of human subjects in a synchronization task is better using auditory stimuli such as metronomes rather than visual stimuli to define the beat (Grondin et al., 1996; Hove et al., 2013; Merchant et al., 2008b; Repp and

Penel, 2002). Furthermore, performance on a synchronization task that employed a continuous visual stimulus (like a swinging pendulum or rotating bars) was better than the performance on a task using static visual stimuli, but was still worse than with auditory stimuli (Grahn, 2012; Hove et al., 2013). These and many other observations support the notion that in humans, the audiomotor system is especially related to the processing of temporal information, while the visuomotor system is more closely related to the processing of spatial relations (Bertelson and Aschersleben, 2003; Repp and Penel, 2002; Hove et al., 2013).

Recent investigations have shown that nonhuman primates do not show the dexterity for rhythm entrainment observed in humans. Nevertheless, monkeys and other nonhuman primates can spontaneously generate rhythmic behaviors. Macaques, for example, generate periodic sounds by drumming or shaking natural or artificial objects in the wild or in captivity (Remedios et al., 2009; Zhao, 1997), and rhythmic tree drumming and chest beating are common displays of chimpanzees and gorillas, respectively (Arcadi et al., 1998, 2004; Pika et al., 2003). These behaviors are often combined with vocalizations and it has been proposed that they accomplish a communicative function (Arcadi et al., 1998; Pika et al., 2003; Remedios et al., 2009). Furthermore, inter-subject differences in the sequential and temporal characteristics of drumming (number of beats per bout, bout duration, and inter-beat interval) have been documented in certain chimpanzee populations (Arcadi et al., 1998). Such differences and the fact that the sounds can be heard at distances of hundreds of meters suggest tree drumming may serve for long distance inter-subject recognition (Arcadi et al., 1998). Finally, it has been observed that many Old World primates execute rhythmic non-ingestive lip movements during face to face or grooming interactions (Ghazanfar, 2013; Morrill et al., 2012) and that some monkeys (marmoset monkeys: Bezerra and Souto, 2008; cottontop tamarins: Ghazanfar et al., 2002; squirrel monkeys: Winter et al., 1966; but not macaque monkeys: Ghazanfar, 2013) and chimpanzees (Parr et al., 2005) commonly perform vocalizations with rhythmic patterns. It is important to note that all these behaviors are associated with communicative functions. Thus, it is possible that social factors were strong pressures for the evolution of rhythm processing in primates as has been proposed to explain the

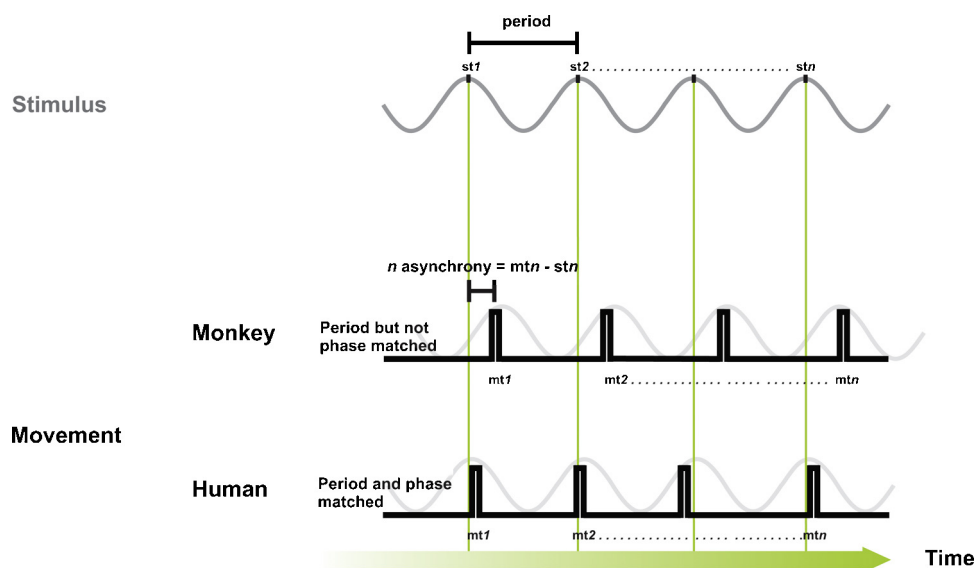


Fig. 5. Schematic representation of main parameters of entrainment tasks employing simple (isochronous) auditory rhythms. The interval between stimulus presentations defines the period. Asynchronies correspond to the interval between movement and stimulus presentation. In contrast to monkeys and apes, human subjects are able to match both period and phase with high fidelity and to produce small negative asynchronies that denotes predictive mechanisms. st: time of stimulus presentation, mt: time of movement.

evolution of other traits of the nervous system of primates (Dunbar and Shultz, 2007). Additionally, it is possible that the neural machinery on which these relatively stereotyped behaviors rest also makes possible the limited levels of rhythmic entrainment observed spontaneously or after intensive training in some nonhuman primates.

The first systematic study evaluating the ability of nonhuman primates to reproduce rhythmic intervals was performed by Merchant and coworkers (Zarco et al., 2009). They intensively trained three rhesus monkeys in a synchronization–continuation tapping task (SCT) in which isochronous sequences of brief auditory or visual stimuli were employed as metronomes for the target rhythms (inter-tap intervals: 450–1000 ms). Monkeys were able to produce rhythmic movements with proper tempo matching. They reproduced the intervals with only slight underestimations (~50 ms), and their inter-tap interval variability increased as a function of the target interval, as observed for human subjects in the same tasks (Merchant et al., 2011b; Zarco et al., 2009). Crucially, monkeys solved the task by adjusting the interval between movements and not their movement's duration (Donnet et al., 2014). This observation suggests that the monkeys, as human subjects, explicitly measured the passage of time. However, an important difference from humans was the inability of macaques to produce negative asynchronies: the movement rarely preceded the stimulus presentation. In fact, movements occurred ~250 ms after each stimulus presentation which resulted in positive asynchronies (Zarco et al., 2009, Fig. 5). Nevertheless, such asynchronies were shorter than those observed in a control reaction task with random inter-stimulus intervals, indicating that during SCT the monkeys showed some level of temporal prediction and synchronization (Zarco et al., 2009). Subsequent studies showed that by using different training strategies, monkeys' asynchronies can be reduced to only ~100 ms (Merchant and Honing, 2014) and that monkeys do not show tempo matching below 350 ms or above 1000 ms (Konoike et al., 2012; Merchant and Honing, 2014).

Rhesus monkeys show a bias toward visual rather than auditory cues in the SCT (Honing and Merchant, 2014; Zarco et al., 2009). Therefore, rhesus monkeys appear to lack the preference for auditory stimuli observed in humans during similar tasks and during rhythmic entrainment in general (Hove et al., 2013). Consistent with this notion is the observation that Japanese macaques facing each other and trained to press two buttons alternately, can show synchronization when visual, but not auditory information, is available (Nagasaka et al., 2013). In addition, a mismatch negativity study using electroencephalographic measurements showed that rhesus monkeys failed to detect beat in a complex rhythmic sequence of auditory stimuli, but suggested that monkeys are able to detect the start of rhythmic groups (Honing et al., 2012). This later observation, has been corroborated in a study that showed that macaques exhibit changes of gaze and facial expressions when a deviant of a regular rhythmic sequence is presented (Selezneva et al., 2013). Hence, it seems that monkeys are sensitive to simple rhythms.

On the other hand, in a recent study three chimpanzees were trained to tap piano keys while listening to isochronous auditory stimulus. One subject showed a significant increase in the number of movements occurring near the auditory beat, suggesting spontaneous synchronization (Hattori et al., 2013). However, this was only true for stimuli with inter-stimulus intervals (ITI) of 600 ms and not for other tempi (Hattori et al., 2013). Therefore, it seems that chimpanzees show abilities for rhythmic entrainment that are between those shown in humans and macaques. Additional work employing conditioning training techniques are needed in order to study the full capacities of apes for rhythmic entrainment.

Based on these findings the gradual audiomotor evolution hypothesis was proposed (Merchant and Honing, 2014). This hypothesis suggests that rhythmic entrainment developed gradually in primates, peaking in humans; only limited features of rhythmic entrainment are present in nonhuman primates, while interval-based timing is shared among human and all nonhuman primates. Thus, this hypothesis accommodates the fact that the performance of rhesus monkeys is comparable to humans' in single-interval tasks such as interval reproduction (Zarco et al., 2009), categorization (Mendez et al., 2011), and interception (Merchant et al., 2003b), but differs in rhythmic entrainment (Zarco et al., 2009).

On the functional side, several fMRI studies have demonstrated that the motor cortico-basal ganglia-thalamo-cortical circuit (mCBGT) is involved in rhythmic behaviors such as music and dance in humans, where the auditory modality plays a critical role (Grahn, 2009; Grahn and Brett, 2007; Lewis et al., 2004; McAuley et al., 2012). Peculiarly, this circuit is activated not only during music production (Bengtsson and Ullén, 2006; Limb and Braun, 2008; Parsons et al., 2005) and rhythmic entrainment but also during rhythm perception (Chen et al., 2008; Grahn and Rowe, 2009; Kung et al., 2013; Merchant et al., 2015b). The mCBGT circuit is usually involved in the control of voluntary skeletomotor movements and includes SMA, pre-SMA and the putamen as the fundamental cortical and neostriatal nodes, respectively (Coull et al., 2011, Fig. 6). In this regard, neurophysiological studies have demonstrated that MPC and the putamen are involved in encoding the sequential and temporal aspects of rhythmic entrainment in macaques performing the SCT (Merchant et al., 2011b, 2013a,b; Perez et al., 2013). SMA and putaminal cells are tuned to the duration of produced intervals during this rhythmic tapping task. Indeed, the same population of neurons is able to simultaneously encode the ordinal structure of a sequence of rhythmic movements and a wide range of durations in the range of hundreds of milliseconds (Bartolo et al., 2014; Merchant et al., 2013b). These results indicate that the MPC and the putamen use interval tuning as an abstract representation of the passage of time, where a cell population–signal functions as a representation of both the duration of the produced interval and its position in the rhythmic sequence of the SCT (comparable to the notes in a musical score, Merchant et al., 2013b; Crowe et al., 2014). In addition, it has been demonstrated that most of the SMA cell responses are aligned to the motor taps, although another considerable proportion of neurons can be aligned to the stimuli of the rhythmic metronome or to a sensorimotor alignment combination (Perez et al., 2013). Consequently, these results corroborate the notion of fMRI studies that the MPC is involved in both rhythm perception and rhythmic entrainment.

The auditory areas of the superior temporal lobe in humans share massive reciprocal connections with the medial, dorsal, and ventral premotor areas of the frontal lobe and they project intensely to the neostriatum, the input node of the basal ganglia (Rilling et al., 2008; Yeterian and Pandya, 1998; see Figs. 4 and 6). In contrast, the projections of these auditory temporal areas in the macaques to medial and ventral premotor areas (Fig. 4, Petrides and Pandya, 1988; Rilling et al., 2008) as well as to the basal ganglia are modest (Borgmann and Jürgens, 1999; Thiebaut de Schotten et al., 2012; Yeterian and Pandya, 1998). It is important to consider that the privileged access of the humans' auditory system to the rhythmic processing machinery of the mCBGT circuit and Broca's region and its associated prefrontal areas arose gradually in the course of evolution from precursors of the great ape lineage. This hypothesis is supported by a DTI study showing that the connectivity between the superior temporal auditory areas and the frontal lobe in chimpanzees has an intermediate level of complexity when compared with macaques and humans (Petrides

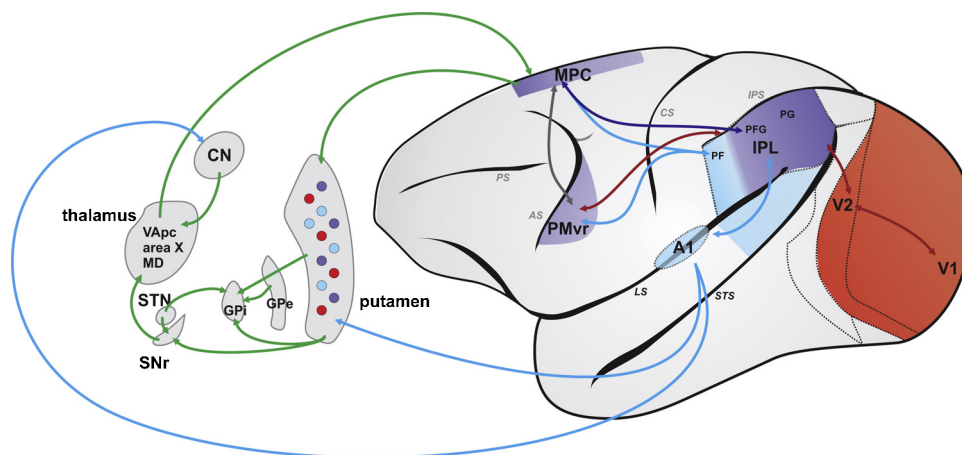


Fig. 6. The motor cortico-basal ganglia-thalamo-cortical circuit (mCBGT) of the monkey is implicated in timing and rhythmic processing. Visual (red) and auditory (blue) dorsal stream inputs are depicted as well as bimodal regions (purple). In the human, the auditory input to the mCBGT is enlarged and more prominent. Intrinsic basal ganglia circuits as well as their connections with MPC are depicted in green. Circles in the putamen represent neurons responsive to the corresponding color coded modality. A1: primary auditory area, AS: arcuate sulcus, CN: caudate nucleus, CS: central sulcus, GPe: globus pallidus externus, GPi: globus pallidus internus, IPL: inferior parietal lobe, IPS: intraparietal sulcus, LS: lateral sulcus, MPC: medial premotor cortex, MD: nucleus medialis dorsalis, PF: part of rostral inferior parietal convexity, caudal to PFG, PG: part of caudal inferior parietal convexity, caudal to PFG, PMvr: rostral ventral premotor area, PS: principal sulcus, SNr: substantia nigra pars reticulata, STN: subthalamic nucleus, STS: superior temporal sulcus, VApC nucleus ventralis anterioris pars parvocellularis, V1: primary visual area, V2: secondary visual area.

and Pandya, 2009; Rilling et al., 2008). In addition, it was shown that the middle region of the human IPL including PFG, which constitutes an important node of the dorsal pathway for auditory processing, is importantly increased in comparison with that of monkeys (Mars et al., 2011). It is clear, however, that more systematic comparative studies are needed to clarify the connections between the auditory system with the basal ganglia and premotor and prefrontal areas of the frontal lobe (Rauschecker, 2012). Taken together, current knowledge suggests that rhythmic entrainment and the sensory appreciation of rhythms developed gradually in primates, peaking in humans, being present with limited properties in macaques, and with intermediate abilities in big apes. The medial, dorsal, and ventral premotor motor areas seem to play a fundamental role in these complex behaviors, in conjunction with the corresponding loops inside the basal ganglia and the motor thalamus. Again, the progressive development of rhythmic abilities across the primate lineage is accompanied by a gradual development of connections, and probably new dynamics in neural processing, linking the parietal and temporal areas with the M1, premotor, and prefrontal areas that handle audiomotor information.

4. Associations among the three high-order behaviors

The first important clue regarding the associations among action imitation, language, and rhythmic entrainment comes from the tight functional coupling between perception and action across these behaviors. It is well known that some neurons in motor and premotor areas display similar activity during the execution and perception of specific motor acts or during the perception of sensory information related with such motor acts (Cisek and Kalaska, 2004; di Pellegrino et al., 1992; Dushanova and Donoghue, 2010; Evangelou et al., 2009; Mukamel et al., 2010; Pulvermüller et al., 2006; Raos et al., 2004, 2007; Savaki, 2010; Suminski et al., 2009; Tkach et al., 2007; Kraskov et al., 2009, 2014). One example is the mirror-like activity found in several cortical areas of the brain of humans and monkeys (Cisek and Kalaska, 2004; di Pellegrino et al., 1992; Dushanova and Donoghue, 2010; Evangelou et al., 2009; Ferrari et al., 2003; Fogassi et al., 2005; Kraskov et al., 2009, 2014; Mukamel et al., 2010; Raos et al., 2004, 2007; Savaki, 2010; Suminski et al., 2009; Tkach et al., 2007). The observation that

speech sounds produce activity in motor areas of the listeners and that such activity resemble the motor patterns necessary for the production of those sounds constitutes another example (Pulvermüller et al., 2006). Importantly, in these studies, human subjects were explicitly instructed to avoid any movement and monkey subjects stayed immobile as corroborated by mean of EMG (see for example: Pulvermüller et al., 2006; Kraskov et al., 2009, 2014). Consequently, the observed neural activity could not be explained in terms of cover motor activity. Finally, several fMRI studies have demonstrated that the motor cortico-basal ganglia-thalamo-cortical circuit (mCBGT) is involved in the motor execution of rhythmic behaviors (Bengtsson and Ullén, 2006; Grahn, 2009; Grahn and Brett, 2007; Limb and Braun, 2008; Lewis et al., 2004; McAuley et al., 2012; Parsons et al., 2005) but also during the perception of rhythms and music without any motor output. (Chen et al., 2008; Grahn and Rowe, 2009; Kung et al., 2013).

Nevertheless, there is the possibility that the activation of motor areas during the perception of high-order behaviors reflects the presence of confounding cognitive processes, such as motor intentionality, effector selection, or unintentional motor output (Mukamel et al., 2010). Although this possibility is hard to prove unambiguously, neurophysiological studies in macaques and fMRI studies in humans have demonstrated, with rigorously controlled methods, the activation of motor and premotor areas in relation to perceptual processes (Coull et al., 2004; Grahn and Brett, 2007; Hernández et al., 2010; Lemus et al., 2009; Macar et al., 2006; Romo et al., 1997).

A critical question, then, is why the motor areas participate not only on the execution but also on the perception of the action of other, the language, and rhythms. One possibility is that the perception-related motor activity arises because comprehension of complex behaviors has been developed through actions since childhood (Johnson, 1987). This notion is closely related to the concept of embodiment (i.e. the existence of a body that shapes different aspects of cognition), and the fact that the internal representation or hypothesis of the external world is acquired by acting in the environment (Clark, 1997; Varela et al., 1991). This idea could help to explain why high-level cognitive processes appear to depend on the partial reactivation of the neural circuitry active in perception and action (Barsalou, 2008). In this sense, the internal representations of such behaviors become a function of

the particular effector embodiment and of its history of experiences (Kontra et al., 2012). We suggest that the gradual evolution of action imitation, language, and rhythmic entrainment in the primate order is also associated with the progressive ability to embody (simulate) the motor elements of these high-order functions. In addition, it is quite possible that these cognitive functions partially depend on similar embodiment mechanisms implemented in part in the motor and premotor areas of the frontal lobe. Although a large number of multidisciplinary studies are needed to refute or prove correct these two hypotheses, there are already some observations supporting them. For example, a large number of papers describe the shared embodiment foundations between language and the gestures that accompany the expression of speech. During speech, gestures are produced by speakers in every culture (McNeill, 1992). They transmit additional information to the listener (Holle et al., 2012; Obermeier et al., 2012) and are tightly timed with speech (McNeill, 1992). Hence, it has been suggested that the speech/gesture co-occurrence reflects a deep functional association that develops during early hand–mouth associations in children (Iverson and Thelen, 1999). On the other hand, it has been proposed that the human audio-visual speech rhythm evolved from rhythmic facial expressions of ancestral primates similar to the lip smacking observed in extant monkeys and apes (Ghazanfar, 2013; Ghazanfar et al., 2010, 2012; MacNeilage, 1998; Morrill et al., 2012). Indirect support to this theory comes from observations that macaque monkey vocal communication is also audio-visual (Chandrasekaran et al., 2011). The ventral premotor areas and Broca's region are core areas of the oro-manual systems (Colby and Goldberg, 1999; Geyer et al., 2000; Petrides and Pandya, 2009). Needless to say, the arm–hand gestures are also closely linked to action imitation (Heyes, 2001). Consequently, it is not surprising that the ventral premotor cortex and the different subdivisions of Broca's area are both involved in the perception and production of speech and the control of gestures associated with language, as well as in action-imitation circuits (Fadiga et al., 2009; Fazio et al., 2009). Moreover, vocal learning and rhythmic entrainment are known to be functionally and anatomically linked (Patel, 2003, 2006; Patel and Iversen, 2014). Speech, music, and dance include complex auditory stimuli used to drive perception and motor behavior, and they strongly depend on large and shared portions of the premotor and motor areas of the human cortex (Honing, 2012; Jürgens, 2002, 2009; Merchant and Honing, 2014; Patel, 2003; Patel and Iversen, 2014). Thus, the gradual development of sensorimotor associations across motor areas during childhood could explain why the perceptual and motor aspects are so deeply intermingled between and within rhythmic entrainment, vocal learning, and language, as well as the imitation of the actions of others.

It is important to notice that recent evidence shows that the complexity of visual, facial and auditory vocal communication signals is correlated with social group size among primates (Dunbar, 2012). In addition, some studies show that rhythmic entrainment in children improves in social contexts (Kirschner and Tomasello, 2009) and that the ability to synchronize movements between different subjects could strengthen social cooperation (Wiltermuth and Heath, 2009). Furthermore, the primate mirror-like systems could provide evolutionary advantages in terms of social cognition (Oberman et al., 2014). This evidence suggests that the challenges of complex social interaction among primates constituted important pressures for the evolution of cognitive functions needed for maintaining social cohesion (Dunbar, 2012). In consequence, it is possible that action understanding/imitation, rhythmic entrainment, and language systems evolved as a result of similar social evolutionary pressures.

The functional properties of the motor system should define the way in which action imitation, rhythmic entrainment, and

language are embodied. In this regard, four intermingled characteristics of the motor system are particularly interesting: motor preparation, motor dynamics, motor timing, and motor cortical connectivity with motoneurons.

4.1. Action prediction and high-order functions

A critical functional property of the motor and premotor areas of the primate cortex is their ability for movement preparation. These areas show responses that encode the temporal and spatial properties of movement and of the stimuli used to drive the behavior, and these responses can be observed hundreds of milliseconds before the onset of actual movement (Godschalk et al., 1985; Matsuzaka et al., 1992; Merchant et al., 2004a,b; Mushiake et al., 1991; Shenoy et al., 2011; Tanji, 1996; Wise, 1985). For example, M1 neurons of monkeys trained to perform a visually instructed push or pull movement show instruction-related activity prior to the signal that cued the movement initiation (Tanji and Evarts, 1976). It is well documented that the neuronal population activity in motor cortex encodes in advance the direction of subsequent instructed movements (Ashe et al., 1993; Georgopoulos et al., 1989a; Smyrnis et al., 1992). Additional evidence shows that motor areas are able to elaborate internal representation of the world in the form of predictions of future incoming sensory events (Kilner et al., 2004). Thus, as early as 1986 neuronal build up activity associated with the prediction of the temporal occurrence of sensory events was described in the PMd of monkeys (Mauritz and Wise, 1986). More recently, it has been shown that the corticomotor system has access to predicted values of dynamic sensory inputs, as in the interception of moving targets that are necessary to trigger a motor response (Merchant and Georgopoulos, 2006; Merchant et al., 2004b, 2009). Predictive signals of this nature could be transmitted in a top-down fashion to the sensory and associative areas in order to generate a congruent construction between the internal representation of a high-order function and the actual sensory input (Schubotz, 2007; Iversen et al., 2009; Fujioka et al., 2012; Bartolo et al., 2014; Teki, 2014). Therefore, preparatory signals associated with action imitation or language, and rhythmic entrainment should occur in premotor and motor areas of the macaque or human cortex. Then, it is probable that in some point of primate evolution such predictive activity was disengaged from actual movement execution in order to serve to more abstract cognitive processes that influenced auditory or, in general, sensory information processing.

Furthermore, it is important to mention that the action simulation for auditory prediction (ASAP) hypothesis by Patel and Iversen (2014), and the motor theory for long-term auditory memory and language by Mishkin and collaborators, are notions that link the predictive nature of the motor system with rhythm perception and language, respectively (Schulze et al., 2012). The idea that the motor system can help to construct internal representations of the sensory world could also be valid for the visual modality. Crowe et al. (2004) trained rhesus monkeys to covertly solved complex mazes and found the M1 neurons encode the direction of the maze path and whether the maze had an exit or not.

4.2. The dynamic nature of both the movement and the corresponding sensory information

It is important to emphasize that voluntary movement is highly dependent on its evolution over time. The kinematics (position and its derivatives) and kinetics (forces, torques, and their derivatives) of movement are determined in large part by its changes over time (i.e. defining the derivatives) (Ashe and Georgopoulos, 1994; Moran and Schwartz, 1999). Hence, the internal representations of

the world are necessarily encoded in a dynamic fashion in the premotor and motor areas (Merchant and Georgopoulos, 2006; Merchant et al., 2008a, 2009; Schubotz, 2007) that generate a representation of chains of rapid movement sequences (Mushiake et al., 1991; Shima and Tanji, 2000; Tanji, 2001). In addition, the sensory information associated with the reviewed high-order behaviors is not static but changes as a function of time, defining in part its sensory properties (Honing, 2012; Jürgens, 2002, 2009; Patel, 2003). Thus, the visual information used for action imitation comes from the well known dorsal stream of visual processing and conveys not only the position in space of the body part, but also its movement over time (Goodale and Milner, 1992). Similarly, the auditory information used in language and rhythmic entrainment fluctuates at high (milliseconds) speeds (Mauk and Buonomano, 2004) and is processed by the dorsal and ventral stream of auditory processing (Hickok and Poeppel, 2004; Rauschecker, 2012). One way in which these dynamic sensory inputs can be represented by the motor system is through their automatic transformation to a chain of rapid motor events, integrated as sets of movement sequences. Therefore, we propose that during the course of a subject's development, high-order behaviors such as action understanding, speech perception and rhythmic entrainment depends on: (1) the fast transformation of the dynamic sensory inputs into a set of movement sequences in the appropriate kinematics and kinetics; (2) the strong bidirectional communication between the pertinent parietal areas, which constitute the highest level in the hierarchy of the dorsal visual and auditory streams, and the corresponding premotor areas (Fig. 6; see Sections 1, 3.3 and 3.4); and (3) the storage of these chains of sensorimotor associations in the motor cortical areas.

4.3. The timing mechanism governing high-order functions

Precise timing on the scale of hundreds of milliseconds is another crucial component of action imitation, language, and rhythmic entrainment. The tight co-occurrence of oro-facial and arm-hand sequence movements during speech accompanied by gestures should depend on a common timing mechanism. Furthermore, it is well known that the mCBGT circuit is strongly involved in the temporalization of the perceptual and motor aspects of behaviors such as speech, music, and dance (Merchant et al., 2013a, 2015b; Merchant and de Lafuente, 2014). In general, the mechanism associated with the quantification of time, across a wide variety of behaviors depends on a partially distributed circuit that has two elements: a core timing circuit that includes the mCBGT, and areas that are selectively engaged during different behavioral contexts (Coull et al., 2011; Merchant et al., 2008b,c, 2013a). Thus, the core timing circuit should precisely align the predictive sensory signals, the motor representation of chains of movement sequences, and the signals associated with the embodiment of the different effectors intervening in a complex behavior.

4.4. The relation between cortical areas and the motoneurons controlling the effectors

The neurophysiology of voluntary motor control has shown that M1 and the premotor areas of the macaque encode different kinematic and kinetic aspects of the preparation and execution of reaching and grasping movements (Ashe and Georgopoulos, 1994; Georgopoulos et al., 1982, 1986; Kakei et al., 1999, 2001; Lillcrap and Scott, 2013; Merchant et al., 2008a; Moran and Schwartz, 1999; Naselaris et al., 2006a,b; Shenoy et al., 2011; Tanji, 2001). All this knowledge has been used to create the field of neuroprosthetics, where the neural activity in these motor cortical areas is used to drive artificial effectors not only in monkeys (Serruya et al.,

2002; Taylor et al., 2002; Velliste et al., 2008; Wessberg et al., 2000), but lately also in tetraplegic human patients (Collinger et al., 2013; Hochberg et al., 2006). Some neurons in the primate's M1 and premotor areas project monosynaptically to motoneurons located in the spinal cord and constitute the cortico-motoneuronal system (Bernhard and Bohm, 1954). This system is more prominent in great apes and humans although it is also present in Old World and some New World monkeys. In contrast, it is absent in all the non-primate species studied and in some primates such as lemurs and marmoset monkeys (Lemon, 2008). The cortico-motoneuronal system is thought to be a recently evolved feature (Lemon, 2008) related to the selective control of small groups of muscles in order to produce fractionated movements (Kuypers, 1978). In particular, it was proposed to be necessary for the voluntary control of independent finger movements observed in Old World monkeys, apes and especially in humans (Lemon, 2008; Lemon and Griffiths, 2005). Of course that the functional correspondence between the activity of M1 neurons and spinal motoneurons in the monkey is complex and shows a large amount of divergence (Taira et al., 1996). Therefore, the tight anatomical relationships between the motor cortical areas and the spinal cord allowed for the unique, complex dexterity that primates have to control their limbs, particularly the hand-arm (Brouwer and Ashby, 1992; Jankowska et al., 1975; Kuypers, 1981). Similar associations exist between the premotor and motor cortex, and the brain stem nuclei involved in the control of the primate vocal apparatus (Jürgens, 2002, 2009). These anatomical properties, which developed progressively in the primate lineage, are especially true in humans where a large fraction of motor and premotor neurons establish direct monosynaptic connections with the spinal and brain-stem motor neurons controlling the hand and the laryngeal movements, respectively (Iwatsubo et al., 1990; Kuypers, 1958; Lemon, 2008; Palmer and Ashby, 1992). Thus, it could be considered that the development of high-order functions such as understanding the actions of others, language, and rhythmic entrainment, that peak in the *Homo sapiens*, can be due at least in part by the direct and strong control of the premotor and motor cortical systems over the motor neuronal pulls governing the contraction of muscles in the hand and the larynx (Petkov and Jarvis, 2012). Nevertheless, the motor and premotor areas of the primate cortex have also shown a gradual increase in their complexity and connectivity with other cortical and subcortical structures across the order of primates. A parsimonious position, therefore, is to consider that all the anatomofunctional aspects that have evolved give the motor cortical system greater access to sensory and cognitive information and a better control over muscular effectors, thus acquiring a predominant role in the incredible emergence of the high-order functions in primates.

5. Concluding remarks

To date there exists a huge corpus of knowledge about the structure, development and function of the brain in mice, rats, cats and monkeys at the molecular, cellular and systems levels. Although the study of the brain has focused on such few species, some groups have started to describe the function and structure of other mammalian species (Beck et al., 1996; Hassiotis et al., 2004; Karlen and Krubitzer, 2007; Stepniewska et al., 2011). Such knowledge diversity boosted the reconstruction of the evolutionary history behind the complexity of modern mammalian nervous systems. In this respect, the comparison of functional and structural data among species has shown to be a useful alternative to overcome the limited information that fossil evidence provides (Kaas, 2008; Krubitzer, 2007). Nevertheless, it is important to note that although this comparative mechanistic approach could shed some light on the evolutionary history of specific cognitive

functions (Krubitzer, 1995), it cannot make clear the selective pressures that gave rise to them (Dunbar and Shultz, 2007). In order to answer these questions, more multidisciplinary studies that include the behavioral advantages of different cognitive functions, their neurobiological underpinnings, and comparative studies within primates.

Two strong notions permeate the studies reviewed here. First, the classical view that the motor and premotor areas of the human and nonhuman primate cortex are only engaged in the preparation and execution of voluntary movement has been replaced by the contemporary notion that these motor cortical areas also perform fundamental computations associated with the perceptual and cognitive aspects of behavior. Second, the increment of motor areas in primates is accompanied with the emergence of new cognitive abilities. The reviewed data show that the evolution of primate's cortex is marked by the quantitative and functional diversification of the motor cortical areas (Kaas, 2004, 2010) in addition to other cortical regions, principally prefrontal and parietal (Genovesio et al., 2014; Semendeferi et al., 2001). This diversification resulted in the emergence of the fronto-parietal-subcortical circuits that we observe in extant primates. Such systems constitute parallel interacting ways for computing specific aspects of sensory-motor transformations and decision making (Buneo and Andersen, 2006; Geyer et al., 2000; Gharbawie et al., 2011; Hernández et al., 2010; Hoshi and Tanji, 2007). In particular, recent evidence shows that the primate motor regions not only control the low-level aspects of planning and control of movements but also participate in the perceptual and motor aspects of more sophisticated cognitive functions such as decision-making, action understanding/imitation, language and rhythmic entrainment. In this regard, we suggest that the gradual emergence of such cognitive abilities in the primate order depended in part on the progressive ability to embody their corresponding motor elements.

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