



Review

The functional significance of mu rhythms: Translating “seeing” and “hearing” into “doing”

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Abstract

Existing evidence indicates that mu and other alpha-like rhythms are independent phenomena because of differences in source generation, sensitivity to sensory events, bilateral coherence, frequency, and power. Although mu suppression and enhancement echo sensorimotor processing in frontoparietal networks, they are also sensitive to cognitive and affective influences and likely reflect more than an idling brain state. Mu rhythms are present at early stages of human development and in other mammalian species. They exhibit adaptive and dynamically changing properties, including frequency acceleration and posterior-to-anterior shifts in focus. Furthermore, individuals can learn to control mu rhythms volitionally in a very short period of time. This raises questions about the mu rhythm’s open neural architecture and ability to respond to cognitive, affective, and motor imagery, implying an even greater developmental and functional role than has previously been ascribed to it. Recent studies have suggested that mu rhythms reflect downstream modulation of motor cortex by prefrontal mirror neurons, i.e., cells that may play a critical role in imitation learning and the ability to understand the actions of others. It is proposed that mu rhythms represent an important information processing function that links perception and action — specifically, the transformation of “seeing” and “hearing” into “doing.” In a broader context, this transformation function results from an entrainment/gating mechanism in which multiple alpha networks (visual-, auditory-, and somatosensory-centered domains), typically producing rhythmic oscillations in a locally independent manner, become coupled and entrained. A global or ‘diffuse and distributed alpha system’ comes into existence when these independent sources of alpha become coherently engaged in transforming perception to action.

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1. Introduction

1.1. Are mu rhythms epiphenomena without significance?

Ever since their discovery by Hans Berger [10], electro-physiological rhythms have held the promise of being key to the understanding of the brain–mind relationship [48]. Scalp-recorded electroencephalographic (EEG) and magnetoencephalographic (MEG) activity, as well as more recent neuroimaging technologies, have been important for understanding the functional significance of these rhythms and the way they are generated by the underlying neural machinery. Indeed, recent work has begun to shed light on the macro-, micro-, and functional architecture of EEG rhythms, from slow theta [82] to fast gamma frequencies [81,100].

The mu rhythm (also known as the central, Rolandic, sensorimotor, wicket, or arceau rhythm), first reported in the 1950s [20,43,44], has not received the kind of attention that other EEG oscillations have, most likely because until recently [103] it was thought to occur infrequently and only in a small percentage of the population [72]. However, new and more sophisticated techniques, such as independent component analysis (ICA), have shown that mu rhythms are found with scalp EEG in most, if not all, healthy adults [83]. A significant amount of work on the mu rhythm has been conducted since the 1950s. Unfortunately, most of this work has occurred in academic fields that, until recently, have not overlapped significantly, resulting in slow progress towards the delineation of the antecedent conditions and the neural basis of this rhythm.

Are mu rhythms merely epiphenomena without functional–behavioral significance? This question has been asked repeatedly over the years [16,82,94]. A number of different hypotheses have been put forth in response, and although most of them link mu rhythms to sensorimotor processes, a comprehensive and satisfactory explanation is still not available. To arrive at such an explanation, it is critically important to understand the neural basis of this rhythm, if only to constrain functional speculations. Hence, one goal of mu research must be to demonstrate that any proposed functional role is affected by the manipulation of the neuronal populations assumed to generate it. Approximately 50 years since it was first reported, we have a variety of insights regarding the mu rhythm but little understanding on how those individual pieces fit together into a rational whole. Conceptual gaps remain in our understanding of the

relationship between mu rhythms, neuronal activity, and information processing, and there have only been a few systematic efforts to integrate the body of results into a coherent theoretical framework [7,16,94,102].

1.2. Goals and organization of this review

This review aims to address some of these conceptual gaps and integrate existing knowledge regarding the phenomenology and neural basis of the mu rhythm in order to elucidate its functional role. More specifically, it presents a synopsis of the evidence suggesting that mu rhythms: (1) are more than an idling state of sensorimotor cortex and instead reflect dynamic and integrative sensory, motor, and mnemonic processes; (2) reflect activity in sensori-, audio-, and visuomotor mirror neurons in frontal and parietal networks; and (3) represent an important information processing function, which is to link perception and action, or more specifically the transformation of “seeing” and “hearing” into “doing.” These proposed functions are consistent with previous empirical and theoretical work on mu rhythms in animals, infants, clinical populations, normal adults, and even the developing brain computer interface field.

The organization of the review will proceed according to the following format: in Section 2, the phenomenology of the mu rhythm, a summary of what is known about its antecedent conditions, and a review of work addressing the neural mechanisms involved in mu generation are described. In Section 3, some supporting evidence from different domains that bear on the functional significance of mu rhythms are reviewed. This section also includes a review of the mirror neuron system, some of its basic properties, and its relationship to mu rhythms. Finally, in Section 4, the concept of the mu rhythm as a perception-to-action process is described.

2. Phenomenology of the mu rhythm

2.1. More than an idling state

The mu rhythm is an EEG oscillation with dominant frequencies in the 8–13 Hz and 15–25 Hz bands [53]. These oscillations are limited to brief periods of 0.5 to 2 s duration [95] and can be recorded over human sensorimotor cortex in the absence of movement. Because it appears to

occur in the absence of processing sensory information or motor output, i.e., “an area that has nothing to do” [1], the mu rhythm was originally conceived to reflect a cortical “idling” or “nil-work” state, similar to the classical alpha rhythm [18,89,109]. Indeed, Pfurtscheller and colleagues [109] have argued that “one example of such an idling cortical area is the enhancement of mu rhythms in the primary hand area during visual processing or during foot movement. In both circumstances, the neurons in the hand area *are not needed* for visual processing or preparation for foot movement. As a result of this, an enhanced hand area mu rhythm can be observed. Another characterization was given earlier by Kuhlman [75] who attempted to isolate variables mediating mu rhythm enhancement. Because no single variable that produced consistent enhancements was found, it was concluded that “. . .mu rhythm had no striking psychological correlates and was present as part of the normal waking state”.

Idling states of the brain, as well as simple explanations concerning their functional significance, are giving way to more complex views reflective of diverse brain functions that comprise sensory, motor, cognitive, mnemonic, and integrative processes [7,9,101]. Today, there is increased interest in the association between EEG rhythms and cognitive processes [8,61,63,69,71], with many studies reporting short- and long-lasting *suppressions* of ongoing alpha-like rhythms with cognitive function [11,62,65,71,104,105,125]. It has been shown, for example, that finger movements in elderly subjects are accompanied by a more widespread alpha-like suppression over motor and premotor areas compared with young subjects [24], presumably because older subjects put more effort into this simple task. Paradoxically, increased attentional demands, such as attentive expectation of relevant stimulus omission, working memory activation, and episodic short-term memory tasks, also produce *enhancements* of alpha-like rhythms [6,67,74,90,116,129]. Recently, a causal connection between alpha-like rhythms and mental rotation has been suggested based on studies using repetitive transcranial magnetic stimulation (rTMS) in which performance on the task was enhanced following alpha-like frequency stimulation [68]. While these reports argue for a relationship between brain rhythms and higher cognitive functions, the precise relationship is not yet clearly established.

2.2. Mu synchronization and desynchronization

It is generally accepted that EEG desynchronization resulting from thalamocortical stimulation is a reliable correlate of excited neural networks or activated cortical areas [49,133], while EEG synchronization is a correlate of deactivated cortex [109]. Both the occipital alpha blocking seen with eyes open as well as frontal mu blocking seen during movement preparation and execution are examples of desynchronized activity. The degree of mu blocking, reactivity, or suppression occurring during movement can

be expressed as a percentage of the peak power value at rest and typically shows an average decrease of about 61% (SD = 25) [142].

According to Nunez and Silberstein [96], frequency-specific electrical scalp activity and hemodynamic activity can change in opposite directions. This inverse relationship is believed to depend upon both the spatial scale and the frequency band of cortical synchrony. During the type of synchrony that is reflected in alpha-like rhythms, activity in a small fraction of neurons within a cortical column may be sufficient to give rise to a strong EEG signal, while the inactive majority maintains overall metabolism low and thus the blood oxygen level dependent (BOLD) effect small [77]. This suggests that widespread thalamocortical synchronization is associated with decreased brain metabolism [37]. Recent functional magnetic resonance imaging (fMRI) studies are also consistent with this negative correlation, showing that, whenever alpha-like oscillations increase, presumably due to increased synchronous activity, inferior frontal, superior temporal, parietal, occipital, and cingulate cortex show a decrease in BOLD signal [77]. In contrast, a positive correlation between alpha rhythm and BOLD signal occurs in some areas, including the thalamus and insula [49]. In PET studies, similar negative correlations between alpha-like power and glucose metabolism have been reported [122], with positive correlations occurring in the pons, midbrain, thalamus, hypothalamus, amygdala, basal prefrontal cortex, insula, and right dorsal premotor cortex [15,122].

Changes in EEG rhythmic activity not only happen spontaneously but can also be induced by external events. These event-related oscillations bridge the gap between single neuron activity and activity in neuronal assemblies. In particular, stimulus-dependent 10 Hz oscillations in the scalp EEG and at the cellular level (evoked by auditory and visual stimuli) share common features. These can be quantified in time and space relative to a predefined reference and hence can be related to specific tasks. Experimental data support the idea that 10 Hz event-related desynchronizations (ERDs) are a correlate of activated cortical networks related to information processing [29,30,63,66,65,124], selective attention [28,137,143], and motor preparation [24,78,110,111,139].

Recordings in normal human adults show that mu ERD starts 2 s before movement onset and that the size and magnitude of the ERD effect reflect the size of the neural network involved in the performance of the task. This is supported by the observation that increasing task complexity increases ERD [11,28,30,143] presumably because a larger group of cells is involved. In general, the two main factors that have been reported to affect the occurrence or maintenance of mu rhythms are motor inactivity and the level and quality of attention. The induction of actual movement is a reliable blocking mechanism of pre-existing mu rhythms, but attention alone (most likely on the motor imagery itself) is also able to provoke the same mu

suppression response [23]. Interestingly, it has been shown that hand dominance, handedness, and type of movement influence the proportion of pre-movement mu rhythm desynchronization in both the left and right peri-Rolandic areas [132].

Since ERD reflects activation of cortical tissue, event-related synchronization (ERS) has been assumed to reflect deactivation, inhibition, or at least the natural “idling” state of the network [93,109]. Koshino and Niedermeyer [73] found synchronized mu rhythms during pattern vision, and Pfurtscheller and Klimesch [105] reported larger and more synchronized mu rhythms during reading. The interpretation has been that, since mu rhythms reflect sensorimotor processing and are not directly involved in visual processing, the network becomes “idle” or “nil-working” and synchronized during such tasks. However, the existence of visuomotor ‘mirror’ neurons in prefrontal cortex (see Section 4), which may provide downstream regulation of sensorimotor neurons, argues for a different interpretation. That is, it is theoretically possible that ERS results from functionally active but increasingly synchronized sensorimotor networks.

2.3. Unique rhythms with independent sources

Alpha-like oscillations, like the mu rhythm, are recorded in nervous systems of different complexities, from the human brain to isolated ganglia of invertebrates. The amplitude of these oscillations is generally inversely proportional to the frequency (higher amplitudes for slower oscillations) and to the number of synchronously active neural elements [34]. These rhythms are believed to arise from the oscillation of postsynaptic potentials in the cortex [10,97] and they are seen in surface EEG if neurons are synchronously active across several centimeters of cortex [97].

Mu rhythms are typically identified as an 8–13 Hz oscillation (although see [53]), maximal over sensorimotor cortex when the individual is at rest. It is attenuated by voluntary movement or somatosensory stimulation, but is minimally affected by visual stimulation. Because mu rhythm frequencies overlap those of the occipital or classical alpha rhythm (~10 Hz), it is sometimes difficult to separate them and more often than not the two have been confused and misidentified. However, mu rhythms show a more anterior focus compared to the more posterior one for the classical alpha oscillations. In general, mu rhythms reflect sensorimotor processing in frontoparietal networks, while classical alpha reflects primarily visual processing in occipital networks. Furthermore, classical alpha is desynchronized and attenuated when eyes are open. This is also true of a recently reported “third rhythm,” an alpha-like oscillation that is independent of classical alpha and shown to be present in approximately 20% of subjects [38]. By contrast, mu rhythms are not affected by opening or closing of the eyes, but rather are desynchronized and attenuated by

actual movement or the motor imagery of movement [91,92,112].

Other marked differences between mu and classical alpha rhythms have been reported in terms of hemispheric source localization and responsiveness to stimulus events. The frequency of mu rhythms has been reported to be significantly higher (mean = 10.5 Hz, SD = 0.9) than that of the classical alpha rhythm (mean = 9.6, SD = 0.7) [135]. This has led some researchers to refer to them as high and low alpha, respectively. However, other reports show opposite numbers [40], suggesting that differentiating these rhythms on the basis of mean frequencies is misleading and may actually require differentiation by spatial or functional criteria. Nonetheless, some differences appear real. Mu rhythms, for example, seem to be asymmetrical in frequency and power and, unlike classical alpha rhythms, do not exhibit bilateral coherence [135]. It is also the case that amplitude or power in the classical alpha rhythm tends to be larger than in mu rhythms [135].

Using high-density magnetoencephalography (MEG), source localization techniques, and independent component analysis (ICA), it has been possible to demonstrate distinct cortical sources (equivalent dipoles) of alpha-like activity [83,84,147]. Furthermore, clinical studies showing asymmetric reactivity of alpha-like activity to eye opening also suggest independent hemispheric generators [146]. Indeed, a number of recent studies [54,94] have identified at least three distinct physiological alpha-like rhythms with independent sources in the two hemispheres: (a) the classical occipital alpha with parietooccipital and calcarine sulci sources; (b) the frontal mu rhythm with sources in the Rolandic fissure; and (c) a midtemporal “third rhythm” that is typically not recorded on the scalp.

Investigators have reported that the human mu and the occipital alpha rhythm both contribute to scalp-recorded EEG in central regions of the brain, with the occipital alpha thought to be volume-conducted into those areas. However, in a study using closely spaced Laplacian derivations, it was possible to rule out volume-conduction effects, providing evidence that both rhythms are, in fact, independently generated by the underlying neocortical circuitry [3]. Whole-head MEG recordings assessing the distribution of the estimated sources of alpha and mu rhythms produced similar conclusions. The results indicate that alpha and mu rhythms have distinct spatial distributions of their equivalent dipolar sources [84].

In a study to determine whether different subtypes of mu rhythms exist, ERD was quantified in the 8–10 and 10–12 Hz bands during self-paced, voluntary finger, and foot movements [111]. The data indicate that the lower frequency component reflects a widespread movement-type non-specific ERD, whereas the upper frequency component shows a more focused and movement-type specific pattern, clearly different with finger and foot movement. The different patterns provide evidence for the existence of at least two different subtypes of mu rhythms, a somatotopi-

cally non-specific lower frequency mu and a somatotopically specific mu characteristically found in the upper alpha frequency band [111].

The relationship between the 8–13 Hz mu rhythm and other EEG rhythms, such as central beta (20–24 Hz) or the 15–25 Hz rhythm reported by Hari and colleagues [53], is also unclear. On the one hand, the most reactive beta-like components (~20 Hz) may be a first harmonic of the mu rhythm. But, the source for these two oscillations seems to be different [108,123], suggesting distinct component frequencies. During a finger movement task, 20-Hz ERD had a focus slightly more anterior than the 10-Hz ERD [108,123]. Furthermore, the time course of recovery following desynchronization differed for these two rhythms, with faster ones recovering more quickly [131]. These data suggest that mu rhythm is not a unitary phenomenon but an aggregation of different processes involved in the transformation of “seeing” and “hearing” into “doing,” with distinct aspects of that process reflected in these different frequencies (i.e., 8–10, 10–12, 15–25 Hz).

Furthermore, all these differences in source localization, bilateral coherence, frequency, power, and functional responsiveness suggest, not only independent sources for mu and classical alpha rhythms, but also independent mu sources in the two hemispheres [83].

2.4. Topography of mu rhythms

Studies have also shown that a correspondence exists between the body area movement which blocks the mu at a given site and the body region that is affected by stimulation at the same site [4]. This suggests that sensorimotor cortex displays a variety of mu rhythms with specific topographic and functional properties rather than one uniform rhythm. Indeed, areas involved in hand, foot, and face movements, which have larger cortical representations in the human brain and an increased number of internal connections but few connections between areas [27] appear to produce distinct mu rhythms [106,110].

Other studies have shown that early ERD, presumably indicative of motor preparation, is located over the contralateral central region covering primary motor cortex. It is then followed by a bilateral suppression occurring over ipsilateral and contralateral central regions during the actual performance of the movement. These results indicate that programming of voluntary movement induces early activation in contralateral sensorimotor areas, while performance of the movement induces bilateral activation in sensorimotor areas [25,138].

While the major focus of studies examining the neural basis of mu rhythms has been in terms of their role in motor preparation and execution, some studies point to a role beyond simple motor control. For example, all the characteristics of the waking mu rhythm, including being blocked by contralateral body movement or contralateral somatosensory stimuli, are present during REM sleep—a

time when motor movement is essentially inhibited [31]. This suggests a larger functional role for mu rhythms in states of wakefulness and REM sleep.

In summary, the extant evidence is compelling that mu rhythms are only superficially similar to other alpha-like rhythms in cortex. Differences in source generation, sensitivity to sensory events, bilateral coherence, frequency, and power suggest that mu and classical alpha rhythms are independent phenomena. Mu rhythms are phasic electrophysiological signals spontaneously induced by internal events or evoked by external stimuli. Functionally, they primarily reflect sensorimotor processing in frontoparietal networks, while classical alpha reflects mainly visual processing in occipital networks. All these argue that mu rhythms are more than an idling state of the brain. Its suppressions and enhancements seem to largely reflect motor processing, but the system is very sensitive to cognitive and affective influences.

3. Other supporting evidence

3.1. Developmental and clinical studies

Stroganova et al. [136] showed that the alpha-like rhythm is blocked by visual stimulation even in 7- to 12-month-old infants, suggesting a functional similarity between infant and adult rhythms. They found a pronounced increase in 6–8 Hz rhythmic activity at parietooccipital sites under a condition of total darkness, compared with a condition of quiet attention. Several other studies [51,52,94] have reported on the appearance of a 4–7 Hz rhythm at central sites at around 4 months of age. Hagne labeled this the ‘central alpha’ and noted that the mean frequency of this rhythm remained around 7 Hz over the first year of life, increasing to 8 Hz by 18 months then to 9 Hz by 4 years, and stabilized at around 10 Hz in mid-adolescence. Most researchers examining the developmental data speculate that the progression of this central rhythm in infants is associated with the development of motor and locomotor skills.

In more recent work, it has been argued that the central rhythm of infants and young children and the sensorimotor mu rhythm in adults have a functional relationship [39,40,85,136]. Observations of 20-month-old infants show a similar slow equivalent of the mu rhythm in the 6–7 Hz range [73]. As individuals get older, alpha-like responses increase in frequency and show stronger phase locking and an increasing locus over frontal brain regions. These results demonstrate a trend towards frequency acceleration and a posterior-to-anterior shift in focus for both the spontaneous and evoked alpha-like activity with increasing age [7].

Clinical studies, in contrast, report a deceleration or slowing of alpha-like rhythms with pathology [94]. Schizophrenic patients, whose EEG is characterized by diminished alpha-like power, exhibit more negative symptoms than those patients who do not show diminished power in the

alpha band [130]. Other clinical studies have reported distinct populations of subjects with characteristically different mu rhythms. In one study, over 5000 patients who received an EEG epileptic assessment were divided into two groups: Group 1 showing typical mu rhythms, i.e., recorded during wakefulness and not affected by visual stimulation but blocked by voluntary movements or tactile stimuli; and Group 2, subjects showing atypical mu rhythms, i.e., accentuated or activated by drowsiness, photic stimuli, or hyperventilation. No difference between the two groups was found with regard to frequency, amplitude, or origin of the mu rhythm. However, although both groups showed a high incidence of epilepsy, Group 2 showed higher incidence of intractable epilepsy, as well as of severe intracranial trauma and of organic brain disease [141].

Clearly, mu and alpha-like rhythms are present at the early stages of human development, suggesting an important functional role. While most current speculation centers on the relationship with developing motor and locomotor skills, our hypothesis would argue for a role in translating “seeing” and “hearing” into “doing,” a necessary component for imitation learning. Hence, it is assumed that mu rhythms play an even greater developmental role than has previously been ascribed. Furthermore, the adaptive and dynamically changing properties of alpha-like rhythms, including frequency acceleration and posterior-to-anterior shifts in focus, underscore a plasticity that is not necessarily lost in adulthood and that may explain the dynamical changes brought about by pathological states.

3.2. Animal studies

Animal experiments in awake cats and monkeys have reported sensorimotor rhythms (SMR) in the 12–16 Hz band. These rhythms are blocked, suppressed, or desynchronized with body movement [18,56,134] when the animal is immobile and/or receiving a reinforcement. Like the human mu rhythm, the SMR develops when the animal is motionless and attentive, i.e., in a state of ‘quiet waking’ [140]. SMR is distinct from other sensorimotor rhythms, with different cortical distributions and different frequencies and appearing under different behavioral and environmental conditions. For example, although similar SMR rhythms are recorded from the primary visual and somatosensory cortex of the cat in the same overall behavioral situations (quiet waking and/or expectancy of an event to occur), these rhythms are independent [19]. The cortical mu focus in the cat is centered within a restricted part of area SI, in the forepaw and wrist projection field. The related thalamic focus is localized in a small zone of the VP nucleus that also corresponds to the hand and wrist projection area [12]. Based on the reported topographical, morphological, and functional similarities between feline SMR and the human mu rhythm, the feline SMR has been described as the first demonstrable model of a spontaneous human EEG rhythm [59].

Although few in number, animal studies of mu and alpha-like rhythms show a remarkable similarity to the analogous human rhythms. From an evolutionary perspective, this gives weight to the growing importance of such a mechanism in more than simply cortical “idling.” Animal models provide a unique opportunity to understand the functional significance of brain rhythms, and there is need for more of this work, especially using non-human primates. In a review of the animal (primarily cat) literature examining the functional role of thalamocortical oscillations, Buser and Rougeul-Buser [16] concluded that SMR-type oscillations have at least two distinct and opposite roles: to lower the level of awareness, such as in slow wave sleep, when the oscillations are globally distributed throughout the cortex; or to contribute to perceptual processing, when these rhythms are of more local origin and possibly of a higher frequency. This local versus global role is an important contextual backdrop for the perception-to-action role that is being ascribed to the human mu rhythms.

3.3. Brain computer interface: volitional control of mu rhythms

Studies show that humans can learn to volitionally control the amplitude of the 8–13 Hz mu rhythm [75,128], as well as central beta (20–24 Hz). Whether this control reflects direct access to the neural mechanisms generating these rhythms or indirect modulation of some general state of the brain is not clear. In brain computer interface (BCI) studies, performance feedback is typically provided by the visual consequences of controlling the mu rhythm, thus creating a closed-loop neurofeedback system. Such learning has been mapped to the control of a variety of applications, from moving a cursor, spelling words, answering questions, selecting among choices on a computer screen, to activating a device [87,88,113,148–150]. This control does not depend on muscle activity per se [144] and thus provides an alternative channel of communication and control for individuals with severe neuromuscular disorders who are unable to use the standard interfaces, i.e., keyboard or mouse.

Some studies use feedback involving 2-dimensional computer representations of mu power in the form of a box or a cursor moving in an upward or downward motion, reflecting high or low levels, respectively [86,149]. The changes in amplitude that provide one- and two-dimensional control involve desynchronization (mu suppression) or synchronization (mu enhancement) of the mu rhythm. Different levels of suppression or enhancement (i.e., different levels of mu amplitude or power) can then be mapped to a variety of computer-controlled functions [150]. Kuhlman [75] used a different form of feedback in which a small white light was illuminated for as long as the subject’s mu power remained at the desired level. In this study, power spectral analysis across 50 sessions of EEG feedback training showed that mu activity could be systematically

enhanced, whereas a 12–14 Hz component of low voltage fast activity could not. Results such as this indicate that long-term modification of mu rhythms with feedback training is possible. However, training per se cannot produce the rhythm [75]. Using a stimulus-rich, realistic, and motivationally engaging environment, Pineda et al. [113] showed that subjects gain control of mu suppression more rapidly than they do mu enhancement. In that study, changes in mu power were reflective of hemispheric coupling (suppression) or uncoupling (enhancement). Overall, subjects learned to control mu rhythms within 3–10 h of training, which required the acquisition of independent control of mu generators in the two hemispheres. Guger et al. [50] reported a similar type of rapid training.

The key to learning volitional control of mu rhythms appears to be the gradual build-up of internal associations with the visual feedback [113]. Since mu rhythms are desynchronized by self-movements, as well as by the observation and imagination of movement [92,112], learning strategies tend to focus on motor imagery. However, recent evidence indicates a strong cognitive and affective influence. In a recent study, for example, it was found that affective inputs regulate mu rhythms by showing that anger induces changes in the spatial distribution of intracortical connections in the alpha-like frequency range over frontal cortex [121].

It is remarkable that individuals learn to control mu rhythm suppressions and enhancements volitionally in a very short period of time. This raises questions about the open architecture of neural systems producing mu rhythms, their ability to respond to cognitive, emotive, and motor imagery, and their ability to reorganize dynamically. Whether dynamical restructuring as a consequence of neurofeedback learning produces improved (or perhaps decreased) performance in motor performance or more broadly defined cognitive processes is only now beginning to be studied.

3.4. Mu rhythms and mirror neurons: a link between perception and action

Single unit studies in the premotor cortex of macaque monkeys indicate that cells in area F5, which are indistinguishable from neighboring neurons in terms of their motor properties, also discharge in response to observed actions [26] (for a review, see [118]). That is, when a monkey observes an action that is in its motor repertoire, these neurons “mirror” the activity and appear to represent the motor action in their own premotor cortex, revealing a type of observation/execution matching system. Mirror neuron activity has also been shown to be selective for goal-directed, meaningful actions [42]. Recently, a population of neurons in the ventral premotor cortex of the monkey has been found that discharge when the animal performs a specific action, when it sees the same action performed by another individual, or when it hears sounds associated with

the same action [60,70]. Thus, mirror neurons respond to the execution of a movement as well as the audiovisual representations of the same movement — therefore providing an audiovisual-to-motor link or a transformation between “seeing” and/or “hearing” and “doing.” Such an observation/execution matching system is capable of performing an on-line automatic execution or “mimicry” of the action it perceives or it may perform an off-line internal simulation of the observed action without concomitant motor movements. It has been speculated that such internal simulation or motor imagery may play a critical role in imitation learning or the ability to understand other individuals’ movements, an ability that may be especially critical for the development of a theory of mind and hence for understanding social interactions [118].

Although individual mirror neurons cannot be studied directly in humans, the existence of an analogous system in the homologous brain regions (Broca’s area or Brodmann’s area 44) has been supported by indirect population-level measures such as TMS [35] and fMRI [57]. Fadiga and colleagues [35] found that motor-evoked potentials over motor cortex were enhanced in response to TMS when subjects observed another individual performing an action relative to when they detected the dimming of a light. They concluded that this specific enhancement was a result of activity of mirror neurons in the prefrontal cortex influencing the motor response. Iacoboni and colleagues [57] measured blood flow in Brodmann’s area 44 and found increases during the observation and performance of actions. Other recent studies have reported activations with similar properties in the parietal cortex [13,14], as well as the superior temporal sulcus [58,115]. These data suggest that the prefrontal mirror neuron system may in fact be part of a broader network, one responsible for biological motion perception [36,99].

The connection between mu rhythms and mirror neuron activity was first suggested by Altschuler et al. [2] and thereafter by other researchers [21,22,55]. More recent studies echoing this line of work give further support to this link [91,92,98]. It is a working hypothesis of this review that mu rhythms reflect the downstream modulation of motor neurons by cells in the premotor cortex, some of which are mirror neurons. However, when the transformation from ‘seeing’ and/or ‘hearing’ to ‘doing’ occurs, or, to put it another way, when action observation/comprehension occurs, then mu rhythms reflect primarily mirror neuron modulation. Various properties of the mu rhythm link it directly to mirror neuron activity. At rest, sensorimotor neurons fire in synchrony [43], leading to large amplitude EEG oscillations in the 8–13 Hz (mu) frequency band. When subjects perform an action, these neurons fire asynchronously, decreasing the power of the mu-band oscillations [107,123]. Mu power recorded from electrodes at scalp locations over sensorimotor cortex is reduced in normal adults by self-initiated movement, imagined movement, and observed movement [5,21,44,112]. More recent

studies have found that the mu rhythm is also modulated by object-directed actions [92], similar to fMRI studies of the mirror neuron system [13]. Since the mu rhythm is generated by activity in sensorimotor areas and mirror neurons have been located primarily in premotor areas, it has been hypothesized that the mu rhythm may specifically index downstream modulation of primary sensorimotor areas by mirror neuron activity [91,92].

In addition to its responsiveness to motor-related imagery, the human mirror system has been implicated in higher-level cognition. Rizzolatti et al. [119] have suggested that the capacity to associate the visual representation of an observed action with the motor representation of that action can lead to imitative learning. Oberman and colleagues have recently reported evidence for a dysfunctional mu rhythm and by implication a dysfunctional mirror neuron system in high functioning individuals with autism spectrum disorders (ASD) [98]. ASD are largely characterized by deficits in imitation, pragmatic language, theory of mind, and empathy. Rizzolatti and Arbib [117] suggest that this observation/execution mechanism is an ideal candidate for a hypothesized evolution of language from an earlier gestural communication system. Gallese [41] suggests that once another individual's actions are represented and understood in terms of one's own actions, it is possible to make predictions about the mental state of the observed individual, leading to "theory of mind" capabilities. Lastly, Leslie et al. [79] found that facial expressions may activate the mirror neuron system. Therefore, empathy may critically depend on one's ability to understand the observed facial expression in terms of one's own motor representations.

In summary, the phenomenology of the mu rhythm resembles the phenomenology of mirror neuron activity. Both are sensitive to movement, as well as to motor and cognitive imagery (i.e., observed meaningful actions). Their overlapping neural sources in sensorimotor frontoparietal networks further support the argument that they are related and involved in linking perception to action, which may be a critical component in the development of higher level cognition.

4. Mu rhythms and perception-to-action processes

4.1. Translating "seeing" and/or "hearing" into "doing"

The existence of mirror systems in the human brain involved in the transformation of perceptual representations to executable actions, together with new conceptualizations about alpha and mu rhythms [102], prompted this elaboration of the mu rhythm–mirror neuron hypothesis. The functional significance of such rhythms in the EEG was one of the major problems in cybernetics put forward early on by Norbert Wiener. Wiener argued that the alpha-like rhythm reflects "the mutual entrainment of an ensemble of non-linear alpha rhythm generators such that the frequencies

of individual members of the ensemble have a tendency to be pulled synchronously toward a central frequency, and serving a type of gating function" [7]. This gating function means that the regulation of incoming signals, or the opening and closing of thalamic gates, occurs with the rhythm of the alpha waves—an idea supported by early, as well as more recent work [45,82]. More recently, it has been suggested that alpha rhythms result from narrowband filtration of a broadband process. In such a model, the synchronicity of rhythmic components is produced by the synchronicity of the broadband inputs to the narrowband filters [38]. That is, there is no need for rhythmic afferent input into such a system [76,151].

The entrainment/gating hypothesis proposed by Wiener, based on deterministic, non-linear oscillators, is a reasonable explanation to account for the multiplicity of local alpha-like rhythms in the context of coherent functions. However, a stochastic (filtered noise) signal resulting from multiple narrowband filters could generate electrical oscillations at their own resonant frequency [38]. Both of these mutually exclusive models can explain the functional interdependence within and between brain areas involved in the generation of alpha-like rhythms. According to our elaboration of these hypotheses, EEG consists of either multiple self-oscillators or narrowband filters producing rhythmic oscillations. These local networks are usually active in an independent manner. However, sensory input causes them to become coupled and entrained (or resonant) and thus to begin acting together coherently. Therefore, our hypothesis assumes that a global or 'diffuse and distributed alpha system' comes into existence when the independent sources of alpha in occipital, frontal, and temporal areas are engaged in some coherent function [7]. In line with arguments derived from information theory, the number of alpha centers decreases with lower complexity of the functional state of the subject [38], presumably reflecting the synchronization of local alpha centers into a more global alpha-like rhythm [97]. Local–global entrainment, then, accounts for suppression and enhancement of alpha-like rhythms. Furthermore, transient global coherence can then organize and instantiate top–down anticipatory processes that facilitate subsequent sensory processing at the local level, say, in visual cortex [80]. Global synchronization of alpha centers may result from neuromodulatory activity extrinsic to cortex, such as that from the brainstem locus coeruleus–noradrenergic or mesocortical dopamine systems, while local intrinsic modulation (e.g., from self-oscillating inhibitory interneurons) may mediate synchrony in small cortical populations [120].

The coupling or resonant state of local alpha networks is also supported by evidence that fronto-occipital and fronto-frontal alpha coherences decouple or become weaker from wakefulness to drowsiness and finally to REM sleep. These networks seem to maintain a mutual inter-dependency during wakefulness, whereas, during the transition to human sleep, the anterior and posterior areas appear to work quite

independently [17]. This coupling–decoupling or local–global coherence is consistent with the idea that synchronized alpha-like rhythms are the result of powerful inhibitory effects on thalamocortical information transfer [64]. Because corticocortical connections have indirect pathways through the thalamus, it provides a neural basis for instantiating the type of gating function proposed. The selective interruption, inhibition, or gating of thalamic activity results in sleep spindles in the range of 7–14 Hz [109,133]. Indeed, zones of mu desynchronization (ERD) and synchronization (ERS), like the focal ERD/surround ERS, likely reflect lateral inhibitory processing resulting from nucleus reticularis (nRT) feedback onto thalamic relay cells [102].

The question that remains is, what is the ‘coherent function’ that involves occipital, frontal, and temporal alpha sources? It is proposed that, within the context of an entrainment/gating neural mechanism and the existence of a system that translates visual (“seeing”) and auditory (“hearing”) representations into action-based representations (“doing”) then a vision-centered domain (classical alpha), an audition-centered domain (third rhythm) and a sensorimotor-centered (mu) domain are the minimal prerequisites for a perception-to-action translation system that is necessary for understanding the behavior of others. Global alpha entrainment would then reflect the spatiotemporal transfer of information from occipitotemporal visual/auditory areas to frontoparietal sensorimotor areas and back [114,145].

Just what causes suppression versus enhancement in this model? These changes in rhythmic activity must be viewed within the context of a local–global organization. Furthermore, the evidence of functionally distinct lower (8–10 Hz), middle (10–12 Hz), and upper (15–25 Hz) bands that may reflect different aspects of this global versus local processing [111] suggests that these bands should be examined independently. Nevertheless, the evidence indicates that several distinct states may be possible: (1) local suppression due to desynchronized activity in a restricted cortical region as a function of asynchronous activation of the network—this produces alpha-like suppression, overall greater cellular firing, and stronger BOLD signals; (2) local enhancement due to synchronized activity of a smaller population of cells in a restricted cortical region—this produces mu enhancement but overall less cellular firing and hence reduced BOLD signals; (3) global enhancement due to synchronized activity across widely distributed networks—this produces alpha-like enhancement, more cellular activity, and stronger BOLD signals; and (4) global suppression due to synchronized activity of a smaller subset of the networks—this produces alpha-like suppression, less cellular activity, and reduced BOLD signals [32,33]. Finally, the optimal performance of a goal-directed movement necessitates the integration of movement-specific and cognitive-related factors [46,47]. In particular, cognitive regulation allows

the subject to plan actions to concrete events and to respond in a flexible manner to changing environments [126,127]. Mu suppression and enhancement appear to be exquisitely responsive to cognitive and affective regulatory processes.

In summary, mu rhythms appear to reflect the translation of “seeing” and/or “hearing” into “doing.” This function requires the entrainment or resonance of multiple alpha generators (visual-, auditory-, and somatosensory-centered domains). These domains typically exhibit synchronized and desynchronized activity in a locally independent manner. However, they become coupled and entrained when they become coherently and globally engaged in translating perception into action.

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