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Claire Calmels, Magaly Hars, Paul Holmes, Gilbert Jarry, Cornelis J Stam. Non-linear EEG synchronization during observation and execution of simple and complex sequential finger movements. *Experimental Brain Research*, Springer Verlag, 2008, 190 (4), pp.389-400. <10.1007/s00221-008-1480-z>. <hal-01575539>

HAL Id: hal-01575539

<https://hal-insep.archives-ouvertes.fr/hal-01575539>

Submitted on 21 Aug 2017

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Non-linear EEG synchronization during observation and execution of simple and complex sequential Finger movements

Claire Calmels · Magaly Hars · Paul Holmes ·
Gilbert Jarry · Cornelis J. Stam

Abstract The main aim of this study was to examine the temporal aspects of neuronal changes during the observation and execution of simple and complex tasks to gain a greater understanding of the mirror neuron system's involvement in complex motor tasks. Eleven right-handed subjects observed simple and complex Wnger movement sequences. Electroencephalograms were recorded from 19 electrodes. Activity was considered in four frequency bands (8–10, 10–13, 13–20, and 20–30 Hz) using a new measure, synchronization likelihood. The results show that motor tasks of diVerent levels of complexity did not have a signiW-cant inXuence on cortical synchronization. The results also provide additional indirect evidence for mirror neuron activity associated with intransitive tasks. Data are discussed in the light of recent Wndings from the cognitive and behavioral neuroscience literature.

Keywords Action observation · Synchronization · Mirror neurons · Movement complexity · Electroencephalography

Introduction

Mirror neurons (MN) were Wrst discovered in the ventral premotor cortex of the macaque monkey with single neuron recording (Di Pellegrino et al. 1992; Gallese et al. 1996; Rizzolatti et al. 1988). These visuomotor neurons show special characteristics; they Wre when the monkey executes a goal-directed hand movement and also when it observes this same action executed by another monkey or by a human.

Evidence for the existence of similar neurons in humans has been provided by researchers who have used electroencephalographic (EEG) techniques (e.g., Cochin et al. 1999; Muthukumaraswamy and Johnson 2004; Muthukumaraswamy et al. 2004) and brain imaging techniques (e.g., Buccino et al. 2001; Grèzes et al. 2003; Iacoboni et al. 1999). EEG research has also provided indirect evidence for the existence of MN in humans. As early as 1954, Gastaut and Bert examined the mu rhythm, an 8–13 Hz rhythm generated in the sensorimotor cortex. It is known to be suppressed or blocked by the execution of actions and somatosensory stimulations. However, of interest here, Gastaut and Bert (1954) also showed that the mu rhythm was blocked during observation of actions performed by conspeciWcs. This result has been corroborated by more recent Wndings (Cochin et al. 1998, 1999; Lepage and Théoret, 2006; Muthukumaraswamy and Johnson 2004; Muthukumaraswamy et al. 2004). For example, Cochin et al. (1999) found that in the 7.5–10.5 Hz frequency band and for the electrode sites F7, T5, C3, P3, F8, F4, T6, C4,

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and P4 logarithmical spectral power values during the resting condition were significantly higher than the values obtained during the observation and execution of thumb and index finger opposition movements. This modulation during the observation of movement led some researchers (i.e., Oberman et al. 2007; Pineda 2005; Ulloa and Pineda 2007) to propose that this suppression could be used as a useful marker of MN system activity (see Pineda 2005 for more details). Brain imaging techniques have also provided evidence in favor of the existence of MN in humans. In contrast to EEG, the greater spatial resolution of brain imaging techniques offers more information concerning the localization of areas involved during the observation and execution of actions. Areas which form the core of the human MN system are located in the frontal and parietal areas and comprise the rostral part of the inferior parietal lobule, the lower part of the precentral gyrus, and the posterior part of the inferior frontal gyrus (Rizzolatti and Craighero 2004).

The existence of the MN system in humans is now widely recognized. While many of its characteristics remain unknown, attempts to explore MN system characteristics have increased dramatically in the past 10 years. In humans, the system acts differently depending upon the forms of observed motor behaviors. For example, the MN system is activated while observing non-object-related actions, so-called intransitive actions (Cochin et al. 1999; Iacoboni et al. 1999; Patuzzo et al. 2003). Further, the MN system shows less activity during observation of objectless actions, where movements are mimicked, compared to the identical movement that includes the object of interest (Buccino et al. 2001; Muthukumaraswamy and Johnson 2004; Muthukumaraswamy et al. 2004). However, two groups of researchers have found different results (Jackson et al. 2006; Jonas et al. 2007). They have reported no involvement of the MN system during the observation of intransitive actions. More specifically, they observed no involvement of ventral premotor cortex or inferior frontal gyrus during the observation of vertical, horizontal, and rotational movements of the hand and foot (Jackson et al. 2006).

Movement complexity has also been suggested to influence the involvement of the MN system. Although not systematically investigated, only Molnar-Szakacs et al. (2006), using functional magnetic resonance imaging (fMRI), have examined the role of the fronto-parietal MN system. In this study, individuals observed manual object manipulation sequences of different levels of complexity with serrated cups and stacking rings. The authors reported the involvement of the parietal and frontal cortices and higher visual area during the observation of all manipulation sequences. Two aspects of complexity were included in the experimental design: (1) the cognitive hierarchical complexity, related

to the complexity of the strategy used and action structure and (2) the motoric complexity related to the motoric manipulation of objects. The authors found that the MN activity was modulated according to the perceived motoric complexity of the action (i.e., the skill required to perform it) but not its cognitive complexity. They concluded that the different object combination strategies were not suitable for adults since the most complex strategy is acquired in childhood at around 3 years. They suggested that future research should examine the involvement of the MN system in more complex action sequences.

Brain mechanisms supporting the execution of simple and complex motor tasks have been broadly investigated using EEG, magnetoencephalography (MEG) (e.g., Leister et al. 2006; Pulvermuller et al. 1995) and imaging techniques (e.g., Catalan et al. 1998; Dassonville et al. 1998; Hummel et al. 2003; Verstynen et al. 2005). A number of studies have examined finger movements where the complexity of such movements can be defined by factors, such as speed and accuracy (e.g., Dhamala et al. 2003), sequence length (e.g., Catalan et al. 1998; Manganotti et al. 1998; Sadato et al. 1996a), and difficulty of transition between subsequent finger movements (e.g., Chen et al. 1997; Hummel et al. 2003). Generally, most of the studies have demonstrated increased brain activity for complex compared to simple movements. For example, Dassonville et al. (1998) used fMRI to investigate cortical motor activity as subjects performed predictable and unpredictable finger movement sequences as quickly as possible. The predictable movement sequence was defined as simple and the unpredictable as complex. Complex movements showed more activity in premotor, cingulate, SMA, pre-SMA, and superior parietal lobule areas compared to simple movements. More specifically, EEG studies have shown that the pattern of brain oscillatory activity varies according to the degree of movement complexity (e.g., Hummel et al. 2003; Kitamura et al. 1993; Manganotti et al. 1998; Pulvermuller et al. 1995). Manganotti et al. (1998) used spectral power and coherence to analyze data collected as right-handed subjects performed four different finger opposition tasks at 2 Hz. In the 8–12 and 13–20 Hz frequency bands, spectral power over the bilateral sensorimotor areas decreased which indicated that processing of the motor system was greater as the task became more complex. High levels of coherence were observed between primary motor cortex, premotor cortex, and the SMA during complex tasks. In contrast, lower levels of coherence were revealed during simple tasks. In addition, Pulvermuller et al. (1995) in the 8–12 Hz frequency band and using spectral analysis found a contralateral activation close to electrode sites C3 or C4 in a simple finger tapping task, and a bilateral activation over the motor cortices in a Luria task which is a complex finger opposition task. Therefore, simple finger movements tended to recruit

unilateral brain areas whereas, more complex movements showed activity in bilateral regions. These findings support the idea of transcortical cell assemblies (Pulvermüller and Mohr 1996) which proposes that “only entities with a certain degree of complexity are represented in transcortical assemblies (i.e., large and strong connected neuron populations), while simple representations are organized as local clusters of neurons” (Pulvermüller and Mohr 1996, pp. 562). Dhamala et al. (2003) have also suggested that as complexity increases, additional eVort is required; the eVort being responsible for the ipsilateral motorcortical activity. The relationship may not be clear as these data propose since Chen et al. (1997) and Dassonville et al. (1998) have shown the existence of ipsilateral activity during simple movement sequences, although ipsilateral activity was still greater for complex movement sequences.

The EEG techniques discussed above provide only a linear analysis of the data. One of the concerns with these approaches is that the analysis presumes that the EEG signal is stationary or varies very slowly (Muthuswamy and Thakor 1998). Since the EEG signal is known to be “noisy”, pseudo-stochastic, time-varying, non-stationary, and non-linear (Friston 2000; Palus 1996; Stam et al. 1999; Thakor and Tong 2004), linear analysis methods have been argued to be inappropriate for characterizing non-stationary data with rapidly changing interdependencies. Further, they do not identify the non-linear interdependencies in the underlying dynamical system (Stam et al. 2002a; Stam and van Dijk 2002). More specifically, spectral analysis technique is the most commonly used method to investigate the MN system in EEG paradigms (e.g., Cochin et al. 1999; Lepage and Théoret 2006). This method has limitations since it has been argued to reveal only part of the relevant information in EEG. It is only as an index of local cortical engagement (Stam et al. 2002b). To address these concerns, Stam and van Dijk (2002) have provided a non-linear index of synchronization in neuronal signaling between distant neuronal populations. Their method estimates the dynamical interdependencies between a time series (e.g., an EEG channel) and one or more other time series (Stam et al. 2002a, b; Stam and van Dijk 2002). Their index, synchronization likelihood (SL), is a marker that describes how strongly a channel is synchronized to all the other channels. Values of SL range from 1 to 0. Scores at or near 1 indicate maximal synchronization. For purely random correlations, SL tends to 0. Details regarding the SL technique can be found in Montez et al. (2006). For example, Micheloyannis et al. (2003, 2005) have also used this non-linear algorithm to examine EEG and (cognitive) task complexity. They showed that SL was able to discriminate cognitive tasks at different complexities. For tasks requiring complex visuo-semantic decision, SL between the temporal sites and parieto-occipital sites compared to the remaining recording

sites was highest in gamma and lowest in alpha bands. With reduced task complexity, the observed trend was reversed.

With the exception of the work conducted by Molnar-Szakacs et al. (2006), the extent of the MN system’s involvement in complex motor tasks has not been investigated. Therefore, examining the temporal aspects of neuronal activity changes during the observation and execution of simple and complex motor tasks requires further study. Therefore, the present study considered complex action sequences in which the level of motoric complexity was similar between the simple and complex actions. The level of complexity was not related to the dexterous manipulation of objects. Consequently, sequential Wnger movements with similar sequence length were chosen for this study with movement complexity being defined by the order in which the Wngers should be moved; a cognitive complexity. In the simple movement condition, adjacent Wngers were moved in one direction. For complex movements, Wngers were required to move in a predetermined order. To allow for the examination of linear and non-linear changes in coupling between different brain areas, the SL measure (Stam and van Dijk 2002) was used.

It was hypothesized that the brain oscillations underlying the observation of sequential Wnger movements would show similarities to those identified in the physical execution of the same movement in areas known to possess mirror properties and in frequency bands lying within a range of 8–30 Hz. In view of the literature results related to brain mechanisms and task complexity, it was also expected that complex movements, argued to include greater cognitive demands, would elicit greater interregional synchronization than simple movements under both the observation and execution conditions.

Method

Subjects

Eleven right-handed subjects (eight women and three men; mean age = 23.3, SD = 4.5) were included in the study. The subjects were assessed as right-handed by the Edinburgh Handedness Inventory (Oldfield 1971). All participants were scored as strongly right-handed and did not report the presence of any neurological or psychiatric disorders. All subjects provided written informed consent and were kept blind to the goals of the study. The study was approved by the local institutional ethics committee.

Task

Subjects were required to perform two sequential Wnger movements of different complexity (i.e., a simple movement

and a complex movement) with their right hand. This choice was made to avoid inter-task priming effects (Solodkin et al. 2001) and to prevent a gradual reduction in cortical activity due to repeated exposure to a same stimulus (Dassonville et al. 1998; Wu et al. 2004). The movements consisted of touching the tip of the right thumb with the tip of the other right hand fingers while the hand and forearm remained in a supinated position supported on a pillow. A simple or complex sequential finger movement comprised eight finger contacts performed at a rate of 2 Hz controlled by a metronome. The duration of the movement was 4 s. Complexity referred to a succession of eight pre-determined, random, and non-repeated contact performed consecutively. The sequence of the simple sequential movement was 1, 2, 3, 4, 1, 2, 3, 4. The complex sequential movement was 1, 2, 4, 3, 4, 2, 1, 3. In both cases, 1 was the index finger, 2 the middle finger, 3 the ring finger, and 4 the little finger.

Experimental procedure

The subjects were examined in five conditions: (1) a simple movement observation condition; (2) a simple movement execution condition; (3) a complex movement observation condition; (4) a complex movement execution condition; and (5) a control condition.

Multichannel EEG was recorded while participants sat in a darkened room with their forearms pronated lying on armrests. To reduce eye movement and other electromyographic artifacts throughout the EEG data collection, subjects were asked to avoid blinking by fixing their attention on a target point placed on a screen situated 1.30 m in front of them and to keep their jaw relaxed. These instructions were provided before each condition. A metronome, set at 2 Hz, was used to regulate temporal consistency and similar experimental parameters in the control, observation, and execution conditions (Manganotti et al. 1998).

Before EEG data collection, the subject memorized and performed the simple and complex finger movements until she/he was able to complete them without making an error

five times in a row. This prevented assessment of a learning process during the EEG acquisition and ensured regular, stable performance throughout the experiment (Catalan et al. 1998).

Movement observation condition

Each subject performed 40 trials for the observation of the simple task and 40 trials for the observation of the complex task. Each trial comprised four stages which were shown to the subjects via a video display. Instructions were provided to the subjects requesting them to observe the movement with the goal of replicating it at a later stage.

During the first stage of each trial ($t = 0-4$ s) the subject watched an amber monitor screen. This screen warned the subject of the impending requirement to observe a video. During the second stage ($t = 4-9$ s), subjects observed a video of a human model performing either a simple or a complex finger movement sequence at 2 Hz. In the third stage ($t = 9-12$ s) a white background was presented requiring the subject to stay focused. In the fourth stage ($t = 12-15$ s), a red monitor screen invited the subject to relax, to think of nothing, and to blink her/his eyes if necessary (see Fig. 1). The time interval between the beginning of viewing the movement and the onset of the next was 15 s (see Fig. 1). During the movement observation conditions, the experimenter controlled for finger movements; where movement was observed, the trial was discarded.

Movement execution condition

Each subject performed physically 40 trials of the simple movement and 40 trials of the complex movement following a similar procedure to the observation trials. The first stage warned the subject about the imminent movement requirement. In the second, a black background was presented to the subject. During this stage, she/he performed the simple or complex finger movement at 2 Hz. In the third stage, a white background invited the subject to remain focused. In the fourth stage, a red background prompted the

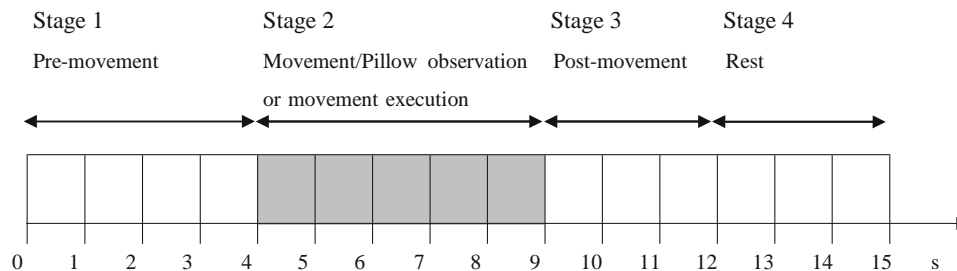


Fig. 1 Schema for one trial to be analyzed on the EEG line irrespective of condition. Shaded sections were used for EEG analysis. Stage 2 lasted 5 s since two periods of 500 ms (i.e., 500 ms before the onset of the movement and 500 ms after its onset/end) were added to the 4 s duration of the

movement. During these time lapses, the subject could see the hand and fingers at rest. This was done to allow the subject to understand the context in which the movement was performed and to avoid abrupt video image changes

subject to stop the movement, to relax, and to blink her/his eyes if required. The time interval between the beginning of one movement and the onset of the next was 15 s (see Fig. 1). During the movement execution condition, the experimenter checked the accuracy of the movements performed by the subjects; only correct series of Wnger–thumb contacts were retained for analysis. Where a subject made more than *W*ve mistakes while performing the movement, the data was discarded.

Control condition

Each subject performed 40 trials observing a pillow. Each trial was conducted similar to those used in the movement observation condition. However, instead of observing a movement, the participant observed a pillow for 5 s (see Fig. 1). Observing a stationary, non-biological object for the control condition was adopted based on the Wndings of Grafton et al. (1996). They reported that observation of movement was better contrasted with observation of an object than observation of a static hand since this can imply movement more than the inert object.

All trials for each of the *W*ve conditions were triggered using a speciWcally designed interface based on a photoresistive diode which responded to the screen color change. Five, 10-min blocks of 40 trials were performed. Each block was separated by a 5-min rest period. Irrespective of the movement complexity, the movement observation was performed *W*rst and was followed by the movement execution condition. The ordering was the same for the eleven subjects since they were required to observe the movement and replicate it at a later stage in order to investigate the role of mirror neurons in imitation (viz., Rizzolatti and Craighero 2004). The *W*ve conditions were structured into three main conditions: (1) The simple movement observation–execution conditions; (2) the complex movement observation–execution conditions; and (3) the control condition. The order of the three main conditions was counter-balanced across subjects.

Data acquisition and recording

Electrical brain activity was recorded from 19 Ag/AgCl pad electrodes held on the head with a rubber cap (Fp1, Fp2, Fz, F7, F8, F3, F4, Cz, C3, C4, PZ, P3, P4, T3, T4, T5, T6, O1, and O2) and placed in accordance with the international 10–20 system (Jasper 1958). Mastoids were used for the reference electrodes and the ground electrode was located on the forehead. Electro-oculograms (EOG) were also registered from the canthi of both eyes (horizontal EOG) and the supra and infra orbital of the right eye (vertical EOG). Electrode impedance was kept homogenously below 5 kQ throughout the experimentation and was checked systemat-

ically between the two blocks of trials. AmpliWer bandwidth was set between 0.15 and 114 Hz using a computer-based EEG recorder (Coherence, Deltamed, Paris, France). Baseline-corrected activity was sampled at 256 Hz. AD resolution was 16 bit.

Synchronization likelihood

Synchronization likelihood is a measure of generalized synchronization between two time series. It is sensitive to linear as well as nonlinear coupling, and suitable for non-stationary data. SL is the likelihood that recurrence of a pattern in time series *X* at two times, *I* and *J* will coincide with recurrence of patterns in time series *Y* at the same times *I* and *J*. The patterns are deWned in terms of state–space vectors obtained by time-delay embedding of the data. The SL takes on values between P_{ref} (no coupling) and 1 (complete coupling). P_{ref} is a parameter of the computation of synchronization likelihood, and is usually chosen as $P_{ref} = 0.01$. Technical details can be found in Stam and van Dijk (2002) and Montez et al. (2006).

Data processing

EEG data were analyzed in four frequency bands: 8–10, 10–13, 13–20, and 20–30 Hz and data processing was composed of three steps: segmentation of EEG trials, removal of artifacts, and SL computation.

Segmentation of EEG trials

Forty trials were completed during each ten-minute condition. Each trial was subdivided into four stages. For all conditions, details of these stages are provided in the experimental procedure section. Only the movement stage (4–9 s) was used for the EEG analysis (see Fig. 1).

Removal of artifacts

The artifact reduction process comprised two stages. First, all movement stage trials were visually inspected and trials

Table 1 Summary of the 5 (conditions) \times 9 (electrode sites) ANOVAs for each frequency band and for the movement stage

	8–10 Hz		10–13 Hz		13–20 Hz		20–30 Hz	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
C \times E	1.669	*	4.659	**	1.275	0.15	1.282	0.15

Only results for conditions \times electrode sites interactions are reported
C condition, E electrode

* $P < 0.02$, ** $P < 0.000001$

with ocular artifacts were corrected via the Semlitsch et al.'s (1986) method. The principle of this method being to subtract a fraction of an electro-oculogram (EOG) from the EEG. More specifically, a regression analysis associated with artifact averaging is used. This artifact removal was performed with Neuroscan 4.1 software (Revision A, 1999). The following options were selected: trigger, positive direction; threshold, 20%; blink values, two minimum sweeps; average artifact duration, 400 ms, and VEOG as the channel used in this computation; review, maxima and blinks enabled; and output, LDR + CNT. Second, for all the movement stage trials, slow drifts were removed by linear trend corrections (linear detrend module of Neuroscan 4.1 software).

Synchronization likelihood computation

Synchronization likelihood (SL) was computed for the movement stage for each of the trials of the Wve conditions, for each subject, frequency band, and electrode site. The SL values of a particular condition were averaged for each subject, frequency band, and electrode site. Parameters for the computation of the SL were: 1 sample for the lag, 10 for the embedding dimension, 10 for the Theiler correction (w_1); 1 for w_2 ; 0.010 for P_{ref} ; and 1 for the speed. These parameter choices were necessary in view of the very short duration of the movement stage to which the synchronization likelihood was applied.

Statistical analysis

All statistical analyses were performed using Statistica 7.1. From the electrode montage employed, F4, F3, P4, P3, FZ, and PZ were chosen for analysis because: (1) in humans, many frontal and parietal areas have been shown to possess mirror properties (Rizzolatti et al. 2002), and (2) the agranular frontal cortex (i.e., motor cortex) and the parietal lobe form the basic components of the motor system (Rizzolatti et al. 1998, 2002). CZ was selected because it overlies the supplementary motor area which is known to be involved in the generation of complex movement and planning of temporally sequential movement (Shibasaki et al. 1993). C4 and C3 were also chosen because oscillations from sites located over sensorimotor areas are thought to reflect the MN system activity (Pineda 2005). SL for these nine electrode sites was considered.

For each of the four frequency bands, 5 (conditions) \times 9 (electrode sites) repeated-measures ANOVAs were completed. There were two within-subject factors; condition (Wve levels: control, simple movement observation, complex movement observation, simple movement execution, and complex movement execution) and electrode site (nine levels corresponding to the nine EEG channels). Post hoc

comparisons were calculated using Fisher's LSD test where ANOVA results were significant. Before the ANOVA computations, the normality of the data was checked with the Kolmogorov-Smirnov test. To verify the sphericity assumption in repeated measures designs, the Mauchly's sphericity test was used.

These ANOVAs were computed to determine whether: (1) control condition SL values were significantly different from observation and execution conditions SL values, (2) simple movement SL values were significantly different from complex movement SL values under the observation and execution conditions, and (3) SL values during observation were significantly different from those during actual execution.

Results

Behavioral results

The percentages of correct Wnger taps performed by the subjects were 87% for the complex movement (13% of trials were removed from analysis) and 100% for the simple movement. No subjects were excluded from the study. During the observation condition, subjects did not move their Wngers and no trials were removed from the subsequent analysis.

SL for electrode sites

Four 5 (conditions) \times 9 (electrode sites) ANOVAs were computed. The EEG data were normally distributed and no sphericity violations were observed. Only results for conditions by electrode sites interactions have been reported here since they were directly linked to the goals of the present study (see Table 1).

No significant conditions \times electrode sites interactions were found for the 13–20 and 20–30 Hz frequency bands (see Table 1). However, significant conditions \times electrode sites interactions were observed in the movement stage for: (1) the 8–10 Hz band, $F(32, 320) = 1.669$, $P < 0.02$; (2) the 10–13 Hz band, $F(32, 320) = 4.659$, $P < 0.000001$ (see Table 1). Fisher's LSD tests were computed and three results were found.

First, during the movement stage, for the 8–10 and 10–13 Hz frequency bands, Fisher's LSD post hoc test analysis revealed significant differences between the simple observation condition and the control condition for all the electrode sites of interest except for P4 in 10–13 Hz. Significant differences were also found between the complex observation condition and the control condition in the two frequency bands except for F4 and P3 in 8–10 Hz and P4 in 10–13 Hz (see Fig. 2). Besides, significant differences were

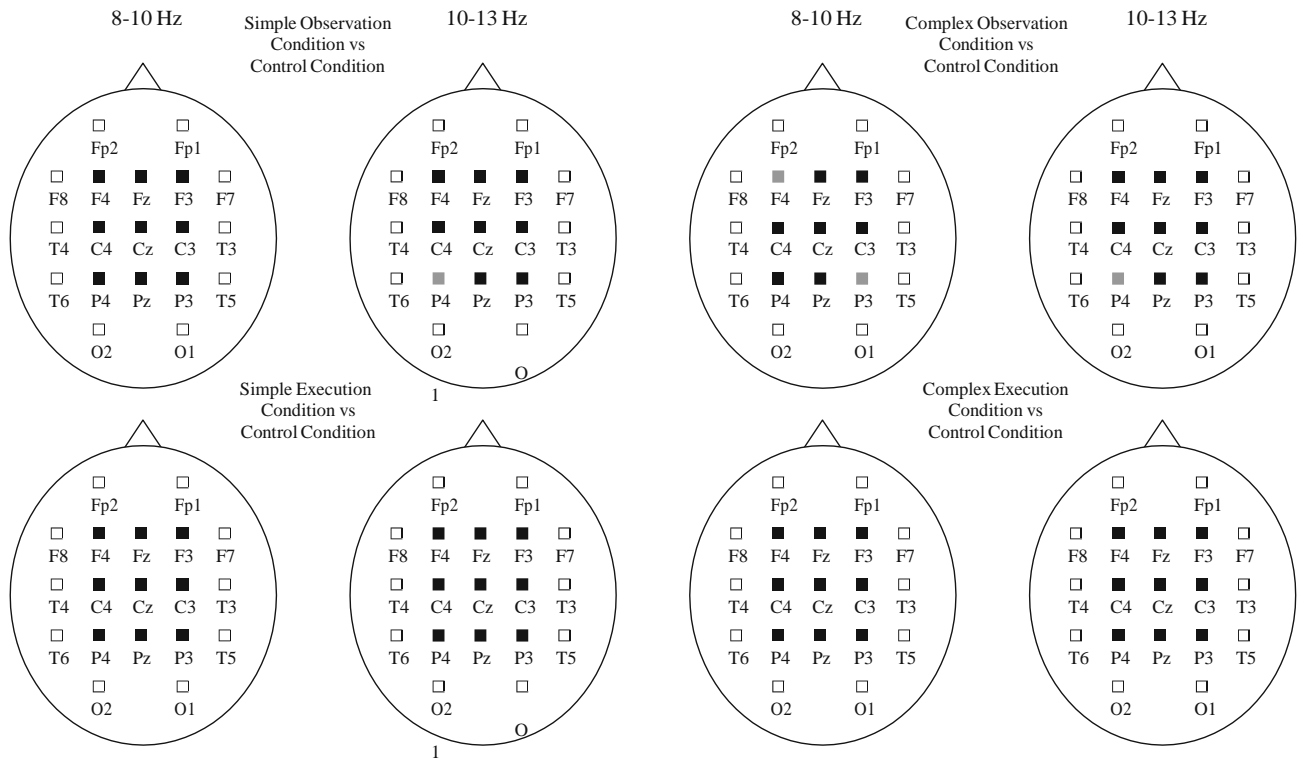


Fig. 2 Schemas indicating the scalp locations. *Black* and *gray squares* indicate the positions of electrodes of interest. SigniWcant diVerences in synchronization likelihood values between: **a** the simple observation condition and the control condition, **b** the complex observation condi-

tion and the control condition, **c** the simple execution condition and the control condition, and **d** the complex execution condition and the control condition are represented by *black squares* ($P < 0.05$). Non signiWcant diVerences are represented by *gray squares* ($P > 0.05$)

detected in each of the two frequency bands between the execution conditions and the control condition for all the nine electrode sites of interest (see Fig. 2). Synchronization values were lower in the control condition compared to the observation and execution conditions.

Second, during the movement stage, for the 8–10 and 10–13 Hz frequency bands, and electrode sites of interest, synchronization values during the simple observation condition were not signiWcantly diVerent from the synchronization values during the complex observation condition. Similar results were found for the execution condition except for C3 and FZ in 10–13 Hz. In these two cases, synchronization values were lower in the simple execution condition compared to the complex execution condition (0.083 vs. 0.088, $P = 0.038$ for C3; 0.090 vs. 0.095, $P = 0.027$ for FZ).

Third, Fisher’s LSD post hoc test analysis showed signiWcant diVerences during the movement stage under the conditions of simple observation and simple execution for the 8–10 Hz band for F4, F3, C4, C3, P3, FZ, and CZ. For the 10–13 Hz band, signiWcant diVerences between simple observation and simple execution were also found for F4, F3, C4, C3, FZ, and CZ (see Figs. 3, 4). Similar results were found for complex observation and complex execution

conditions for the 8–10 and 10–13 Hz frequency bands. In both frequency bands, SL during execution was higher than during observation (see Figs. 3, 4). These Wndings show that for the 8–10 and 10–13 Hz frequency bands, the observation–execution comparisons between the simple movement condition and the complex movement condition displayed similar synchronization patterns: SigniWcant and non signiWcant diVerences in SL were found at the same electrode sites (see Figs. 3, 4). More speciWcally, although there were some exceptions for parietal sites, the main Wnding was one of no signiWcant diVerences in SL for electrodes located in the parietal cortex (i.e., P4, PZ, P3) (see Figs. 3, 4).

Discussion

The primary aim of this study was to examine EEG synchronization during the physical execution and observation of simple and complex sequential Wnger movements. EEG functional connectivity was analyzed for the 8–30 Hz frequency band using a general measure, SL, sensitive to linear and non-linear coupling. The discussion has been organized into three sections. The Wrst discusses methodological considerations. The second considers task complexity,

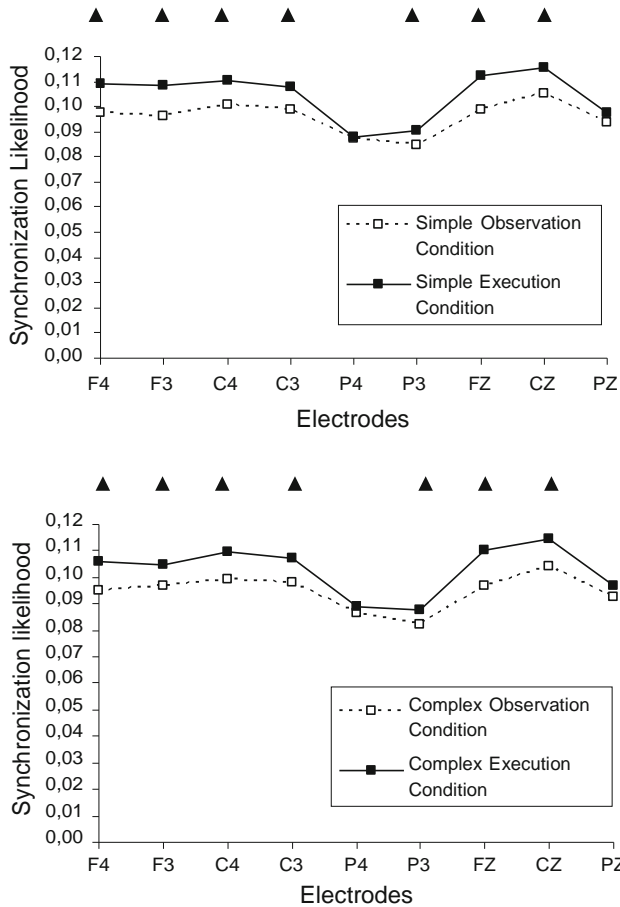


Fig. 3 Mean synchronization likelihood for each of the nine electrodes in the conditions of observation and execution in the 8–10 Hz frequency band during the movement stage. *Filled triangle*, P is considered significant

and the third reviews the existence of a human MN system. Our interpretation of the results has been made cautiously, since a lack of significant difference in EEG activity between two experimental conditions does not automatically imply equality. Activity differences may exist but EEG as a technique may be unable to detect the differences which may be related to deeper motor structures (e.g., basal ganglia) whose activity is not present at the scalp.

Methodological considerations

Cortical synchronization during the resting state (i.e., during the control condition) for the nine electrode sites of interest was used as the control. Higher SL values were found during the execution and observation conditions in comparison to those obtained during the control condition for electrodes located in the fronto-centro-parietal cortex in the 8–10 and 10–13 Hz frequency bands. However, no significant differences were detected between the observation and execution conditions and the control condition for the

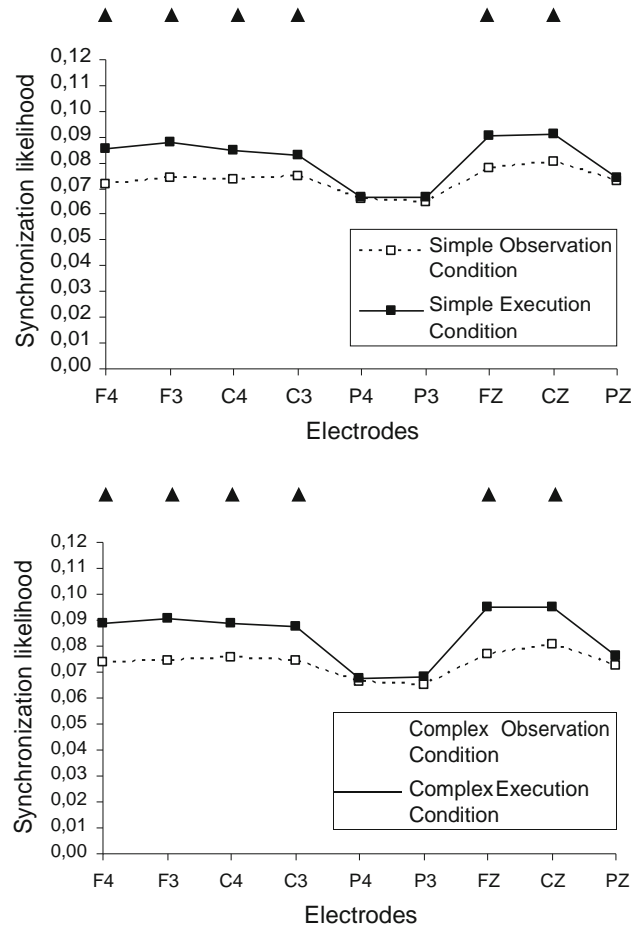


Fig. 4 Mean synchronization likelihood for each of the nine electrodes in the conditions of observation and execution in the 10–13 Hz frequency band during the movement stage. *Filled triangle*, P is considered significant

13–20 and 20–30 Hz frequency bands. An explanation for the results found in these higher bands is not clear.

One reason may be attributed to the oscillations in different frequency bands that serve different functions (Chen et al. 2003; GerloV et al. 1998). The 8–10 Hz band is known to be related to attentional processes, whereas the 10–13 Hz band is related to semantic long-term memory processes (Klimesch 1996, 1999). In contrast, the 13–20 and 20–30 Hz frequency bands are closely associated with motor learning, motor preparation (Alegre et al. 2004), attentional mechanisms (Chen et al. 2003) and more cognitive tasks such as face recognition (Ozgoren et al. 2005). Therefore, it could be suggested that the 8–10 and 10–13 Hz frequencies may reflect aspects of information processing which are distinguishable from those occurring during the control condition, whereas frequencies within the 13–30 Hz range do not. A second reason could be related to the choice of the control condition used for the baseline. It seems an ideal baseline condition does not exist. Wicker et al. (2003) have also stressed the problem of choosing an appropriate baseline for

cognitive tasks involving integrated brain areas and Morcom and Fletcher (2007) have stated that “Any control state, no matter how carefully it is selected, is just another task state with its own unique areas of activation” (pp. 1074). Indeed, baseline values will show variation both within and across participants; therefore, a resting state is far from being an inactive state (Binder et al. 1999; Buzsaki 2006). When an individual is not actively committed to a behavior, mental activities can occur spontaneously, such as day dreams (e.g., Stark and Squire 2001), free association (e.g., Mazoyer et al. 2001), autobiographic episodes (e.g., Mazoyer et al. 2001), and inner speech and imagery (e.g., Mazoyer et al. 2001). Some researchers have demonstrated that, during a resting state, interactions between brain areas can be more extensive than during the completion of diverse transitive actions (e.g., Mazoyer et al. 2001; Shulman et al. 1997; Wicker et al. 2003).

In the literature, four possible conditions have been considered. First, in EEG/MEG studies, baseline periods are measured a few seconds prior to the event of interest (Pfurtscheller and Lopes da Silva 1999). Second, when the experimental task is performed with the eyes closed, researchers have designed rest conditions with the eyes closed also (e.g., Stam et al. 2002a, b). Third, baseline conditions have consisted of observing a static picture of a hand (e.g., Jonas et al. 2007). Finally, baselines have comprised viewing a fixation cross or a monochrome background without a hand stimulus (e.g., Muthukumaraswamy and Johnson 2004). In the present study, the wrist option was not chosen because of the specificity of the experimental procedure. The period before the onset of the task was a preparation stage for the impending task. The second option was also not selected because the experimental tasks required the subjects to have their eyes open. The third was not appropriate because the exposure to a static hand stimulus may have reduced the responsiveness of the mirror neuron system (Jonas et al. 2007). Recently, it has been shown that viewing static body postures suggesting a transition to action may activate the MN system (Urgesi et al. 2006). The problem, however, is knowing whether the static body stimulus is perceived as containing implied motion or not. Therefore, the fourth option seemed to be the most appropriate since cortical activations were clearer when action observation was compared to object observation rather than a static hand (Grafton et al. 1996).

Complexity

Contrary to our hypothesis, complex movements, compared to simple movements, did not generate greater inter-regional synchronization under the observation and execution conditions in the four frequency bands with the exception of C3 and F3 in the 10–13 Hz frequency band

under the execution condition. Apart from these two cases, during the movement stage, and for all other frequency bands, no significant differences in SL were found between simple and complex movements irrespective of condition. This finding may be explained by a number of reasons. First, the lack of synchronization difference between the simple and complex execution conditions in the present study may be due to a saturation or ceiling effect. This effect has been observed by Sadato et al. (1996b) with positron emission tomography (PET). They showed that regional cerebral blood flow (rCBF) increased in the primary sensorimotor cortex (SM1) with finger movement frequencies up to 2 Hz and tended to a plateau at higher frequencies. Though Sadato et al. (1996b) have examined activation and not synchronization, it may be possible that a similar ceiling effect occurred in EEG at 2 Hz as has been suggested by Manganotti et al. (1998). Synchronization values may have reached a steady-state and synchronization measurements between simple and complex movement could not, therefore, be differentiated. Second, it is possible that SL is not an appropriate marker to detect differences in the synchronization of distant neuronal populations between simple and complex motor acts. However, Micheloyannis et al. (2003, 2005) have shown that synchronization likelihood was able to discriminate cognitive tasks at different complexities, so this over seems unlikely. Third, it may be possible that what was defined as the simple sequential movement may actually be a complex sequential movement since the moveable hand was outside of the subject’s visual array. Since the task required the touching of the tip of the thumb with the tips of the four fingers, with no visual guidance, it may have been perceived as more complex than wrist thought. Through anecdotal debriefs, some subjects reported being concerned about missing the contact between the thumb and the other four fingers. Therefore, it may be that participants observed and executed two complex sequential movements. Finally, it may be possible that, because of the pre-experimental training session, the two movements could not be differentiated by level of difficulty since they both became overlearned and were performed quasi-automatically. The subjects may have reached an automatic stage of learning for each movement; whether the subjects had reached an automatic stage is debatable. Automaticity is used “to indicate that a person performs a skill or engages in an information-processing activity without demands on attention capacity” (Magill 2004, pp. 151). Assessment of automaticity has been shown through dual task paradigms where minimum interference should be observed on the primary task to conclude that it had reached automaticity (Passingham 1996). For example, Wu et al. (2004) developed a dual task paradigm with a finger movement and a letter-counting task for the interference task.

The results of the present study also showed for all frequency bands that similar synchronization patterns under the simple and complex movement conditions were found when observation and execution conditions were compared. This strengthens the proposition that the MN system may not be sensitive to motor acts which have different degrees of complexity or, as mentioned above, that the simple experimental task may have been perceived as more complex than was thought.

The present study does not allow us to support claims for one reason over another one. Additional investigations will be necessary to resolve this issue.

Existence of a mirror neuron system

Consistent with our prediction, the data tend to provide evidence for an EEG equivalence between the observation and execution conditions; this was true for the 13–20 and 20–30 Hz frequency bands. For the two movements, no significant differences in SL were found between the observation and execution conditions during the movement stage for the nine electrode sites of interest. These findings suggest the validity of the mirror neuron system activity through the 13–20 and 20–30 Hz frequency bands, as usually defined by Rizzolatti and Craighero (2004), since similar or, more correctly, non-different, cortical oscillations for an action, either observed or executed, were generated. Further, interpretation of these results should be made cautiously as the lack of any statistical significance between the control condition and the observation or execution conditions is of concern. However, in the present study, there were differences, albeit not statistically significant, between SL values in the control condition and those in the other conditions. In these cases, control SL values were lower than observation and execution SL values.

However, in the 8–10 and 10–13 Hz frequency bands, SL data revealed that congruence between the observation and execution conditions was not complete. Significant differences across the observation and execution conditions were observed for the finger movements and for all the electrodes of interest except for some located in the parietal cortex. The pattern of synchronization under the observation condition was similar but weaker in intensity to that recorded when subjects perform the observed action. The fact that, the areas of interest, known to be involved in motor control, display patterns of synchronization during observation of an action akin to those revealed during the execution of the same action can be reported as an indirect evidence for a human MN system. This viewpoint is supported by the MN research findings of a number of groups (Fadiga et al. 1995; Iacoboni et al. 1999, 2001; Koski et al. 2002, 2003; Muthukumaraswamy and Johnson 2004;

Muthukumaraswamy et al. 2004; Patuzzo et al. 2003). These authors have shown, with a variety of different methods, that observation of intransitive, non-object-related actions, can activate the human MN system. More specifically, Muthukumaraswamy et al. (2004) reported that the human MN system was active during the observation of transitive and intransitive actions and that the magnitude of the mu rhythm was related to the characteristics of the observed action. Desynchronization of the mu rhythm was greater during the observation of a manipulandum grip than during the observation of an empty grip (Muthukumaraswamy et al. 2004). The proposal from these findings was that the cortical representations of motoric actions, directed towards objects, are either different or more salient than those of non-object directed actions.

We also feel it is important to offer an explanation for the lack of significance between the observation and execution condition in the 8–10 and 10–13 Hz frequency bands for some of the parietal electrode sites. Apart from some results to the contrary (e.g., Iacoboni et al. 1999), execution, in contrast to observation mainly involves fronto-central areas as recognized by Rao et al. (1993), Shibasaki et al. (1993), and Sadato et al. (1996a). This may explain why synchronization likelihood (SL) values for parietal electrode sites are lower than the SL values of electrodes located in the central and frontal areas. The parietal SL values collected during the execution condition are very close to parietal SL values recorded during the observation condition since it is known that parietal areas play an important role in the observation process (Iacoboni et al. 1999, Rizzolatti et al. 2002).

Finally, taken all together, the results in frequency bands lying with a range of 8–30 Hz seem to provide additional, albeit indirect, evidence for MN activity associated with intransitive tasks.

Conclusions

The use of the non-linear SL technique (Stam and van Dijk 2002) allowed for detailed consideration of some of the mechanisms of functional integration in observation and execution conditions. The results indicated that cortical connectivity did not seem to be sensitive to motor acts of different levels of complexity under the observation and execution conditions. They also provided additional, indirect evidence, for human MN activity for intransitive tasks.

Acknowledgments This study was supported by a grant from the French Ministry of Health, Youth, and Sports. The authors are grateful to the participants who participated in the study. They would also like to thank M. Paisley for the video footage editing and the two anonymous reviewers for their helpful suggestions and comments. This study is dedicated to Gui Calmels.

References

- Alegre M, Garcia de Gurtubay I, Labarga A, Iriarte J, Malanda A, Artieda J (2004) Alpha and beta oscillatory activity during a sequence of two movements. *Clin Neurophysiol* 115:124–130
- Binder JR, Frost JA, Hammeke TA, Bellgowan PSF, Rao SM, Cox RW (1999) Conceptual processing during the conscious resting state: a functional MRI study. *J Cogn Neurosci* 11:80–93
- Buccino G, Binkofski F, Fink GR, Fadiga L, Fogassi L, Gallese V, Seitz RJ, Zilles K, Rizzolatti G, Freund HJ (2001) Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *Eur J Neurosci* 13:400–404
- Buzsaki G (2006) *Rhythms of the brain*. Oxford University Press, New York
- Catalan MJ, Honda M, Weeks RA, Cohen LG, Hallett M (1998) The functional neuroanatomy of simple and sequential Wnger movements: a PET study. *Brain* 121:253–264
- Chen R, GerloV C, Hallett M, Cohen LG (1997) Involvement of the ipsilateral motor cortex in Wnger movements of diVerent complexities. *Ann Neurol* 41:247–254
- Chen Y, Ding M, Kelso JAS (2003) Task-related power and coherence changes in neuromagnetic activity during visuomotor coordination. *Exp Brain Res* 148:105–116
- Cochin S, Bathelémy C, Lejeune B, Roux S, Martineau J (1998) Perception of motion and qEEG activity in human adults. *Electroencephalogr Clin Neurophysiol* 107:287–295
- Cochin S, Bathelémy C, Roux S, Martineau J (1999) Observation and execution of movement: similarities demonstrated by quantitative electroencephalography. *Eur J Neurosci* 11:1839–1842
- Dassonville P, Lewis SM, Zhu XH, Ugurbil K, Kim SG, Ashe J (1998) Effects of movement predictability on cortical motor activation. *Neurosci Res* 32:65–74
- Dhamala M, Pagnoni G, Wiesenfeld K, Zink CF, Martin M, Berns GS (2003) Neural correlates of the complexity of rhythmic Wnger tapping. *Neuroimage* 20:918–926
- Di Pellegrino G, Fadiga L, Fogassi L, Gallese V, Rizzolatti G (1992) Understanding motor events: a neurophysiological study. *Exp Brain Res* 91:176–180
- Fadiga L, Fogassi L, Pavesi G, Rizzolatti G (1995) Motor facilitation during action observation: a magnetic stimulation study. *J Neurophysiol* 73:2608–2611
- Friston KJ (2000) The labile brain. I. Neuronal transients and non linear coupling. *Philos Trans R Soc Lond B Biol Sci* 355:215–236
- Gallese V, Fadiga L, Fogassi L, Rizzolatti G (1996) Action recognition in the premotor cortex. *Brain* 119:593–609
- Gastaut HJ, Bert J (1954) EEG changes during cinematographic presentation. *Electroencephalogr Clin Neurophysiol* 6:433–444
- GerloV C, Richard J, Hadley J, Schulman AE, Honda M, Hallett M (1998) Functional coupling and regional activation of human cortical motor areas during simple, internally paced and externally paced Wnger movements. *Brain* 121:1513–1531
- Grafton ST, Arbib MA, Fadiga L, Rizzolatti G (1996) Localization of grasp representations in humans by positron emission tomography. 2. Observation compared with imagination. *Exp Brain Res* 112:103–111
- Grèzes J, Armony JL, Rowe J, Passingham RE (2003) Activations related to “Mirror” and “Canonical” neurones in the human brain: a fMRI study. *Neuroimage* 18:928–937
- Hummel F, Kirsammer R, GerloV C (2003) Ipsilateral cortical activation during Wnger sequences of increasing complexity: representation of movement difficulty or memory load? *Clin Neurophysiol* 114:605–613
- Iacoboni M, Woods RP, Brass M, Bekkering H, Mazziotta JC (1999) Cortical mechanisms of human imitation. *Science* 286:2526–2528
- Iacoboni M, Koski LM, Brass M, Bekkering H, Woods RP, Dubeau MC, Mazziotta JC, Rizzolatti G (2001) ReaVerent copies of imitated actions in the right superior temporal cortex. *Proc Natl Acad Sci USA* 98:13995–13999
- Jackson PL, MeltzoV AN, Decety J (2006) Neural circuits involved in imitation and perspective-taking. *Neuroimage* 31:429–439
- Jasper HH (1958) Report of the committee on methods of clinical examination in electroencephalography. *Electroencephalogr Clin Neurophysiol* 10:370–375
- Jonas M, Siebner HR, Biermann-Ruben K, Kessler K, Baumer T, Buchel C, Schnitzler A, Munchau A (2007) Do simple intransitive Wnger movements consistently activate frontoparietal mirror neuron areas in humans? *Neuroimage* 36:T44–T53
- Kitamura J, Shibasaki H, Takagi A, Nabeshima H, Yamaguchi A (1993) Enhanced negative slope of cortical potentials before sequential as compared with simultaneous extensions of two Wngers. *Electroencephalogr Clin Neurophysiol* 86:176–182
- Klimesch W (1996) Memory processes, brain oscillations and EEG synchronization. *Int J Psychophysiol* 24:61–100
- Klimesch W (1999) Event-related band power changes and memory performance. In: Pfurtscheller G, Lopes da Silva FH (eds) *Event-related desynchronization*. Handbook of electroencephalography and clinical neurophysiology. Revised series, vol 6. Elsevier, New York, pp 161–178
- Koski L, Wohlschlager A, Bekkering H, Woods RP, Dubeau MC, Mazziotta JC, Iacoboni M (2002) Modulation of motor and premotor activity during imitation of target-directed actions. *Cereb Cortex* 12:847–855
- Koski L, Iacoboni M, Dubeau MC, Woods RP, Mazziotta JC (2003) Modulation of cortical activity during diVerent imitative behaviors. *J Neurophysiol* 89:460–471
- Leistner S, Wubbeler G, Trahms L, Curio G, Mackert BM (2006) Tonic neuronal activation during simple and complex Wnger movements analyzed by DC-magnetoencephalography. *Neurosci Lett* 394:42–47
- Lepage JF, Théoret H (2006) EEG evidence for the presence of an action observation-execution matching system in children. *Eur J Neurosci* 23:2505–2510
- Magill RA (2004) *Motor learning and control*. Concepts and applications. McGraw-Hill, Boston
- Manganotti P, GerloV C, Toro C, Katsuda H, Sadato N, Zhuang P, Leocani L, Hallett M (1998) Task-related coherence and task-related spectral power changes during sequential Wnger movements. *Electroencephalogr Clin Neurophysiol* 109:50–62
- Mazoyer B, Zago L, Mellet E, Bricogne S, Etard O, Houdé O, Crivello F, Joliot M, Petit L, Tzourio-Mazoyer N (2001) Cortical networks for working memory and executive functions sustain the conscious resting state in man. *Brain Res Bull* 54:287–298
- Micheloyannis S, Vourkas M, Bizas M, Simos PG, Stam CJ (2003) Changes in linear and nonlinear EEG measures as a function of task complexity: evidence for local and distant signal synchronization. *Brain Topogr* 15:239–247
- Micheloyannis S, Sakkalis V, Vourkas M, Stam CJ, Simos PG (2005) Neural networks involved in mathematical thinking: evidence from linear and non-linear analysis of electroencephalographic activity. *Neurosci Lett* 373:212–217
- Molnar-Szakacs I, Kaplan J, GreenWeld PM, Iacoboni M (2006) Observing complex action sequences: the role of the fronto-parietal mirror neuron system. *Neuroimage* 33:923–935
- Montez T, Linkenkaer-Hansen K, van Dijk BW, Stam CJ (2006) Synchronization likelihood with explicit time-frequency priors. *Neuroimage* 33:1117–1125
- Morcom AM, Fletcher PC (2007) Does the brain have a baseline? Why we should be resisting a rest. *Neuroimage* 37:1073–1082

- Muthukumaraswamy SD, Johnson BW (2004) Changes in rolandic mu rhythm during observation of a precision grip. *Psychophysiology* 41:152–156
- Muthuswamy J, Thakor NV (1998) Spectral analysis methods for neurological signals. *J Neurosci Methods* 83:1–14
- Muthukumaraswamy SD, Johnson BW, McNair NA (2004) Mu rhythm modulation during observation of an object-directed grasp. *Cogn Brain Res* 19:195–201
- Oberman LM, McCleery JP, Ramachandran VS, Pineda JM (2007) EEG evidence for mirror neuron activity during the observation of human and robot actions: towards an analysis of the human qualities of interactive robots. *Neurocomputing* 70:2194–2203
- OldWeld RC (1971) The assessment and analysis of handedness: the Edinburgh Inventory. *Neuropsychologia* 9:77–113
- Ozgoren M, Basar-Eroglu C, Basar E (2005) Beta oscillations in face recognition. *Int J Psychophysiol* 55:51–59
- Palus M (1996) Nonlinear in normal human EEG: cycles, temporal asymmetry, nonstationarity and randomness, not chaos. *Biol Cybern* 75:389–396
- Passingham RE (1996) Attention to action. *Philos Trans R Soc Lond B Biol Sci* 351:1473–1479
- Patuzzo S, Fiaschi A, Manganotti P (2003) Modulation of motor cortex excitability in the left hemisphere during action observation: a single- and paired-pulse transcranial magnetic stimulation study of self- and non-self-action observation. *Neuropsychologia* 41:1272–1278
- Pfurtscheller G, Lopes da Silva FH (1999) Event-related. EEG/MEG synchronization and desynchronization: basic principles. *Clin Neurophysiol* 110:1842–1857
- Pineda JA (2005) The functional significance of mu rhythms: translating “seeing” and “hearing” into “doing”. *Brain Res Rev* 50:57–68
- Pulvermüller F, Mohr B (1996) The concept of transcortical cell assemblies: a key to the understanding of cortical lateralization and interhemispheric interaction. *Neurosci Biobehav Rev* 20:557–566
- Pulvermuller F, Lutzenberger W, Preissl H, Birbaumer N (1995) Motor programming in both hemispheres: an EEG study of the human brain. *Neurosci Lett* 190:5–8
- Rao SM, Binder JR, Bandettini PA, Hammeke TA, Yetkin FZ, Jesmanowicz A, Lisk LM, Morris GL, Mueller WM, Estkowski LD, Wong EC, Haughton VM, Hyde JS (1993) Functional magnetic resonance imaging of complex human movements. *Neurology* 43:2311–2318
- Rizzolatti G, Craighero L (2004) The mirror-neuron system. *Ann Rev Neurosci* 27:169–192
- Rizzolatti G, Carmada R, Fogassi L, Gentilucci M, Luppino G, Matelli M (1988) Functional organization of inferior area 6 in the macaque monkey: II. Area F5 and the control of distal movements. *Exp Brain Res* 71:491–507
- Rizzolatti G, Luppino G, Matelli M (1998) The organization of the cortical motor system: new concepts. *Electroencephalogr Clin Neurophysiol* 106:283–296
- Rizzolatti G, Craighero L, Fadiga L (2002) The mirror system in human. In: Stamenov MI, Gallese V (eds) *Mirror neurons and the evolution of brain and language*. John Benjamins Publishing Company, Philadelphia, pp 37–63
- Sadato N, Campbell G, Ibanez V, Deiber MP, Hallett M (1996a) Complexity affects regional cerebral blood flow change during sequential Wnger movements. *J Neurosci* 16:2691–2700
- Sadato N, Ibanez V, Deiber MP, Campbell G, Leonardo M, Hallett M (1996b) Frequency-dependent changes of regional cerebral blood flow during Wnger movements. *J Cereb Blood Flow Metab* 16:23–33
- Semlitsch H, Anderer P, Schuster P, Presslich O (1986) A solution for reliable and valid reduction of ocular artifacts, applied to the P300 ERP. *Psychophysiology* 23:695–703
- Shibasaki H, Sadato N, Lyshkow H, Yonekura Y, Honda M, Nagamine T, Suwazono S, Magata Y, Ikeda A, Miyazaki M (1993) Both primary motor cortex and supplementary motor area play an important role in complex Wnger movement. *Brain* 116:1387–1398
- Shulman GL, Fiez JA, Corbetta M, Buckner RL, Miezin F, Raichle ME, Petersen SE (1997) Common blood flow changes across visual tasks: II. Decreases in cerebral cortex. *J Cogn Neurosci* 9:648–663
- Solodkin A, Hlustik P, Noll DC, Small SL (2001) Lateralization of motor circuits and handedness during Wnger movements. *Eur J Neurol* 8:425–434
- Stam CJ, van Dijk BW (2002) Synchronization likelihood: an unbiased measure of generalized synchronization in multivariate data sets. *Physica D* 163:236–251
- Stam CJ, Pijn JP, SuVczynski P, Lopes da Silva FH (1999) Dynamics of the human alpha rhythm: evidence for non-linearity? *Clin Neurophysiol* 110:1801–1813
- Stam CJ, van Walsum AM, Micheloyannis S (2002a) Variability of EEG synchronization during a working memory task in healthy subjects. *Int J Psychophysiol* 46:53–66
- Stam CJ, van Walsum AM, Pijnenburg YAL, Berendse HW, de Munck JC, Ph Scheltens, van Dijk BW (2002b) Generalized synchronization of MEG recordings in Alzheimer’s disease: evidence for involvement of the gamma band. *J Clin Neurophysiol* 19:562–574
- Stark CE, Squire LR (2001) When zero is not zero: the problem of ambiguous baseline conditions in fMRI. *Proc Natl Acad Sci USA* 98:12760–12765
- Thakor NV, Tong S (2004) Advances in quantitative electroencephalogram analysis methods. *Annu Rev Biomed Eng* 6:453–495
- Ulloa ER, Pineda JA (2007) Recognition of point-light biological motion: mu rhythms and mirror neuron activity. *Behav Brain Res* 183:188–194
- Urgesi C, Candidi M, Fabbro F, Romani M, Aglioti S (2006) Motor facilitation during action observation: topographic mapping of the target muscle and influence of the onlooker’s posture. *Eur J Neurosci* 23:2522–2530
- Verstynen T, Diedrichsen J, Albert N, Aparicio P, Ivry RB (2005) Ipsilateral motor cortex activity during unimanual hand movements relates to task complexity. *J Neurophysiol* 93:1209–1222
- Wicker B, Ruby P, Royet JP, Fonlupt P (2003) A relation between rest and the self in the brain? *Brain Res Rev* 43:224–230
- Wu T, Kansaku K, Hallett M (2004) How self-initiated memorized movements become automatic: a functional MRI study. *J Neurophysiol* 91:1690–1698