Changes in local and distant EEG activities before, during and after the observation and execution of sequential finger movements

Claire Calmels, Gilbert Jarry, Cornelis J Stam

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Oscillations électrocorticales locales et interrégionales générées avant, pendant et après l'observation et l'exécution de mouvements digitaux séquentiels

C. Calmels[a,*], G. Jarry[b], C.J. Stam[c]

[a] Mission recherche, Institut national du sport et de l'éducation physique, 11, avenue du Tremblay, 75012 Paris, France
[b] EA 4391, université Paris-XII, hôpital Henri-Mondor, Créteil, France
[c] Department of Clinical Neurophysiology, VU University Medical Centre, Amsterdam, The Netherlands

Summary

Aim of the study. — To consider cortical oscillations at local and distant/large scale levels during the time course of motor events under both an observation and an execution condition.

Methods. — Local and distant changes in EEG cortical oscillations were respectively assessed by the Event-Related Desynchronization/Synchronization technique and the Synchronization Likelihood technique. Data collected prior to, during, and after observation and execution of complex sequential finger movements were used to investigate these changes. EEGs were recorded from 19 active sites across the cortex of 10 subjects. Sensorimotor activity was examined in alpha frequency bands.

Results. — Local power changes and global interregional synchronizations were two distinct phenomena, which occurred simultaneously and displayed different spatiotemporal patterns.

Discussion and conclusions. — These findings demonstrate the complementary character of both analysis techniques. Results are discussed in light of the recent findings from the cognitive and behavioural neuroscience literature.

* Corresponding author.
 E-mail address: claire.calmels@insep.fr (C. Calmels).

Résumé

But de l'étude. — Examiner, au cours du temps, les oscillations électrocorticales locales et interrégionales générées lors de l'observation et lors de l'exécution d'actions motrices.

Méthodes. — La technique linéaire de synchronisation/désynchronisation liée à un événement (SLE/DLE) et la technique du seuil de synchronisation (SS) ont été utilisées pour mettre en évidence respectivement les oscillations locales et interrégionales. Les données, collectées avant, pendant et après l'observation et l'exécution de mouvements complexes séquentiels digitaux ont permis d'examiner les changements oscillatoires corticaux. L'activité électrique cérébrale a été enregistrée à partir de 19 électrodes positionnées sur le scalp de dix sujets. L'activité sensorimotrice a été considérée dans les bandes de fréquence alpha.

Résultats. — Les variations locales de puissance des activités rythmiques (SLE/DLS) et les synchronisations interrégionales (SS) sont deux phénomènes distincts qui se déroulent simultanément mais qui produisent des patterns spatiotemporels différents.

Discussion et conclusions. — Les résultats de cette étude ont permis de mettre en évidence le caractère complémentaire de ces deux techniques d'analyse du signal EEG. Les résultats sont discutés en relation avec les travaux récents réalisés dans le domaine des neurosciences cognitives et comportementales.

Introduction

Electroencephalographic (EEG) markers of cortical activity offer many possibilities for off-line analysis. The methods that are used could be categorized by different approaches: linear vs. non-linear analyses; parametric vs. non-parametric methods; analyses at local level vs. analyses at a distal or interregional level.

Power-spectrum and event-related change of EEG activity analyses are examples of techniques that provide an index of local cortical activity [33,53]. Traditionally, power-spectrum analysis has been the most common method to analyze the raw EEG signal [5,16]. Event-related change in EEG power in a given frequency band is a procedure that has been extensively studied by Pfurtscheller et al. [43,44,45]. In the context of movement planning, Pfurtscheller et al. [43,45] defined change in power in a frequency band as a change relative to a baseline period recorded a few seconds before the occurrence of the event. A decrease in relative power is termed event-related desynchronization (ERD), while an increase is defined as event-related synchronization (ERS). ERD is a marker of an active cortical processing [44,45], whereas ERS reflects an idling state [46] or even a state of cortical inhibition [27,28]. Research that has considered ERD/ERS patterns of voluntary movements has tended to examine brisk finger movements [13,47] mainly at C3 and C4 electrode sites [47] and before, during, and after the movement stage.

Event-related coherence [29,49], imaginary coherence [38], partial direct coherence [4], direct transfer function [24], and synchronization likelihood (SL) [54] are various methods that allow investigation of the interactions between brain areas. More specifically, the SL measure reflects a non-linear index of synchronization in neuronal signalling between distant neuronal populations. This method involves the estimation of the dynamical interdependencies between a time series (e.g., an EEG channel) and one or more other time series. The SL index is sensitive to linear as well as non-linear coupling, and suitable for non-stationary data. SL is a measure which describes how strongly a specific channel, at a particular time, is synchronized to all the other channels. The SL takes on values between P_{ref} (no coupling) and 1 (complete coupling). P_{ref} is a parameter in the computation of SL, and is usually chosen as $P_{ref} = 0.01$ (Appendix 1). The SL method has been used to examine EEG patterns in different contexts: detecting EEG patterns to predict the occurrence of epileptic seizure [54] or examining EEG changes associated to cognitive activities [32,33] or to the execution and observation of motor tasks [6,7].

Associating the ERD/ERS technique with the SL technique would be of prime interest since it will provide information on the coexistence of local and distant cortical activities over time. The comparison of the SL technique, which is a novel measure, with the well established measure of ERD/ERS would also contribute to 'validate' the SL measure, as recommended by the scientific community [12]. The relationship between local and distant EEG activities has been investigated mainly during the execution stage by Andres et al. [1], Gerloff et al. [18], Leocani et al. [29], Manganotti et al. [31], and Rappelsberger et al. [49]. These authors have shown that parallel EEG activities occur at different spatial levels in the neuronal network (i.e., both a local level and a distant level) and describe different aspects of cortical activity. For instance, work by Rappelsberger et al. [49], who are the rare researchers to have examined the movement preparation stage, demonstrated before the beginning of a left finger movement a coexistence of a 10 Hz ERD in C4 with an increase in event-related coherence between C4-F4 electrodes and a decrease between C4-T4 electrodes. During the movement, they found similar oscillations, but with an increase in event-related coherence between C3-C4 electrodes.

Examining different conditions, such as an execution and an observation conditions would refine this investigation. Over the last decade, a large number of studies in the field

of neurosciences have been conducted on observation processes [3,8,9,22,58]. The increased interest in the process of observation was probably due to the discovery of mirror neurons [15,50]. First discovered in the ventral premotor cortex of the macaque monkey, these neurons display special characteristics. They fire when the monkey executes a goal-directed hand movement and also when it observes the same action executed by another monkey or by a human [15,50]. Evidence for the existence of similar neurons in humans has been provided by researchers who had used brain imaging techniques or EEG techniques [11,35,36].

Using mainly power-spectrum analyses, research using EEG has shown that the mu rhythm, an 8—13 Hz rhythm generated in the sensorimotor cortex, was suppressed or blocked during observation of actions [10,11,17,19,30,35,36]. This mu modulation detected during the observation of movement led some researchers [39,48,57] to propose that this suppression could be used as a marker of the mirror neuron system activity.

Therefore, the aim of this study was to consider cortical oscillations at local- and distant/large-scale levels during the time course of motor events under specific conditions (i.e., an observation condition and an execution condition). To our knowledge, investigation of these oscillations after an event and under an observation condition has never been undertaken previously and will be of prime interest. The ERD/ERS and SL techniques respectively have been used to identify local cortical activity and distant cortical activity. Data were collected prior to, during, and after observation and execution of sequential finger movements. C3 and C4 electrode sites were selected since:

· they overlie the sensorimotor area, an area that has been extensively examined [12];
· they are located on the hand area [21].

The 8—13 Hz frequency band was chosen since it was the frequency range — in which a modulation has been detected during the observation of biological movements [39,48,57]. It would therefore be interesting to examine how this modulation is reflected at a larger scale level.

Materials and methods

Subjects

Ten strongly right-handed (seven women and three men; mean age = 23.8, SD = 4.76) subjects participated in this study. The subjects were assessed as right-handed by the Edinburgh Handedness Inventory [40] and had normal vision. The study was approved by the local ethics committee (Comité de Protection des Personnes d'Île-de-France 9 [CPP]).

Task

Subjects were asked to perform two sequential finger movements of differing complexity (i.e., a complex movement and a simple movement) with their right hand. The movements required the subjects to touch the tip of their right
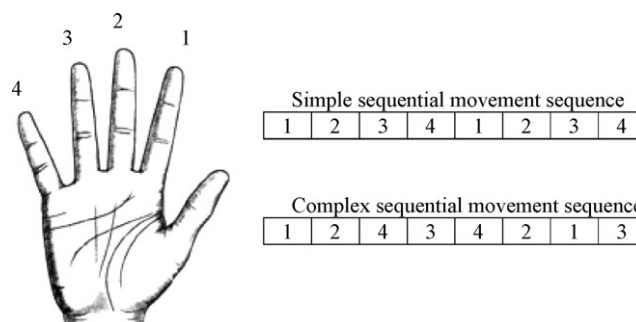

Figure 1 Experimental task. Subjects performed simple and complex movements which involved touching the tip of the right thumb with the tip of the other right hand fingers as specified in the sequences.

thumb with the tip of the other right hand fingers at a rate of 2 Hz controlled by a metronome (Fig. 1).

Experimental procedure

The procedure of the present study was similar to that previously described in Calmels et al. [6]. The EEGs were recorded whilst the subjects completed five conditions:

· a simple movement observation condition;
· a simple movement execution condition;
· a complex movement observation condition;
· a complex movement execution condition;
· a control condition.

Before EEG data collection, there was a short training session which ended after subjects were able to complete five movement sequences at 2 Hz without making any sequential errors.

Subjects performed 40 observation trials for the complex and simple task. Each trial comprised four stages, which were shown to the subjects on a video display. The subjects received instructions requesting them to observe the movement with the aim of replicating it at a later stage. Subject watched an amber monitor screen for the first four-second stage. The screen informed the subject of the impending requirement to observe the video. During the second, five-second stage, the subjects observed a video of a human model performing the simple or complex finger movement sequence. In the third stage, lasting 3 s, subjects were presented with a white background on the screen. In the fourth stage, also lasting 3 s, the screen changed to red and invited the subjects to relax.

Subjects performed 40 physical trials of the simple and complex movements. These followed a similar procedure to the observation trials. The second stage was different in that a black background was presented and the subjects were invited to perform the simple or complex finger movement at 2 Hz.

Finally, each subject performed 40 trials observing an inert pillow. These trials were conducted in a similar way to those used in the movement observation conditions except that instead of observing a movement, the subject observed a pillow for the five-second epoch.

In each condition, a metronome, set at 2 Hz, was used. Five, ten-minute blocks of 40 trials were performed. Each block was separated by a five-minute rest period. The movement observation was performed first and was followed by the movement execution condition irrespective of the movement complexity. The order of the control, observation/execution of the simple movement, and observation/execution of the complex movement was counterbalanced across subjects.

Data acquisition and recording

EEG data were 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 [23]. Mastoids were used for the reference electrodes and the ground electrode was located on the forehead. Electrooculograms (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 experiment. Amplifier 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.

The EEG recordings in the present study have been subjected to a different form of analysis and published in an earlier paper [6]. In the previous study, the authors examined cortical connectivity using the SL during the observation and execution of simple and complex movements in right-handed individuals through a full electrode montage in alpha and beta frequency bands. In this study, cortical changes before, during, and after the observation and execution of complex finger movements were analyzed using the SL technique and the ERD/ERS technique [43,44]. Cortical changes were examined in alpha frequency bands and the electrodes of interest were C3 and C4. With regards to the computation of ERD/ERS, it is recommended that EEG power, within identified frequency bands, recorded during the period of interest is displayed (as a percentage) to the power of those recorded during the baseline period, which was taken a few seconds prior to the event [44,45]. In the present study, the baseline period therefore corresponded to 1101.56—1976.56 ms (Appendix 2). Although data were also recorded from a control condition, these were not subjected to further analysis since they were not directly linked to the goal of the present study. Only data related to the observation and execution of the complex finger movement were considered. One female subject from the 2008s research has been discarded since her EEG data, in the pre-movement stage, were substantially contaminated by artifacts and could not be corrected by specialized software.

Data processing

EEG data were analyzed using two different techniques: the SL technique [54], and the ERD/ERS computation technique [43,44]; and in two frequency bands (i.e., 8—10 Hz and 10—13 Hz).
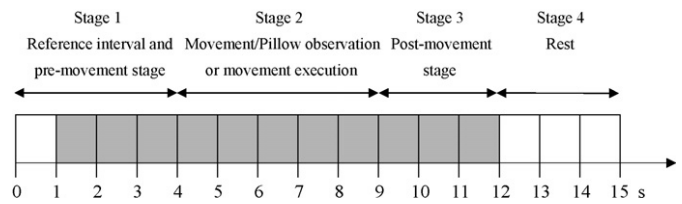

Figure 2 Schema for one trial to be analyzed off-line irrespective of condition. Shaded sections were used for EEG analysis. Stage 2 lasted 5 s since two periods of 500 ms (i.e, 500 ms before the onset of the movement and 500 ms after its offset) were added to the 4-s duration of the movement. During this period, subjects could see the hand and fingers at rest.
The time interval between the beginning of the viewing of the movement and the onset of the next was 15 s.

Segmentation of EEG trials and artifact corrections
First, only the first three stages were used for the EEG analysis. Off-line analysis of the first stage revealed that muscular artifacts had contaminated the data in the first second of some trials. Consequently, this stage was reduced to 3 s in length and the first second was discarded from further analysis (Fig. 2). Second, ocular artifacts were corrected via Semlitsch et al.'s [52] method and slow drifts were removed by linear trend corrections.

ERD/ERS computation technique
First, the Laplacian operator method [20] was used to transform the EEG data to reference-free data. Second, to quantify ERD/ERS in the time domain, EEG signals of all trials were bandpass filtered. The band pass filter was zero phase. The filtered values were squared to obtain power values which were averaged across all trials. A change in power within a particular frequency band was determined as a percentage measurement: ERD% = (A−R)/R × 100 (R is defined as a reference period and A as a test period) [43—45]. All these computations were performed using Neuroscan 4.3. Details related to these computations can be found in Appendix 2.

For each subject, electrode site, trial, and frequency band, the 16 power values of the pre-movement stage were averaged producing values for this stage. The same process was applied for the 40 power values of the movement stage and the 20-power values of the post-movement stage. This averaging process is not commonly presented in the ERD/ERS literature. Researchers generally prefer to examine 4- or 8-power values per second. However, the current averaging process was undertaken in this way, since it was the only means to allow a comparison with the SL technique which cannot provide (SL) values for short periods of time around 100 ms.

Synchronization likelihood computation technique
SL was computed for each trial of the two conditions, for each subject, frequency band, electrode site, and movement stage. The durations of all movement stages matched those defined for the ERD/ERS computation. All the SL values of a particular condition were averaged for each subject, frequency band, electrode site, and movement stage. Parameters for the computation of the SL were: 1 sample for the lag; 10 for the embedding dimension; 10 for the Theiler

correction; 0.010 for P_{ref}. These parameter choices were necessary because of the very short durations of the stages to which the SL was implemented. Further information concerning this technique can be obtained in the studies by Stam and Van Dijk [54] (2002) and Montez et al. [34].

Statistical analysis

All statistical analyses were performed using Statistica software 7.1. C3 and C4 were selected for analyses. To compare the ERD/ERS technique with the SL technique, changes in power and in cortical connectivity were analyzed using similar statistical analyses. For each condition (observation and execution), each electrode (C3 and C4), each frequency band (8—10 Hz and 10—13 Hz), and each technique (SL and ERD/ERS), 16 3 (stages) repeated measures ANOVAs were completed. There was one within-participant factor: stages (three levels: pre-movement stage, movement stage, and the post-movement stage).

Post-hoc comparisons were calculated using Fisher's LSD test when ANOVA results were significant. Before the ANOVA computations, the normality of the data was checked using the Kolmogorov Smirnov test. To verify the sphericity assumption in repeated measures designs, Mauchley's sphericity test was used and to correct possible violations against this assumption, Greenhouse-Geisser corrected p-values were used where necessary.

Results

Sixteen 3 (stages) repeated measures ANOVAs were computed. The EEG data were normally distributed and some sphericity violations were observed. Greenhouse-Geisser corrected p-values were implemented.

SL technique

No main effect for the stages factor was found at any frequency bands and electrode sites during the execution condition (Table 1). However, in the observation condition, ANOVAs yielded a significant main effect for the stages factor for all the frequency bands and electrode sites (Table 1). Fisher's LSD post-hoc tests showed that for the 8—10 Hz and 10—13 Hz frequency bands and C3 and C4 electrode sites, significant differences were found between the pre-movement and movement stages and between the movement and post-movement stages. SL values for the pre-movement stage were significantly higher than those for the movement stage and SL values for the movement stage were significantly lower than those for the post-movement stage (Fig. 3).

ERD/ERS technique

For the 8—10 Hz and 10—13 Hz frequency bands, ANOVAs revealed a significant main effect for the stages factor for all the electrodes during the observation and execution conditions (Table 1). For the 8—10 Hz frequency band, Fisher's LSD post-hoc tests showed that for all the frequency bands, electrode sites, and conditions, significant differ-

Table 1 Summary of the three (stages) repeated measures ANOVAs for each frequency band and for the SL and ERD/ERS analysis techniques under the observation and execution conditions.

		C3								C4							
		8—10 HZ				10—13 Hz				8—10 HZ				10—13 HZ			
		Observation		Execution		Observation		Execution		Observation		Execution		Observation		Execution	
		F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p
SL technique	Stage	17.972 ***		1.684	0.22	14.567 ***		1.310	0.29	11.918 ***		2.571	0.14	12.136 ***		0.351	0.71
ERD/ERS technique	Stage	26.108 ***		19.294	**	14.987 ***		14.896	**	9.500	**	22.547 ***		3.795	*	4.517	*

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$; Greenhouse-Geisser corrected where necessary.
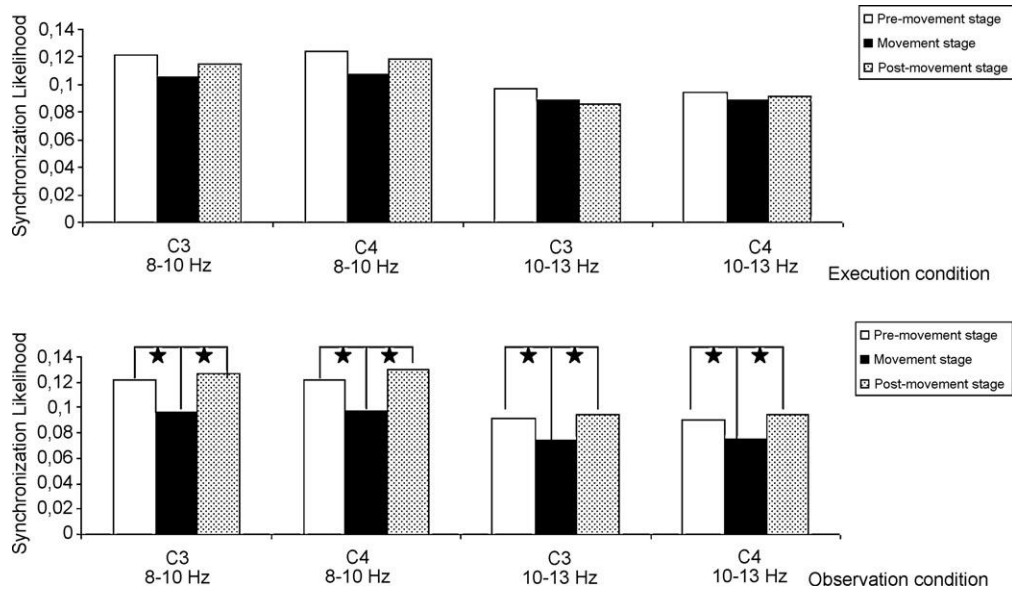
Figure 3 Pre-movement, movement, and post-movement SL values in alpha bands under the execution and observation conditions.
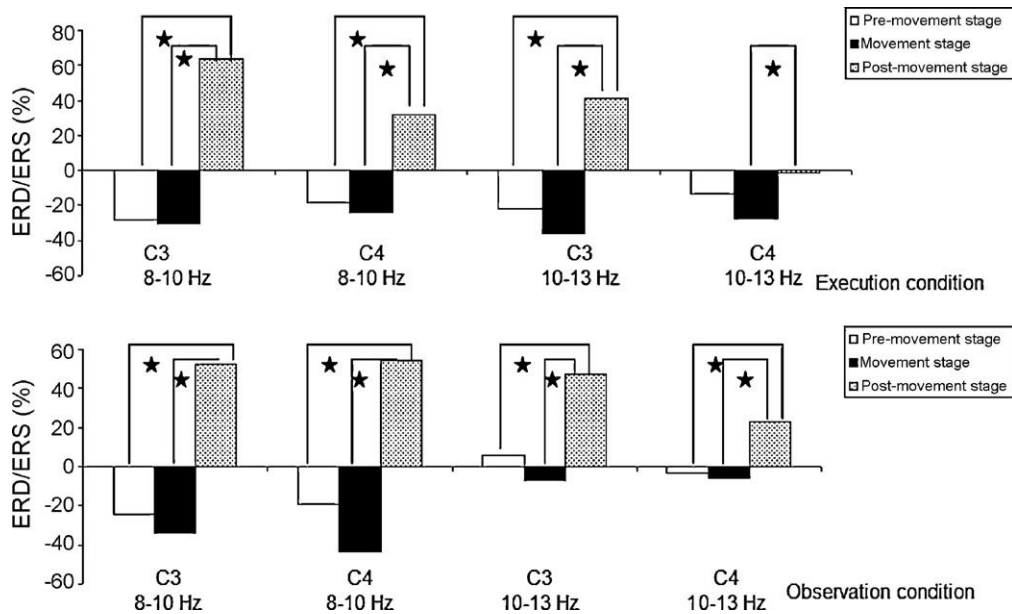

Figure 4 Pre-movement, movement, and post-movement ERD/ERS values in alpha bands under the execution and observation conditions.

ences were found between the pre- and post-movement stages and between the movement and post-movement stages. Irrespective of condition, pre-movement ERD values were less than the post-movement ERS values and movement ERD values were also less than the post-movement ERS values (Fig. 4). For the 10—13 Hz frequency band, Fisher's LSD post-hoc tests displayed similar results at the C3 electrode site under the observation and execution conditions and at the C4 electrode site under the observation condition (Fig. 4). Under the execution condition, only one significant difference was obtained with this occurring at the C4 electrode site: movement ERD value was less than the post-movement ERS value (Fig. 4).

To summarize, under the execution condition at the C3 and C4 electrode sites, we observed different aspects of cortical activity (Table 2). The same result was obtained for the observation condition (Table 3).

Discussion

The aim of the present study was to investigate cortical oscillations at local and large scale levels before, during, and after the observation and execution of sequential finger movements in frequency bands 8—13 Hz. The discussion has been organized into two sections. The first discusses the results under the execution condition, whereas the second considers the observation condition.

Table 2 Coexistence of local and distant EEG activities assessed respectively by the ERD/ERS and SL techniques during the pre-movement, movement, and post-movement stages under the execution condition.

	C3		C4	
Stages	8—10 Hz	10—13 Hz	8—10 Hz	10—13 Hz
Pre-movement	ERD	ERD	ERD	ERD
	High SL value	High SL value	High SL value	High SL value
Movement	ERD	ERD	ERD	ERD
	High SL value	High SL value	High SL value	High SL value
Post-movement	ERS	ERS	ERS	Weak ERD
	High SL value	High SL value	High SL value	High SL value

From a functional point of view, a local power change (ERD/ERS) was detected in the alpha bands, between the movement and post-movement stages. However, no such change was observed in the interregional synchronization (SL) between the same movement stages.

Execution Condition

During the pre-movement and movement stages of the execution condition, alpha band ERD was detected at electrode sites C3 and C4. These ERDs were followed by an alpha band ERS during the post-movement stage except for the C4 electrode site in the 10—13 Hz frequency band. These results are broadly consistent with those presented in the classical ERD/ERS literature, since changes in brain oscillations were reported to be associated with the different stages of the movement [44,45]. More specifically, the classical ERD/ERS literature [44,45] showed that for voluntary self-paced finger movements, alpha-band ERD was observed at 2.5 s before the beginning of the movement. This ERD occurred over the contralateral hemisphere to the movement and spread to the ipsilateral side immediately prior to the start of the movement. During the movement execution, alpha ERD developed symmetrically in the hemispheres. In the present study, pre-movement ERD can be viewed as a readiness state, since the amber screen, which served as a warning stimulus, informed the subject of the impending requirement to perform the movement. To perform the required task, subjects searched long-term memory for information. Sensorimotor areas were pre-activated or primed and a desynchronization occurred [37]. Alpha post-movement ERS has not been reported in the literature contrary to beta post-movement ERS [46]. Researchers have only mentioned a slow recovery lasting a few seconds to reach baseline level activity after the end of the movement for the alpha rhythm [44,45]. They have also shown the existence of simultaneous occurrence of alpha ERD and alpha ERS during voluntary hand movements [41]. A sensorimotor ERD coupled with an ERS in parieto-occipital areas has been observed. Pfurtscheller [42] suggested that this alpha ERS expresses an 'idling' state or 'a correlate of a deactivated cortical network.' Similarly, Klimesch et al. [26,28] proposed that this 'idling' state is important as it may be a state in which strong inhibitory processes allow a memory search to spread only within relevant parts of the cortical memory network.

During all the movement stages, alpha SL values at electrode sites C3 and C4 were not statistically different. The interpretation of this result in relation to previous research is not easy to undertake. First, to our knowledge, only the study carried out by Calmels et al. [7] has examined and compared SL patterns in movement preparation and execution. While Calmels et al. [7] employed similar methods, the results of their study cannot be compared to the current data. In their study, the observation and execution condition variables were indistinguishable because they were averaged in the post-hoc comparisons. Moreover, the frequency bands were different and the post-movement stage was not included in their analysis whereas the baseline stage was included. Second, SL findings do not allow for

Table 3 Coexistence of local and distant EEG activities assessed respectively by the ERD/ERS and SL techniques during the pre-movement, movement, and post-movement stages under the observation condition.

	C3		C4	
	8—10 Hz	10—13 Hz	8—10 Hz	10—13 Hz
Pre-movement	ERD	Weak ERS	ERD	Weak ERD
	High SL value	High SL value	High SL value	High SL value
Movement	ERD	Weak ERD	ERD	Weak ERD
	Low SL value	Low SL value	Low SL value	Low SL value
Post-movement	ERS	ERS	ERS	ERS
	High SL value	High SL value	High SL value	High SL value

From a functional point of view, changes were detected in the alpha bands, between the movement and post-movement stages using both techniques. Changes were also observed between the pre-movement and movement stages using the SL technique whereas no such change in local power (ERD/ERS) was identified.

absolute comparison with research that has not used this analysis technique. However a comparison of the current findings with different measures of coherence, synchronicity, or event-related coherence is merited. Unfortunately, as far as we know, apart from studies by Leocani et al. [29] and Rappelsberger et al. [49], no research using this type of measures has investigated the EEG activity during the stages occurring before and/or after an event. Comparing our results with those of Leocani et al. [29] and Rappelsberger et al. [49] is delicate since the movements they chose were more simple and brisk compared to ours which were more complex and longer. The movement studied by Leocani et al. [29] was also self-paced or internally generated whereas this was externally paced or triggered in our study. Comparing these two kinds of movements, which involve different neuronal pathways [14,18], would be erroneous. We, therefore, can only extrapolate from the lack of significant SL changes throughout the three stages under the execution condition. It may be possible that, because of the pre-experimental training session, the movement became over-learned. Besides, the ordering of the conditions (i.e., observation condition performed first and followed by the execution condition) could have also contributed to reinforce the learning and led the subject to perform the movement quasi-automatically. This automaticity can be reflected, at a large scale level, by synchronization congruence throughout the three stages of the movement. The results of the present study do not allow us to support claims for this suggestion. Additional investigations will be necessary to test this suggestion.

Observation condition

Under the observation condition, an alpha band ERD, occurring during the pre-movement and movement stages, was followed by a post-movement ERS at the C3 and C4 electrode sites except for the C3 electrode site in the 10—13 Hz frequency band, which displayed a different pattern. The results related to the movement stage are in agreement with the EEG findings reported in the classical literature of the mirror neurons [2,10,11,17,19,30,35,36]. A suppression, a block, or a modulation of the mu rhythm was uncovered during the observation of actions performed by conspecifics. For instance, Babiloni et al. [2] showed the existence of a bilateral central desynchronization during the observation of fast finger extension movements. The results on the alpha pre-movement desynchronization are in accordance with those reported by Kilner et al. [25]. These authors showed that a readiness potential, which is an electrophysiological marker of motor preparation, was present prior to the observation of an action performed by a human being. As suggested by Kilner et al. [25], the observed ERD could be due to the knowledge of an impending event. The pre-movement stage can be viewed as a preparatory phase in which individuals had to be ready for observation. The results related to the ERS of the post-movement stage cannot be discussed in the context of any previous research because no studies have addressed this topic.

Pre-movement alpha SL values were higher than movement SL values which were lower than post-movement SL values. As previously mentioned, these results cannot be dis-

cussed in the context of any earlier research. We can only suggest that during the observation of a movement the modulation detected at a local level in alpha frequency band and in sensorimotor areas [10,11,17,19,30,35,36] may be reflected by a decrease in synchronization at a large scale level. This suggestion has yet to be tested.

Conclusion

In the present study, different aspects of cortical activity have been depicted: local changes in activation assessed by measures of ERD/ERS power and global integration and synchronization of brain activity considered by SL measures. The coexistence of these two kinds of activity within a same period of time, which occurred simultaneously and varied differently in time and space, provided an accurate description of oscillatory cortical activity.

Acknowledgements

Appendix 1. Mathematical background of synchronization likelihood

The synchronization likelihood (SL) is a measure of the *generalized synchronization* between two dynamical systems X and Y [54]. Generalized synchronization [51] exists between X and Y if the state of the response system is a function of the driver system: Y = F(X). The first step in the computation of the synchronization likelihood is to convert the time series x_i and y_i recorded from X and Y as a series of state space vectors using the method of time delay embedding [55]:

$$X_i = (x_i, x_{i+L}, x_{i+2 \times L}, x_{i+3 \times L} \ldots, x_{i+(m-1) \times L}) \qquad (1)$$

where L is the time lag, and m the embedding dimension. From a time series of N samples, N-(m × L) vectors can be reconstructed. State space vectors Y_i are reconstructed in the same way.

Synchronization likelihood is defined as the conditional likelihood that the distance between Y_i and Y_j will be smaller than a cutoff distance r_y, given that the distance between X_i and X_j is smaller than a cutoff distance r_x. In the case of maximal synchronization, this likelihood is 1; in the case of independent systems, it is a small, but nonzero number, namely P_{ref}. This small number is the likelihood that two randomly chosen vectors Y (or X) will be closer than the cut-off distance r. In practice, the cut-off distance is chosen such that the likelihood of random vectors being close is fixed at P_{ref}, which is chosen the same for X and for Y. To understand how P_{ref} is used to fix r_x and r_y, we first consider the correlation integral:

$$C_r = \frac{2}{N(N-w)} \sum_{i=1}^{N} \sum_{j=i+w}^{N-w} (r - X_i - X_j) \qquad (2)$$

Here, the correlation integral C_r is the likelihood that two randomly chosen vectors X will be closer than r. The vertical bars represent the euclidian distance between the vectors. N is the number of vectors, w is the Theiler correction for autocorrelation [56] and θ is the Heaviside function: $\theta(X)=0$ if $X \geq 0$ and $\theta(X)=1$ if $X < 0$. Now, r_x is chosen such that $Cr_x = P_{ref}$ and r_y is chosen such that $Cr_y = P_{ref}$. The synchronization likelihood between X and Y can now be formally defined as:

$$SL = \frac{2}{N(N-w)p_{ref}} \sum_{i=1}^{N} \sum_{j=i+w}^{N-w} \theta(r_x - |X_i - X_j|) \theta(r_y - |Y_i - Y_j|) \tag{3}$$

SL is a symmetric measure of the strength of synchronization between X and Y ($SL_{XY} = SL_{YX}$). In equation (3), the averaging is done over all i and j; by doing the averaging only over j, SL can be computed as a function of time i. From (3), it can be seen that in the case of complete synchronization $SL = 1$; in the case of complete independence, $SL = P_{ref}$. In the case of intermediate levels of synchronization, $P_{ref} < SL < 1$.

Appendix 2. Additional information about the ERD/ERS computation

To compute ERD/ERS, the following options in Neuroscan 4.3 were selected: band power; bandpass filter in a centered symmetric frequency band with a rolloff of 48 dB/octave; envelope; warmup filter from the right with 101.56 ms trim left and trim right; reference interval with a start of 101.56 ms and a stop of 1000 ms; percent decrease scaling; averaging window span to 125ms with the collapse option; and ERD/ERS mixture for the phase locking. For each subject, and each of the two frequency bands, 83-power values (one every 125 ms) were obtained for the 19 electrode sites during observation and execution.

Three stages that were slightly different in time duration from those described above were identified within a trial after the ERD/ERS computation. These time differences are due to the characteristics of the Neuroscan 4.3 software which has been devised for a 250 AD rate rather than a 256 AD rate. With a dwell time of 3.90625 (i.e., 1000/256), a trim time of 100 ms is unobtainable since it does not give a whole number for the points. Therefore, 101.56 ms was used instead. The first stage comprised a reference interval [1101.56—1976.56 ms] and a pre-movement stage [1976.56—3976.56 ms]. The second, a movement stage [3976.56—8976.56 ms]; and the third stage, a post-movement stage [8976.56—11476.56 ms]. The reference for all time intervals was the onset of the first stage, even if the first second of the first stage had been removed from the EEG analysis.

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