LARGE-SCALE SYNCHRONIZATION RELATED TO STRUCTURES MANIFESTING SIMULTANEOUS EEG BASELINE SHIFTS IN THE PRE-MOVEMENT PERIOD

Miloslav Kukleta^{*1,2}, Petr Bob^{1,2}, Baris Turak³, Jacques Louvel³

¹Central European Institute of Technology (CEITEC), Masaryk University,
Brno, Czech Republic

²Center for Neuropsychiatric Research of Traumatic Stress, Department of Psychiatry and UHSL,
First Faculty of Medicine, Charles University, Prague, Czech Republic

³Service de Neurochirurgie Stéréotaxique, Hôpital Ste Anne, Paris, France

Abstract

Several current data indicate that intracranial records of the Bereitschaftspotential from some brain loci manifest baseline shifts (EBS) in the early pre-movement period that are separated from the movement components by a distinct plateau. In this context, main purpose of this study was to assess whether structures generating the EBSs that are simultaneously widespread in various structures of the brain will be specifically linked to higher levels of large-scale integration in comparison to structures that were not involved in EBS generation. In this study were included 21 epilepsy surgery candidates (12 men, 9 women; aged from 18 to 49 years), who were measured during self-paced clenching movements of the hand. Brain activities during the task were recorded using intracerebral electrodes and were evaluated in pairs. Eighty two percent of the EBSs started in various distant brain structures at the same time, eighteen percent at different time. Approximately half of the EBSs of the first group started in the prefrontal regions; the second half was obtained from pairs located in parietal and temporal regions. The first, the second, and the third groups exhibited a special degree of activity synchronization. The simultaneous EBS onsets associated synchronization strongly suggests significantly higher functional coupling of these brain areas which is supposed to be a basic mechanism of integration of various areas of the brain participating in cognitive and intentional functions.

Key words: Intracerebral EEG recordings; Bereitschaftspotential; Voluntary movement

1. INTRODUCTION

Recent research documented that processes preceding volitional movement and movement planning actions are closely related to preattentive processing and attentional functions (Johnson et al., 1996; Burnod et al., 1999; Andersen & Cui, 2009). In this context, experimental research using the slow cortical potentials preceding self-initiated movement (Bereitschaftspotential - BP) described various functional parameters of the BP components (Jahanshahi & Hallett, 2003; Shibasaki & Hallett, 2006).

^{*}Correspondence to: Petr Bob, email: petrbbob@netscape.net

Received May 30, 2015; accepted June 25, 2015; Act Nerv Super 57(3-4), 101-109; ISSN-1802-9698

In this previous research neural cognitive networks underlying generation and executive activities of self-paced movements were studied using measurements of regional cerebral blood flow changes during various tasks in numerous reported studies (Jahanshahi et al., 1995; Jenkins et al., 2000). In addition comparison of these changes observed under selfinitiated versus externally triggered movements shows that the networks engaged in the early “volitional” part of the task are widespread in many structures of the brain (Jenkins et al., 2000). These processes are related to large-scale integration of neural activities coupled to cognitive processing preceding movement have also been described in the form of “early baseline shift” (EBS) (Kukleta et al., 2001, 2012). Those reported data are in agreement with recent findings that complex cognitive functions are organized at a global level in the brain and are related to large-scale information processing that requires mechanisms of functional integration of multiple disparate neural assemblies which enables to integrate more primitive functions organized in localized brain regions (Bressler & Kelso, 2001; Fries et al., 2001; Jensen et al., 2007; Kukleta et al., 2010; Varela et al., 2001).

In this context of recent findings, the present study examined a hypothesis whether structures generating the “Early Baseline Shifts” that are simultaneously widespread in various structures of the brain will be specifically linked to higher levels of large-scale integration in comparison to structures that were not involved in EBS generation. To test this hypothesis we have assessed the temporo-spatial characteristics of the EBSs found in depth EEG recordings that were obtained during self-paced movement.

2. METHODS AND MATERIALS

2.1. Subjects

The study included 21 epilepsy surgery candidates (12 men, 9 women, aged 18 - 49 years) in whom the early pre-movement baseline shifts of the intracerebral EEG (iEEG) records during repeated self-paced hand movements were analyzed. We have selected subjects who had at least two distinct records with EBS responses. In these patients we have investigated whether the EBSs started at the same time or they had different onsets. In addition we have also assessed levels of linking between sites exhibiting identical onsets with special focus to specific prefrontal and parietal brain sites engaged in the accomplishment of a self-paced task.

These shifts were conceived as a difference between distinguished periods of iEEG amplitudes which may be described by the Boltzmann sigmoid function used to perform the curve fitting as was previously documented (Devanne et al., 1997). The subjects were selected from a sample of archived data including 42 patients participating in BP experiment and their selection was based on a presence of EBS in at least two EEG electrodes (per patient; neighboring contacts of one electrode were not included). The intracerebral locations of recording contacts from which the EBSs records were included are in Table 1.

All patients had implanted chronic depth multilead electrodes for diagnostic reasons (Hôpital Sainte-Anne, Service de Neurochirurgie; INSERM, U 97) and were informed that the experiment had no relevance to their clinical examination. All of them agreed to participate in the study. With exception of epilepsy the selected patients had no other neurological or psychiatric disorder and all of them were treated by antiepileptic medication. During the period of diagnostic iEEG recording, the doses of medication were reduced to allow seizures to develop spontaneously or in response to a focal repetitive electrical stimulation.

2.2. Recording procedures

Deep (DIXI Besançon) intracerebral stainless steel or platinum electrodes orthogonally implanted were used for experimental recording. Each 0.8 mm diameter electrode had a series

of 2 mm long recording contacts (5 - 15), with a distance of 1.5 mm between the contacts. The positions of the electrodes were indicated in relation to the axes defined by the Talairach system using the 'x, y, z' format where 'x' is lateral, millimeters to midline, positive right hemisphere, 'y' is anteroposterior, millimeters to the AC (anterior commissure) line, positive anterior, and 'z' is vertical, millimeters to the AC/PC (posterior commissure) line, positive up (Talairach et al., 1967). In one patient, an additional diagonal electrode was inserted into the mesial prefrontal cortex.

Table 1. Location of recording contacts from which the paired EEG records with early baseline shifts (EBS) were derived, distances between these contacts, mean amplitudes of EBS obtained from the sigmoid fits of the paired records, differences of EBS onsets in paired records, and the correlation coefficient calculated from paired records in the pre-movement period from -4.0 sec to -0.8 sec.

Patient and No. of EBS pair	Location of paired records with EBS and coordinates x, y, and z of Talairach		Distance (mm)	EBS amplitude (μV)		Differences of EBS onsets (msec)	R-value in window from -4.0 to -0.8 sec	
Aa	1	G temp superior (40, -27, 6)	G parahippocampi (23, -58, -3)	38	28.1	22.6	220	0.65
	2	G supramarginalis (57, -40, 31)	G parahippocampi (23, -58, -3)	52	28.1	12.5	210	0.61
	3	G temp superior (40, -27, 6)	G supramarginalis (57, -40, 31)	34	22.6	12.5	0	0.61
Ab	4	G cing anterior (12, 35, 6)	G front inferior (51, 35, 6)	39	8.5	6.9	0	0.63
	5	G cing anterior (12, 35, 6)	L parietalis inferior (50, -28, 32)	73	8.5	14.5	0	0.60
	6	G front inferior (51, 35, 6)	L parietalis inferior (50, -28, 32)	58	6.9	14.5	0	0.62
Ba	7	G temp superior (54, -27, 9)	G cing posterior (12, -47, 12)	49	10.7	11.9	760	0.41
	8	Precuneus (11, -39, 46)	G cing posterior (12, -47, 12)	35	10.7	8.0	720	0.47
	9	G temp superior (54, -27, 9)	Precuneus (11, -39, 46)	58	8.0	11.9	60	0.48
Bb	10	G cing anterior (9, 26, 16)	G front inferior (51, 26, 16)	42	4.0	6.3	0	0.69
	11	G cing anterior (9, 26, 16)	G cing posterior (13, -32, 30)	59	4.0	5.3	0	0.63
	12	G cing posterior (13, -32, 30)	G front inferior (51, 26, 16)	69	6.3	5.3	30	0.38
Ca	13	G cing posterior (12, -28, 28)	Precuneus (14, -58, 30)	29	4.5	3.4	0	0.75
	14	G cing posterior (12, -28, 28)	G temp superior (54, -29, 10)	45	4.5	4.0	130	0.40
	15	Precuneus (14, -58, 30)	G temp superior (54, -29, 10)	54	3.4	4.0	150	0.18
Cb	16	G cing anterior 1 (12, 30, 19)	G cing anterior 2 (10, 43, 1)	22	4.2	3.9	0	0.78
	17	G cing anterior 1 (12, 30, 19)	G temp superior (51, 18, -18)	55	4.2	18.9	0	0.31
	18	G cing anterior 2 (10, 43, 1)	G temp superior (51, 18, -18)	52	3.9	18.9	0	0.31
Da	19	G temp medialis (-50, -31, -6)	G front medialis -8, 30, -12)	78	17.1	32.1	0	0.76
Db	20	G cing anterior 1 (10, 22, 20)	G cing anterior 2 (14, 31, -7)	18	23.8	19.5	0	0.99
	21	G cing anterior 1 ((10, 22, 20)	G front inferior (47, 30, -1)	46	23.8	10.3	0	0.55
	22	G cing anterior 2 (14, 31, -7)	G front inferior (47, 30, -1)	46	19.5	10.3	0	0.58

Table1.Continues.

Ga	23 G cing anterior 1 (10, 22, 20)	G cing anterior 2 (14, 31, -7)	42	19.4 17.0	0	0.89
24	G cing anterior 1 (10, 22, 20)	L parietalis inferior (51, -34, 28)	70	19.4 21.6	0	0.86
25	L parietalis inferior (51, -34, 28)	G cing anterior 2 (14, 31, -7)	83	21.6 17.0	0	0.80
26	G front inferior (52, 22, 20)	L parietalis inferior (51, -34, 28)	57	25.4 21.6	0	0.72
27	G cing anterior 1 (10, 22, 20)	G front inferior (52, 22, 20)	42	19.4 25.4	0	0.85
28	G front inferior (52, 22, 20)	G cing anterior 2 (14, 31, -7)	48	25.4 17.0	0	0.79
Gb	29 G cing anterior 1 (-14, 37, 10)	G front medialis 1 (-8, 49, 2)	16	21.3 18.4	0	0.72
	30 G cing anterior 1 (-14, 37, 10)	G front medialis 2 (-8, 16, -16)	36	21.3 30.9	0	0.94
	31 G cing anterior 1 (-14, 37, 10)	G cing anterior 2 (-10, 28, 17)	12	21.3 12.7	0	0.91
32	G front medialis 1 (-8, 49, 2)	G front medialis 2 (-8, 16, -16)	36	18.4 30.9	0	0.94
33	G front medialis 1 (-8, 49, 2)	G cing anterior 2 (-10, 28, 17)	26	18.4 12.7	0	0.82
34	G front medialis 2 (-8, 16, -16)	G cing anterior 2 (-10, 28, 17)	34	30.9 12.7	0	0.90
35	G cing anterior 2 (-10, 28, 17)	G front inferior (-43, 28, -4)	39	12.7 16.3	0	0.80
36	G front medialis 2 (-8, 16, -16)	G front inferior (-43, 28, -4)	36	30.9 16.3	0	0.63
37	G front medialis 1 (-43, 28, -4)	G front inferior (-43, 28, -4)	43	18.4 16.3	0	0.69
38	G cing anterior 1 (-14, 37, 10)	G front inferior (-43, 28, -4)	41	21.3 16.3	0	0.64
Ka	39 G cing posterior (-10, -43, 34)	G lingualis (-16, -68, 3)	41	8.3 9.3	680	-0.01
La	40 G front inferior (-59, 9, 22)	G supramarginalis (-48, -38, 32)	51	8.8 9.3	0	0.33
Lb	41 G front inferior (52, 33, 11)	G front medius (50, 28, 42)	33	7.0 15.1	0	0.72
Lc	42 G cing posterior (10, -32, 32)	L parietalis inferior (52, -32, 32)	42	12.1 15.4	0	0.66
43	G front inferior (44, 39, -2)	G cing posterior (10, -32, 32)	86	12.1 18.6	0	0.86
44	G front inferior (44, 39, -2)	L parietalis inferior (52, -32, 32)	79	18.6 15.4	250	0.62
Ld	45 G front medialis 1 (-10, 42, 29)	G front medialis 2 (-11, 34, -12)	44	11.2 11.5	0	0.82
	46 G cing anterior (-14, 40, 5)	G front medialis 2 (-11, 34, -12)	20	7.4 11.5	0	0.86
	47 G cing anterior (-14, 40, 5)	G front medialis 1 (-10, 42, 29)	24	7.4 11.2	0	0.81
Na	48 G precentralis (-36, -11, 26)	G cing posterior (-13, -31, 39)	34	14.9 8.1	270	0.48
Pa	49 G cing anterior (13, 37, -1)	G front medius (46, 40, -12)	38	11.6 19.2	0	0.71
	50 G cing anterior (13, 37, -1)	G front medialis (12, 40, -12)	20	11.6 14.7	0	0.91
	51 G front medialis (12, 40, -12)	G front medius (46, 40, -12)	34	14.7 19.2	0	0.71
Pb	52 L parietalis inferior (61, -37, 25)	Precuneus (7, -65, 41)	79	4.4 26.7	0	0.56
Ra	53 G parahippocampalis (-26, -51, 3)	Insula (-52, -38, 21)	36	12.0 16.0	0	0.52

Table 1. Continues.

	54	G parahippocampalis (-26, -51, 3)	G supramarginalis (-55, -60, 31)	41	12.0	16.0	0	0.55
	55	Insula (-52, -38, 21)	G supramarginalis (-55, -60, 31)	38	16.0	16.0	0	0.60
Sa	56	G cing anterior (9, 8, 29)	G cing posterior (15, -32, 38)	55	12.2	9.9	0	0.88
	57	G cing posterior (15, -32, 38)	G postcentralis (43, -18, 28)	33	9.9	14.7	0	0.79
	58	G cing anterior (9, 8, 29)	G postcentralis (43, -18, 28)	43	12.2	14.7	0	0.72
Ta	59	G cing anterior (14, 36, 3)	L parietalis inferior (54, -43, 28)	90	9.5	36.4	0	0.59
	60	G cing posterior (15, -43, 28)	L parietalis inferior (54, -43, 28)	39	23.0	36.4	0	0.64
	61	G cing anterior (14, 36, 3)	G cing posterior (15, -43, 28)	81	9.5	23.0	0	0.70

All electrode positions were verified radiologically in anteroposterior and lateral views. Surface electromyograms (EMG) were recorded with a pair of cup electrodes placed on the skin over the flexor digitorum communis.

2. 3. Experimental design

During the experiment, a patient laid comfortably on bed and watched a point on the video screen positioned approximately 150 cm in front of their eyes. Experimental data were recorder during two periods. In the first control period, the patient watched the screen on which a letter lasting 200 ms irregularly replaced the central point. In the second experimental period, the patient was instructed spontaneously and irregularly to move a joystick and was asked to maintain intervals of at least 10 sec between the successive movements without counting or maintaining any other rhythmic activity. Due to anatomical cross of the hemisphere and hand, the opposite hand to the explored hemisphere was used to move the joystick with approximately 35 movements in the second experimental period.

2. 4. Data acquisition and processing

The intracerebral EEG activity was recorded and averaged using a 32-channel amplifier device (Nihon-Kohden, bandpass between 0.016 and 100 Hz), and using Cambridge electronic device (CED) 1401 + interface with SIGNAL 2 software. Each data frame had duration of 5 sec (4 sec before the EMG onset in the experimental block and 4 sec before the visual signal in the control block) and was digitized at a frequency of 100 Hz. All the records were taken with a binaural reference. The data processing was performed offline using artifact-free iEEG records only (the selection was based on visual inspection of the records by two experienced persons). In experimental block, all available trials were used for averaging so that the number of trials averaged slightly varied across the patients (minimal number was 28). The averaging was triggered by the onset of the EMG. The fitted curves (see Figure 1) were calculated in the early pre-movement period (from -4.0 to -0.8 sec) using the sigmoid fitting function from the analysis menu of Signal 5 program. This arbitrary choice of the -0.8 sec time point as the proximate limit of the analyzed pre-movement period was determined by our intention to exclude all possible contamination by processes associated with the late BP processes.

Figure 1. The fitted curves calculated in the early pre-movement period (from -4.0 to -0.8 sec) using the sigmoid fitting function.

The selection of one record with EBS from usually quasi-identical responses obtained from the neighboring contacts of an electrode was based on evaluation of EBS amplitude and the result of the fitting procedure. In order to disclose a possible functional relationship between the brain loci which yielded the EBSs, we arranged the collected records into 61 pairs and assessed the level of phase correlation of iEEG oscillations in each of these pairs. As a measure of synchronization we have used correlation coefficients calculated in the period from -4.0 to -0.8 sec. The determination of EBS onsets in pairs was based on visual assessment of differences between iEEG records. To reduce a subjective factor the determination was based on a consensus of two persons.

2. 5. Statistical evaluation

Statistical evaluation of the results was performed by software package Statistica'99 (StatSoft Inc., Tulsa, U.S.A.). The binominal distribution was calculated on the whole data set using the chi-squared test, the correlation between the EBS amplitude and the distance was calculated also on the whole set using Spearman R-value. The correlation between levels of activity synchrony in paired loci was calculated in every pair using the same test, and the comparisons of levels of activity synchrony between subgroups were calculated in these subgroups using ANOVA test.

3. RESULTS

Main result represents significant difference of correlations between the two groups of pairs of loci, the first containing EBS and the second including pairs without EBS, both obtained during early premovement period from 15 anatomically delineated cortical regions and calculated in the time windows from -4.0 to -0.8 sec (see Table 1 and Figure 2).

Figure 2. Topographic distribution of brain sites in sections A and B. Rectangles (■) corresponds to the sites localized in the left hemisphere and circles (●) correspond to right hemispheric brain locations generating Early Baseline Shifts (EBS).

Other important finding was the time synchrony of EBSs onsets in the great majority of pairs. In single subjects, the number of analyzed pairs varied between 1 and 10 (median 3 pairs). The onsets of EBSs were from 1.6 to 3.2 sec (median 2.4 sec). The mean amplitude value of the shift was 14.1 ± 7.6 μ V (minimum 3.4 μ V, maximum 36.4 μ V). The amplitude change was electrically positive in 46 cases and negative in 15 cases; binominal distribution was not found (chi-squared test, $p > 0.05$). In single persons, the EBS change had identical polarity just with one exception in the subject, who had one positive and one negative EBS. In 50 EBSs, the potential change was generated at the same time. The variability of the distance between the paired recording sites (45.8 ± 18.2 mm; minimal value 12 mm, maximal value 90 mm) shows

that some pairs described local field potentials within one anatomical structure and other pairs of the activity in different brain regions. Any significant correlation between the distances and the r -values was not found (Spearman $R = -0.24$; $p > 0.05$).

As evident from Table 2, part A, testing of the same structures under different conditions (observation of the screen without any movement) was followed by different responses – only one identical onset from the 16 EBS responses was observed, decreased level of mean r values in the time window -4.0 sec to -0.8 sec was found (ANOVA, $F(1,120) = 43.7$; $p < 0.001$). Other spatiotemporal relations of the EBSs and mean r -values are presented in Table 2, part B. The allocation of pairs according to their brain location and the presence or absence of identical EBS onsets into subgroups have shown influence of these factors. As can be seen, the prefrontal location of the pair and identical EBS onsets had the highest r -values, lower values had parietotemporal locations with the identical EBS onsets, and lowest values had variously localized pairs without identical EBS onsets. All the differences were significant (ANOVA; $F(2,58) = 21.48$; $p < 0.001$). Post hoc Scheffe test showed p -value lower than 0.008 between first and second groups, lower than 0.001 between first and third groups, and lower than 0.002 between second and third groups. With the exception of one pair, the correlation of activity in

all the other pairs was significant (number of compared items was 320). Important and interesting finding represents also synchronization between the loci in the lobulus parietalis inferior and the prefrontal loci. All these pairs had identical EBS onsets and the mean r -value was 0.69 ± 0.10 (pairs 5, 6, 24, 25, 26, 44, and 59).

Table 2. Relation between the location of paired iEEG records with early baseline shifts (EBS) and the level of their phase synchrony in the premovement period.

A			
Group of pairs	N	Number of pairs with identical EBS onsets	Mean r -values in window from -4.0 to -0.8 sec
Self-paced condition	61	50	0.66 ± 0.20
Observation without task	61	1	0.35 ± 0.32

B			
Subgroups of self-paced condition of pairs (N61)	N	Mean r -values in window from -4.0 to -0.8 sec	Identification of EBS
Pairs in prefrontal region with identical EBS onsets	26	0.78 ± 12	4,10,16,20,21,22,23,27,28,29,30,31,32,33,34,35,36,37,38,41,45,46,47,49,50,51
Pairs in prefrontal and parietotemporal regions with identical EBSs onsets	24	0.64 ± 0.16	3,5,6,11,13,16,17,18,24,25,26,40,42,43,52,53,54,55,56,57,58,59,60,61
Pairs without identical EBSs onsets	11	0.42 ± 0.20	1,2,7,8,9,12,14,15,39,44,48

9. DISCUSSION

The data show that the great majority of the EBSs (82 %) started at different, frequently distant brain structures at the same time. In the context of recent findings we have also found that the “early baseline shifts” simultaneously widespread in various structures of the brain are specifically linked to higher levels of large-scale integration compared to structures which were not involved in EBS generation. In addition, the prefrontal pairs exhibited a significantly higher level of synchronization of their activities in comparison to the other pairs. The simultaneous EBS onsets together with the associated transitory increase of synchronization in node pairs from prefrontal sites and the lobulus parietalis inferior indicate a strong functional

coupling of these brain areas during the task. The analysis of parameters from this experimental period could be of interest for further research of recently discussed relationship between consciousness and will (Dirnberger et al., 2011; Haggard, 2011; Travena & Miller, 2002).

According to Haggard, in this relationship the competition of prefrontal neurons could play an important role and might provide an efficient mechanism of regulation (Haggard, 2011). The presented data showed that EBSs could be considered as the end of estimating the time interval which elapsed from previous trial and reflect beginning of a new task and action. In addition compared to other reported findings (Ball et al., 1999; Deiber et al., 1991, 1996, 1999; Jahanshahi et al., 1995; Jannerod, 1994, 2006, 2009; Jenkins et al., 2000; McKinnon et al., 1996; Toro et al., 1994), the local sites generating EBSs are also mainly involved in processes related to selective increase of cerebral blood flow in the self-paced variant of movement triggering (Jahanshahi et al., 1995; Jenkins et al., 2000; Soon et al., 2008).

No significant correlations between the distances and r -values of correlations between pairs were found, which is in agreement with recent findings about large scale synchronization in the brain. The large-scale coupling between structures generating EBS in comparison to other structures is in agreement with other studies focused on EEG analysis that also observed functionally relevant epochs of synchronization in various brain structures during attention, perception, motor and memory task performance (Jensen et al., 2007; Singer, 2001), which participate in intentional activities related to action planning, and decision making (Johnson et al., 1996; Andersen & Cui, 2009). The data of the present study suggest that structures generating EBS specifically participate in large-scale integration and binding mechanisms (Bressler & Kelso, 2001; Fries et al., 2001; Jensen et al., 2007; Kukleta et al., 2010). In this context, the present study provides novel findings about specific large scale integration related to structures involved in the pre-movement period manifesting EBSs that most likely reflect voluntary actions. The data directly indicate that these structures belong to large scale integrated and highly specialized systems that enable flow of information among various areas of the brain participating in cognitive and intentional functions.

ACKNOWLEDGEMENTS

The study was supported by the project CEITEC CZ.1.05/1.1.00/02.0068 from European Regional Development Fund and the grant MSM 002 1620849 research grant provided by Charles University (PRVOUK). The data were collected in Paris (Hôpital Ste Anne, Service de Neurochirurgie; INSERM, U 97) by a currently no more existent research group headed by Michel Lamarche. The authors thank to Pierre Buser and Ivan Rektor for their help.

REFERENCES

- Andersen, R.A., & Cui, H. (2009). Intention, action planning, and decision making in parietalfrontal circuits. *Neuron*, 63, 568-583.
- Ball, T., Schreiber, A., Feige, B., Wagner, M., Lucking, C.H., & Kristeva-Feige, R. (1999). The role of higher-order motor areas in voluntary movement as revealed by high-resolution EEG and fMRI. *Neuroimage*, 10, 682-694.
- Bressler, S.L., & Kelso, J.A.S. (2001). Cortical coordination dynamics and cognition. *Trends Cogn Sci (Regul Ed)* 5, 26-36.
- Burnod, Y., Baraduc, P., Battaglia-Mayer, A., Guigon, E., Koechlin, E., Ferraina, S., Lacquaniti, F., & Caminiti, R. (1999). Parieto-frontal coding of reaching: An integrated framework. *Experimental Brain Research* 129, 325-46.

- Deiber, M.-P., Passingham, R.E., Colebatch, J.G., Friston, K.J., Nixon, P.D., Frackowiak, R.S.J. (1991). Cortical areas and the selection of movement: a study with positron emission tomography. *Experimental Brain Research*, 84, 393-402.
- Deiber, M.-P., Ibañez, V., Sadato, N., & Hallett, M. (1996). Cerebral structures participating in motor preparation in humans: a positron emission tomography study. *Journal of Neurophysiology*, 75, 233-247.
- Deiber, M.-P., Honda, M., Ibañez, V., Sadato, N., & Hallett, M. (1999). Mesial motor areas in self-initiated versus externally triggered movements examined with fMRI: effect of movement type and rate. *Journal of Neurophysiology*, 81, 3065-77.
- Devanne, H. Lavoie, B.A., & Capaday, C. (1997). Input-output properties and gain changes in the human corticospinal pathway. *Experimental Brain Research*, 114, 329-338.
- Dirnberger, G., Dürreger, C., Lindinger, G., Lang, W. (2011). On the regularity of preparatory activity preceding movements with the dominant and nondominant hand: a readiness potential study. *International Journal of Psychophysiology*, 81, 127-131.
- Fries, P., Reynolds, J.H., Rorie, A.E., & Desimone, R. (2001). Modulation of oscillatory neuronal synchronization by selective visual attention. *Science*, 291 (5508), 1560-3.
- Haggard, P. (2011). Decision time for free will. *Neuron*, 69, 404-406.
- Jahanshahi, M., Jenkins, I.H., Brown, R.G., Marsden, C.D., Passingham, R.E., & Brooks, D.J. (1995). Self-initiated versus externally triggered movements. I. An investigation using measurement of regional cerebral blood flow with PET and movement-related potentials in normal and Parkinson's disease subjects. *Brain*, 118, 913-933.
- Jahanshahi, M., Hallett, M. (2003). *The Bereitschaftspotential. Movement-related cortical potentials*. Kluwer Academic/Plenum Publishers, New York.
- Jannerod, M. (1994). The representing brain. Neural correlates of motor intention and imagery. *Behavioral and Brain Sciences*, 17, 187-245.
- Jannerod, M. (2006). The origin of voluntary action. History of a physiological concept. *C. R. Biologies*, 329, 354-362.
- Jannerod, M. (2009). *Le cerveau volontaire*. Odile Jacob, Paris.
- Jenkins, I.H., Jueptner, M., Passingham, R.E., & Brooks, D.J. (2000). Self-initiated versus externally triggered movements. II. The effect of movement predictability on regional cerebral blood flow. *Brain*, 123, 1216-28.
- Jensen, O., Kaiser, J., & Lachaux, J., 2007. Human gamma-frequency oscillations associated with attention and memory. *Trends in Neurosciences*, 30 (7), 317-324.
- Jonhson, P.B., Ferraina, S., Bianchi, I., & Caminiti, R. (1996). Cortical networks for visual reaching: Physiological and anatomical organization of frontal and parietal lobe arm regions. *Cerebral Cortex*, 6, 102-119.
- Kukleta, M., & Lamarche, M. (2001). Steep early negative slopes can be demonstrated in premovement Bereitschaftspotential. *Clinical Neurophysiology*, 112, 1642-1649.
- Kukleta, M., Bob, P., Brazdil, M., Roman, R., & Rektor, I. (2010). The level of frontal-temporal beta-2 band EEG synchronization distinguishes anterior cingulate cortex from other frontal regions. *Consciousness and Cognition*, 19, 879-886.
- Kukleta, M., Turak, B., & Louvel, J. (2012). Intracerebral recordings of the Bereitschaftspotential demonstrate the heterogeneity of its components. *International Journal of Psychophysiology*, 83, 65-70.
- McKinnon, C.D., Capur, S., Hussey, D., Verrier, M.C., Houle, S., Tatton, W.G. (1996). Contribution of the mesial frontal cortex to the premovement potentials associated with intermittent hand movements in humans. *Human Brain Mapping*, 4, 1-20.
- Shibasaki, H., & Hallett, M. (2006). What is the Bereitschaftspotential? *Clinical Neurophysiology*, 117, 2341-56.
- Singer, W. (2001). Consciousness and the binding problem. *Annals of the New York Academy of Sciences*, 929, 123-46.
- Soon, Ch.S., Brass, M., Heinze, H.J., & Haynes, J.D. (2008). Unconscious determinants of free decisions in the human brain. *Nature Neuroscience*, 11, 543-545.

- Talairach, J., Szikla, G., Tournoux, P., Prossalenti, A., Bordas-Ferrer, M., & Covello, L. (1967). *Atlas d'Anatomie Stéréotaxique du Télencéphale*. Mason, Paris.
- Toro, C., Wang, B., Zeffiro, T., Thatcher, R.W., & Hallett, M. (1994). Movement-related cortical potentials: source analysis and PET/MRI correlation. In: Thatcher, R.W., Hallett, M., Zeffiro, T., John, E.R., Huerta, M., editors. *Functional Neuroimaging: Technical Foundations*. Orlando, FL: Academic Press, pp. 259-267.
- Travena, J., & Miller, J. (2002). Cortical movement preparation before and after a conscious decision to move. *Consciousness and Cognition*, 11, 162-190.
- Varela, F., Lachaux, J., Rodriguez, E., & Martinerie, J. (2001). Phase synchronization and largescale integration. *Nature Reviews Neuroscience*, 2, 229-239.