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Influences of Instructions and Expertise on the Mechanisms Involved During a Working Memory Task

An EEG Study

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Abstract. The purpose of this study was to examine the effects of instructions and expertise upon cortical mechanisms during a working memory task. Ten professional pianists and ten musically naïve subjects were instructed to retain for a short period of time, sequential finger movements viewed previously with the aim of either replicating them or recognizing them at a later stage. The results showed that in the 20–30 Hz frequency band and in musically naïve subjects, functional connectivity was greater within the occipital, parietal, central, frontal, right, and left temporal areas when the subjects were invited to remember the observed movement in order to replicate it compared to the recognition condition in which they had to recognize it. In professional pianists, incomplete connectivity equivalence was detected between the two conditions. In addition, under the condition for replica, functional connectivity in musically naïve subjects was greater in the central area compared to professional pianists. Explanations related to the: (i) level of expertise, (ii) nature of operations involved during the retention period, and (iii) task demand are discussed.

Keywords: working memory, movement, instructions, expertise, EEG, functional connectivity

In the classical working memory literature, mechanisms underlying the maintenance of information in memory have been extensively investigated. Different techniques such as functional magnetic resonance imaging (fMRI) (Pochon et al., 2001; Postle, Berger, Taich, & d'Esposito, 2000; Sakai, Rowe, & Passingham, 2002) or electroencephalography (EEG; Hwang et al., 2005; Sarnthein, Petsche, Rappelsberger, Shaw, & Von Stein, 1998; Sauseng et al., 2005; Stam, van Cappellen van Walsum, & Micheloyannis, 2002; Tallon-Baudry, Bertrand, Peronnet, & Pernier, 1998; Tallon-Baudry, Kreiter, & Bertrand, 1999) have been employed. fMRI research for example, has identified the major role played by the prefrontal cortex in working memory (see Curtis & d'Esposito, 2003; Passingham & Sakai, 2004 for a review). Working memory is defined as the process that controls the maintenance, manipulation, and utilization of mental representations (Levy & Goldman-Rakic, 2000). More specifically, Passingham and Sakai (2004) described in a review of the literature that sustained activity, recorded in the prefrontal cortex during working memory tasks, was reflected in different operations, such as the

maintenance of sensory information, the response preparation, the transformation of the sensory input into a response, or the expectation of a reward.

EEG research has also examined oscillations during the retention or delay stage. Subjects were invited to perform either a Sternberg task (Hwang et al., 2005; Sauseng et al., 2005; Tallon-Baudry et al., 1998, 1999) or a stimulus recall task (Sarnthein et al., 1998; Stam et al., 2002). The study by Tallon-Baudry et al. (1998) used a Sternberg task to examine the oscillatory activity during the delay stage in the 20–80 Hz frequency band. Sustained activity was detected at the occipito-temporal and frontal electrodes. The authors suggested that this activity may reflect the rehearsal of stimulus representations in memory. More recently, Hwang et al. (2005) considered oscillatory activities after the presentation of stimuli which were easy or difficult to verbally rehearse and which had to be subsequently recognized. The authors revealed that easily verbally rehearsable stimuli generated more power in the frontal and occipital areas in the retention stage compared to the stage where the stimuli were viewed. This result was only observed in

the 14–28 Hz frequency band and led researchers to consider that verbal rehearsal is connected to this frequency band. Research by Sauseng et al. (2005) has also shown that in the beginning of the retention period, there was a stronger coupling between prefrontal and occipital areas in the alpha frequency band as subjects had to manipulate spatial information and to maintain it in memory compared to the situation in which they had only to keep this information in memory before completing a recognition task. Sarnthein et al. (1998) used a stimulus recall task to investigate the EEG relationship between the prefrontal and posterior regions in the 4–7 Hz frequency band. The authors reported an increase in coherence between these two regions during the retention stage. In the same vein, Stam et al. (2002) investigated synchronization in frequency bands lying within a range of 2–50 Hz in 60-years old elderly volunteers recalling previously viewed stimuli. Results demonstrated a synchronization increase in the 2–6 Hz frequency band at frontal and posterior parieto-temporo occipital sites and a decrease in the 6–10 Hz, 14–18 Hz, and 18–22 Hz frequency bands.

In all the aforementioned studies, the stimuli used only included still images (e.g., letters, digits, words, smooth shapes, pictures, matrixes containing colored targets, and spatial locations). To our knowledge, dynamic displays, such as biological movements, have not been employed in experimental paradigms. More specifically, no studies have investigated the mechanisms to hold movement representations active in the memory for short periods of time in order to accomplish a recognition or a reproduction task at a later stage. An investigation into this issue is, therefore, warranted.

Similarly, there is to our knowledge no research that has investigated EEG mechanisms during a working memory task in novices and experts. Experts are described as individuals who possess a high level of performance in a particular domain, which has been acquired through a long-lasting and high involvement (Ericsson, Krampe, & Tesch-Romer, 1993). What is known in the literature is that experts possess a higher working memory storage capacity compared to novices. Research by Starkes, Deakin, Lindley, and Crips (1987) has reported higher recall performances in expert dancers compared to novices and Millslagle (2002) reported similar results in a recognition task in experienced basketball players. It is also recognized that experience in a particular task is reflected in different structural and functional brain architectures (Karni, 1996). For instance, it has been demonstrated that long term and regular piano practice led to cortical changes (Amunts et al., 1997; Gaser & Schlaug, 2003; Koeneke, Lutz, Wüstenberg, & Jäncke, 2004). An increase in grey matter volumes in the motor network of experienced pianists has been detected (Gaser & Schlaug, 2003). Similarly, an increase in the size of the hand motor cortex in expert keyboard players has been identified (Amunts et al., 1997). Research by Koeneke et al. (2004) has also demonstrated a lower recruitment of neurons among experienced pianists compared to non-pianists during unimanual and bimanual tasks. Examining the influence of expertise on cortical mechanisms during a working memory task would be of prime importance.

Therefore, the aim of the present study was to investigate the cortical mechanisms at play among experts and novices

during a working memory task where individuals had to keep in memory, movement information to perform subsequently a reproduction or a recognition task. The electroencephalographic (EEG) analysis technique was selected since it allows the examination of cerebral activities with an excellent temporal resolution. Experts were selected among a population of professional pianists who are considered experts in manual dexterity. Nonexperts were composed of individuals who were musically naïve. The investigation of cerebral rhythmic activities was completed with the synchronization likelihood (SL) measure which is a marker of linear and non-linear changes in functional connectivity between different brain areas (Montez, Linkenkaer-Hansen, van Dijk, & Stam, 2006; Stam & van Dijk, 2002).

Three hypotheses were tested. First, functional connectivity in musically naïve subjects, in the retention stage, would be greater when subjects were required to retain information related to observed movements in order to reproduce them at a later stage compared to the condition in which subjects were asked to recognize these movements. Under the former requirement, the retention activity could reflect different factors such as response preparation and visuomotor transformation (Passingham & Sakai, 2004) both of which are considered unnecessary in the latter requirement. These factors are recognized as requiring greater neuronal activity (e.g., Pochon et al., 2001) and have a cost that could be the consequence of additional functional connectivity. Second, in the professional pianists, a difference is not expected since these subjects were familiar with the process of visuomotor transformation and finger movement preparation (Palmer, 1997) due to their daily and long piano practice. Thanks to their high level of expertise, professional pianists would not need to recruit extra neuronal networks to accomplish the visuomotor transformation and movement preparation which are required when performing a reproduction task. Thirdly, as a consequence of testing two hypotheses, a difference in functional connectivity between musically naïve subjects and professional pianists is foreseeable when the instructions provided are to observe with the purpose of replication or recognition. However, it is presumed that the difference between musically naïve subjects and professional pianists in the recognition task would be weaker than the difference detected in the reproduction task. Modifications in functional coupling would be mainly conjectured to occur in theta band (4–8 Hz) and in beta bands (20–30 Hz), since oscillations in these two bands play an important role during the retention of information (Hwang et al., 2005; Sarnthein et al., 1998, 1999; Stam et al., 2002; Tallon-Baudry et al., 1998).

Materials and Methods

Subjects

Ten right-handed professional pianists (eight males and two females; mean age = 25.2, $SD = 4.26$) and ten right-handed musically naïve subjects (six males and four females; mean age = 24.9, $SD = 3.78$) participated after providing written

informed consent. The professional pianists were classical pianists who possessed at least 10 years of musical training and on average, did 25 hours of piano practice per week. In contrast, the musically naïve subjects had no previous experience in playing any type of musical instrument. The subjects were assessed using the Edinburgh Handedness Inventory (Oldfield, 1971) and all were considered to be right-handed. No neurological or psychiatric disorders were observed in any of the subjects. The study was approved by the local institutional ethics committee.

Task

The task was a sequential finger movement which involved touching four times, the tip of the right thumb with the tip of the other right hand fingers with the hand in a supine position. There were 40 different movements with nonrepeated contact performed consecutively (e.g., 1321, 4312, 2423). 1 was the index finger, 2 the middle finger, 3 the ring finger, and 4 the little finger. These 40 movements were matched for difficulty. They were selected by drawing lots among the 108 possible movements. These 108 movements were determined by a combinatorial analysis ($9 \cdot 3 \cdot 4$) which took into account the fact that a movement should be composed of four taps and that repeated tap was not allowed. A final stage of this movement selection involved assessment of the difficulty or easiness in memorizing each movement by using a 5 point-Likert scale. This assessment was achieved by two musically naïve PhD students of the Department. Movements that were assessed as easy to remember (i.e., assessed 1 or 2) were discarded from the study and replaced by another movement which was selected by drawing lots.

Experimental Procedure

The experimental procedure comprised two parts: An EEG recording and an interview. The first part of the experimental procedure in the present study has been described in an

earlier paper (Calmels, Hars, Jarry, & Stam, 2010). More accurately, the current paper reported additional analysis of EEG data collected previously. In the earlier paper, the authors examined the cortical mechanisms during observation of sequential finger movements, whereas in the present study, mechanisms during the retention, the memorization of information related to the finger movements viewed previously were investigated. The investigated mechanisms, subjects, electrode montages, stages, sets of EEG data, and computation of functional coupling were different between the two studies.

During the EEG recording, the subjects sat in a darkened room with their pronated forearms lying on armrests. They were invited to complete three conditions with different videos and instructions. Altogether, 40 trials were included in each condition. Each trial was comprised of five separate stages which were displayed using a video monitor. Different screen colors (blue, amber, black, and red) helped the subject follow the procedure (see Figure 1). In the first condition (i.e., condition for replica), the subjects watched videos in which a human model performing a finger movement sequenced at 2 Hz from an egocentric perspective was displayed (stage 2). The instruction given to the subject in stage 1 (blue screen) was to observe the movement with the goal of replicating it at a later stage. After the movement observation (stage 2), the subject was asked to stay focused during 3.76 sec (stage 3, retention stage, amber screen) before performing the finger movement viewed previously (stage 4, black screen) (see Figure 1). In this condition, the subject observed 40 different finger movement sequences. In the second condition (i.e., condition for recognition), the subjects observed the same set of movement sequences that were displayed in the condition for replica, however, the instructions were different. The subject was invited to observe the movement with the goal of recognizing it at a later stage (stage 2). A 3.76 sec focusing period (stage 3, retention stage, amber screen) followed before the recognition task was performed (stage 4). A second video was presented and the subject had to determine whether this video was similar or dissimilar to that watched in stage 2. 50% of the videos were similar. Clenching or not clenching the fist was used to indicate the response in stage 5 (red screen).






Stages	Stage 1	Stage 2 (observation)	Stage 3 (retention)	Stage 4 (observation or execution)	Stage 5 (rest)
Stage duration	4s	3.24 s	3.76 s	3.24 s	6 s
Characteristics of the videos	Blue screen with or without instructions	Finger movements or picture of a pillow	Amber screen	Black screen or Finger movements	Red screen with or without instructions
Condition for replica	Observe to perform				
Condition for recognition	Observe to recognize				Answer
Control condition					

Figure 1. Schema for one trial according to condition.

The third condition was used as a control and was contrasted with the two experimental conditions by a subtracting procedure. In this control condition, instead of observing movements, the subject observed an object (i.e., pillow) in stages 2 and 4 (see Figure 1). Observing a background without a static hand stimulus was adopted based on the findings in the scientific literature. Grafton, Arbib, Fadiga, and Rizzolatti (1996) reported that observing a movement was better contrasted with the observation of an inert object than the observation of a static hand. More recently, Jonas et al. (2007) and Urgesi, Candidi, Fabbro, Romani, and Aglioti (2006) have suggested that viewing a stationary hand (suggesting a transition to action) was capable of activating motor related areas. Additional information concerning this experimental procedure can also be obtained in a companion paper (Calmels et al., 2010).

Synchronization between the EEG signal and the videos was carried out using a photoresistive diode which responded to the screen color change. The 120 trials (i.e., 40 trials for replica, 40 trials for recognition, and 40 trials for control) were randomized across time and distributed at random among four ten minute blocks. Each block was thus composed of 30 trials stemming from the three conditions. A five minute rest period separated each block. The experimenter monitored the accuracy of the movement performed in the observation condition for replica and the correctness of the answer provided in the observation condition for recognition. Incorrect answers were discarded from further analysis. The experimenter also verified that the subjects did not move their fingers during the observation and retention stages.

After the EEG recordings, interviews (Vermersch, 2003) were conducted to provide an opportunity to associate the subjective experience of the individual with more objective results stemming from a scientific investigation. The interviews ranged in duration from 10 to 15 minutes. The 20 subjects were asked to identify the strategies they had used during the retention phase (i.e., stage 3) and to assess the difficulty of the conditions for replica and recognition.

Data Acquisition and Recording

To investigate electrical brain activity, data were obtained using 19 electrodes (Fp1, Fp2, Fz, F7, F8, F3, F4, Cz, C3, C4, Pz, P3, P4, T3, T4, T5, T6, O1, and O2) mounted on an elastic lycra cap worn by each subject (Electro-cap International, Eaton, OH, USA). Mastoids were used for the reference electrodes and the ground electrode was positioned on the forehead. In addition, electro-oculograms (EOG) were also registered from the canthi of each eye (horizontal EOG) and the supra and infra orbital of the right eye (vertical EOG). Throughout the experimentation, electrode impedance was kept homogeneously below 5 k Ω and 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 and AD resolution was 16 bit.

Data Processing

EEG data were analyzed in five frequency bands (4–8 Hz, 8–10 Hz, 10–13 Hz, 13–20 Hz, and 20–30 Hz) and in the third stage, that is, retention stage (7.24–11 s). Ocular artifacts were corrected via Semlitsch, Anderer, Schuster, and Presslich's (1986) method where a regression analysis in combination with artifact averaging was used (Neuroscan 4.3 software).

To measure linear and nonlinear EEG activity (Friston, 2000), the index of synchronization provided by Stam and van Dijk (2002) was chosen. This index, called synchronization likelihood (SL), estimates the dynamical interdependencies between a time series and one or more other time series (Montez et al., 2006; Stam and van Dijk, 2002).

More specifically, the SL was computed between each single electrode and the 18 remaining electrode sites for each of the trials of the three conditions, both for each subject and frequency band. In other words, the SL describes how strongly an electrode site is synchronized to all the other electrode sites. The use of this technique and in this way has allowed researchers to successfully investigate functional connectivity (Gootjes, Bouma, van Strien, Scheltens, & Stam, 2006; Micheloyannis, Sakkalis, Vourkas, Stam, & Simos, 2005; Micheloyannis, Vourkas, Bizas, Simos, & Stam, 2003; Simos, Papanikolaou, Sakkalis, & Micheloyannis, 2002; Stam & van Dijk, 2002; Stam et al., 2002). The retention stage was considered for this computation.

The subsequent SL values obtained for the retention stage were averaged across trials at each electrode site for each subject, condition, and frequency band. To reduce the variability between subjects and electrodes (Andres et al., 1999; Classen, Gerloff, Honda, & Hallett, 1998; Gerloff et al., 1998; Leocani, Toro, Manganotti, Zhuang, & Hallett, 1997; Manganotti et al., 1998), the SL value under the control condition was subtracted from the SL value under the condition for replica as stated by the formula: $SL_{\text{final}} = SL_{\text{condition for replica}} - SL_{\text{control condition}}$ (Andres et al., 1998; Classen et al., 1998; Gerloff et al., 1998; Leocani et al., 1997; Manganotti et al., 1998). The same procedure was applied in the recognition condition. A positive SL_{final} value indicated a SL increase between control and experimental conditions, whereas a negative value represented a SL decrease. The subtraction of control SL values from experimental SL values was also undertaken. This was done to remove synchronizations which occurred during the control and experimental conditions and which were not related to the task to be performed, for example, the synchronization introduced by volume conduction (Rappelsberger, 1989). This procedure displays limitations in reducing the problem of volume conduction. Indeed, Nunez et al. (1997) and Srinivasan, Winter, Ding, and Nunez (2007) have shown that nearby EEG electrodes (i.e., distance inferior to 10 cm) were more prone to display substantial effects of volume conduction whereas distant EEG electrodes (i.e., distance superior to 20 cm) exhibited small volume conduction effects. Finally, this subtraction procedure mitigated the bias related to the synchronization inflation initiated by the reference electrodes (Classen

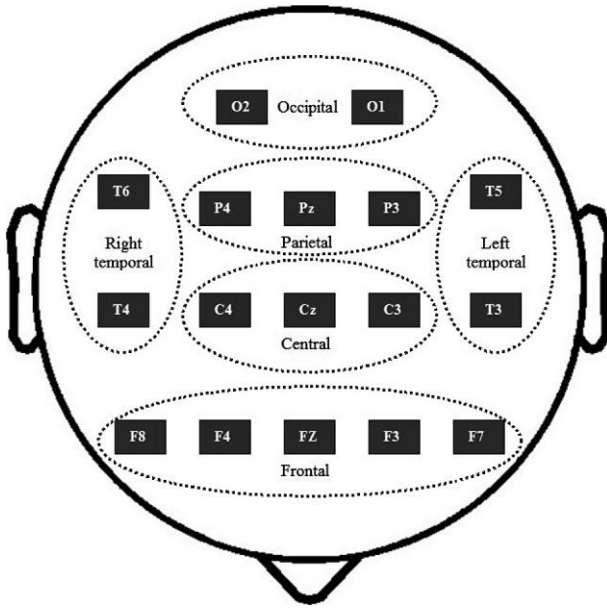


Figure 2. The six areas of interest.

et al., 1998; Fein, Raz, Brown, & Merrin, 1988; Rappelsberger & Petsche, 1988).

To reduce the degrees of freedom in the statistical analyses, SL_{final} from neighbouring electrode sites were averaged together to form six areas: occipital (O1, O2), parietal (P3, P4, Pz), central (C3, C4, Cz), frontal (F3, F4, F7, F8, Fz), right temporal (T4, T6), and left temporal (T3, T5) (see Figure 2). This averaging procedure has frequently been employed in other investigations (Gootjes et al., 2006; Micheloyannis et al., 2003, 2005; Simos et al., 2002; Stam & van Dijk, 2002; Stam et al., 2002) and the SL_{final} value obtained in a particular area represents the mean synchronization of the signal of this particular area with the signals of the whole scalp.

Statistical Analysis

All statistical analyses were performed using Statistica software 7.

2 (conditions) · 6 (areas) · 2 (groups) MANOVAs were completed for all the frequency bands. There were two within-subject factors; condition (two levels: replica, recognition); area (six levels: occipital area, parietal area, central area, frontal area, right temporal area, and left temporal area) and one between-subject factor; group (two levels: musically naïve subjects, professional pianists). Post hoc comparisons were made using Fisher's LSD test where MANOVA results were significant. Before the MANOVA computations, the normality of the data was checked using the Kolmogorov-Smirnov test. The MANOVAs were computed to determine within the areas of interest whether: (i) SL_{final} values during the condition for replica were significantly different to SL_{final} values during the condition for recognition in musically naïve subjects and in professional

pianists, (ii) SL_{final} values in musically naïve subjects were significantly different to SL_{final} values in professional pianists under the condition for replica and the condition for recognition.

Results

Qualitative Results

Regardless of condition, four (memory) strategies were identified as being used by the subjects during the retention stage. The first was mental imagery and was used by three musically naïve subjects. The second, subvocal rehearsal, was employed by one musically naïve subjects and two professional pianists. The third was an association of subvocal rehearsals and mental imagery. This association was used by six musically naïve subjects and two professional pianists. Finally, six professional pianists used no strategies. The majority of the subjects also perceived the condition for replica to be more difficult and felt they required more energy and concentration than the condition for recognition.

Behavioral Results

The performance data of the musically naïve subjects and professional pianists were examined. During observation for replica, the percentages of correct finger taps performed by the subjects were 82.50% for the musically naïve subjects and 96.75% for the professional pianists. This difference was statistically significant (Mann-Whitney, $U = 12$, $p = .002879$). During observation for recognition, the percentages were 90% for the musically naïve subjects and 99.25% for professional pianists. This difference was statistically significant (Mann-Whitney, $U = 12.50$, $p = .002879$). In musically naïve subjects, the percentages of correct finger taps under the observation for replica (82.50%) and under the observation for recognition (90%) were statistically different (Wilcoxon, $T = 0.00$, $p = .007686$). In professional pianists, this difference was not statistically different (96.75% vs. 99.25%).

Synchronization Likelihood Results

The EEG data were normally distributed. Results of the MANOVAs in each frequency band were provided in Table 1. Significant main effects for the Condition factor for the 10–13 Hz, 13–20 Hz, and 20–30 Hz bands were found (see Table 1). A Fisher's LSD post hoc test indicated that irrespective of area and group, the SL_{final} value during the condition for replica (.003472) was greater than SL_{final} value during the condition for recognition (.000418) ($p = .000031$) in the 10–13 Hz band. In the 13–20 Hz and 20–30 Hz bands, SL_{final} values were opposite in sign: positive under the condition for replica and negative under the condition of recognition (.000312 vs. -.00074,

Table 1. SL summary of the 2 (conditions) · 6 (areas) · 2 (groups) MANOVAs for each frequency band

	4–8 Hz		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>	<i>F</i>	<i>p</i>
Condition	0.225	.64	0.003	.95	30.323	****	8.429	*	23.724	***
Condition · Group	0.367	.55	0.018	.89	1.729	.20	0.050	.83	2.067	.17
Area	0.166	.97	2.342	*	0.529	.75	1.021	.41	12.078	****
Area · Group	1.363	.25	1.965	.09	1.615	.16	1.828	.11	0.917	.47
Condition · Area	0.552	.74	0.918	.47	4.956	***	4.380	**	15.910	****
Condition · Area · Group	1.410	.23	1.047	.39	0.344	.88	1.546	.18	3.539	**

Notes. **p* < .05. ***p* < .006. ****p* < .0005. *****p* < .00005.

p = .009479, 13–20 Hz band; .001097 vs. -.000626, *p* = .000123, 20–30 Hz band).

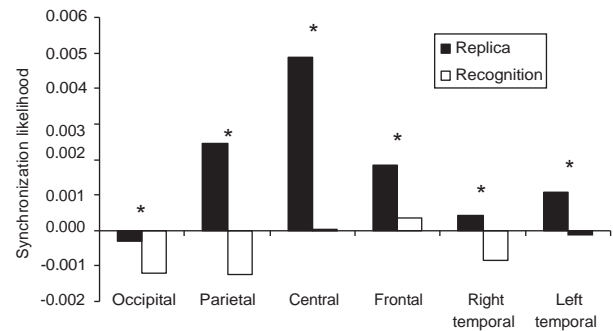
Significant effects for the Area factor were also detected for the 8–10 Hz and 20–30 Hz bands (see Table 1) but were not examined and reported since they were not directly linked to the goal of the study.

Significant Condition by Area interactions were observed for: (i) 10–13 Hz band, (ii) 13–20 Hz band, and (iii) 20–30 Hz band (see Table 1). These results were not investigated since these were not directed related to the goal of the study which focused on expertise. Moreover, if the interaction Condition by Area had been considered, it would have introduced a bias in the experimental procedure due to the lack of homogeneity of the subjects. Musically naïve subjects and professional pianists are very different when taking into consideration the strong ability of the latter to perform finger movements and to treat information collected during the observation of finger movements. Musically naïve subjects do not display such ability. This point was confirmed by the scores of correct finger taps obtained by the musically naïve subjects and professional pianists.

A significant Condition by Area by Group interaction was found for the 20–30 Hz band, $F(5, 90) = 3.539$, $p < .006$. No other significant results were revealed at any frequency bands (see Table 1).

Condition by Area by Group interaction was examined and Fisher's LSD post hoc tests revealed three results. First, during the retention stage and for the musically naïve subjects, significant differences between the condition for replica and the condition for recognition were reported within the occipital, parietal, central, frontal, right temporal, and left temporal areas (Occipital, $p = .024539$; Parietal, $p = .000000$; Central, $p = .000000$; Frontal, $p = .000355$; Right temporal, $p = .00202$; Left Temporal, $p = .003264$) (see Figure 3). SL_{final} values were greater in the condition for replica compared to those obtained during the condition for recognition. More specifically, in the central and frontal areas, SL_{final} values were higher in the condition for replica. In the parietal, right, and left temporal areas, they were opposite in signs: positive under the condition for replica and negative under the condition for recognition. In the occipital area, the negative SL_{final} value obtained under the condition for replica was weaker when compared to that obtained under the condition for recognition (see Figure 3). Second, in the professional pianists, significant differences between the two conditions were also detected within the

(a) Musically naïve subjects



(b) Professional pianists

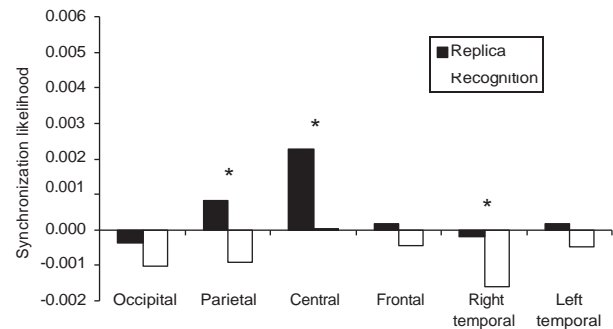
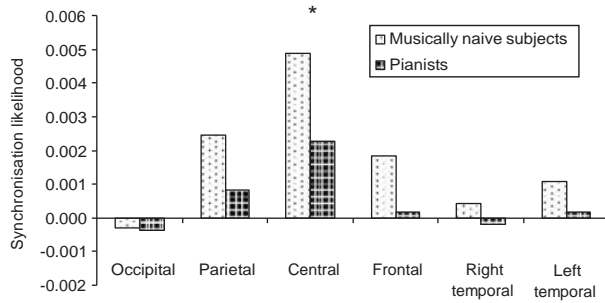


Figure 3. (a) SL_{final} values in the 20–30 Hz frequency band in musically naïve subjects during the retention stage under the condition for replica and the condition for recognition. (b) SL_{final} values in professional pianists under the two conditions. Asterisks (*) indicate statistically significant differences between condition for replica and condition for recognition.

parietal, central, and right temporal areas. In the parietal area, SL_{final} values were opposite in sign: positive under the condition for replica and negative under the condition of recognition ($p = .000042$). In the central area, SL_{final} value in the condition for replica was higher compared to SL_{final} value in the condition for recognition ($p = .000000$). In the condition for replica and within the right temporal area, the negative SL_{final} value was weaker when compared to that obtained under the condition for recognition, (Right Temporal, $p = .000736$; see Figure 3). Third,

(a) Condition for replica



(b) Condition for recognition

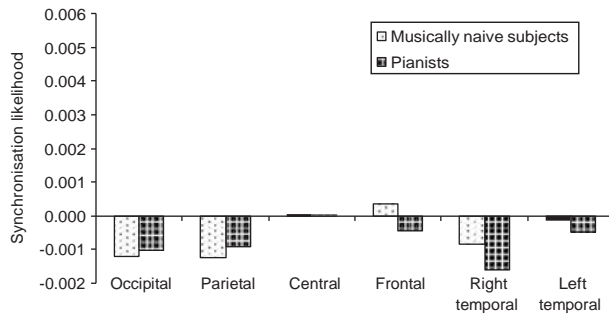


Figure 4. (a) SL_{final} values in the 20–30 Hz frequency band under the condition for replica in musically naïve subjects and professional pianists. (b) SL_{final} values under the condition for recognition in musically naïve subjects and professional pianists. Asterisks (*) indicate statistically significant differences between musically naïve subjects and professional pianists.

a significant difference was identified under the condition for replica between musically naïve subjects and professional pianists within the central area (Central, $p = .031378$). Musically naïve subjects had higher SL_{final} values in comparison to professional pianists (see Figure 4).

Discussion

The aim of the present study was to examine EEG functional connectivity when expert and nonexpert individuals in manual dexterity retain motor representations in memory to subsequently perform a recognition or a reproduction task. The reader should bear in mind that caution must be exerted when interpreting the results of this study. Stimuli presented to subjects (i.e., biological movements) were different to those reported in the classical working memory literature (i.e., verbal, visual, or semantic content). Results based on EEG signals do not reflect similar aspects of cortical activity obtained by other neuroimaging techniques, such as fMRI and Positron Emission Tomography (PET). Attention should also be paid to the different techniques employed to treat the EEG signal.

EEG Activity

The presence of functional connectivity differences in upper beta frequency band (i.e., 20–30 Hz) is in accordance with the results from earlier studies. Previous studies have shown that beta oscillations are related to the retention of information and more specifically to the rehearsing process of the sensory trace in memory (Tallon-Baudry, Bertrand, & Fischer, 2001; Tallon-Baudry et al., 1998, 1999). This point is corroborated by the subjects' reports. Most of the subjects stated the use of mental imagery and subvocal rehearsal to remember the movement during the retention stage. In the same vein, research by Hwang et al. (2005) also showed that the process of subvocal rehearsal was linked to beta activity.

Functional Connectivity in the Retention Stage Among Musically Naïve Subjects

In accordance with our first hypothesis, functional connectivity was greater when musically naïve subjects were invited to remember the observed movement in order to reproduce it at a later stage. This result could be explained by the cost of the mechanisms, such as the response preparation and the visuomotor transformation, which are required under the condition for replica and needless under the condition for recognition. Operations to perform under the condition for replica can be perceived as more demanding than those to be achieved under the condition for recognition. Subjects may thus allocate most of their attention to the most demanding condition (i.e., condition for replica). This suggestion is supported by the subjective reports of the subjects. One musically naïve subject declared that condition for replica was more difficult than condition for recognition because the former required a motor transfer. The other musically naïve subjects reported that the former condition required more energy and attention.

This result observed in musically naïve subjects is also in line with research by Pochon et al. (2001) and Curtis, Rao, and d'Esposito (2004). These authors reported greater activity in Brodmann Area 46 when individuals could prepare the forthcoming response compared to when they could not. More specifically, Pochon et al. (2001), using a fMRI paradigm, have shown that when subjects were invited to reproduce a previously viewed visuospatial sequence, the dorsolateral prefrontal cortex was activated during the retention period. This was not the case when the same subjects had to perform a recognition task, since these only had to maintain the information in memory and not to prepare, to program a response.

Finally, the result related to the great synchronization within the central area and under the condition for replica is consistent with the findings reported by Pfurtscheller's research group (Pfurtscheller & Lopes da Silva, 1999; Pfurtscheller, Stancak, & Edlinger, 1997). The authors demonstrated that central beta activity reflected motor preparation. In the 15–26 Hz frequency band, a power decrease was observed in the contralateral sensorimotor areas at

2.5 s before the onset of the movement, which spread to the ipsilateral side immediately prior to the beginning of the movement. As underlined by Curtis and d'Esposito (2003) and Passingham and Sakai (2004), motor preparation is a mechanism which takes place during the retention period when subjects have to remember spatial locations in order to recall them. This mechanism or operation can reflect different EEG activities occurring at different scale levels: a local level like the results described by Pfurtscheller and co-workers and an interregional level like the great synchronization observed in the present study.

Functional Connectivity in the Retention Stage Among Professional Pianists

Contrary to our second hypothesis, the data do not tend to provide evidence for a complete functional connectivity equivalence when the pianists had to maintain the movement in memory for replica and when they held it in memory for recognition. Parietal, central, and right temporal areas displayed significant differences between these two conditions. One may believe that the many years of training in pianists could have brought about an increase in the efficiency of the neuronal system by a reduction of the processing treatment (Haslinger et al., 2004; Krings, Töpper et al., 2000; Meister et al., 2005). Skills required in musical training include processing complex visuomotor transformation (Palmer, 1997) learned by observation in order to reproduce the teacher's actions (Haslinger et al., 2005). The pianists were thus used to retaining behaviors in representational forms in memory in order to reproduce them in a short time delay and to processing visuomotor transformations. This expertise, gained throughout the years, could induce a nil cost to process the visuomotor transformation and response preparation during the retention stage. This explanation concurs with the results obtained from the analysis of the occipital, frontal, and left temporal areas. However, the reasons for the functional connectivity difference between the two experimental conditions within the parietal, central, and right temporal areas remain to be explained.

First, the difference between the two conditions within the central area, an area known to be devoted to control the selection and preparation of motor program, is mainly due to the positive value of synchronization under the condition for replica and the near zero synchronization value under the condition for recognition. The high and positive value of synchronization in the central area can be explained by the fact that the sequential finger to thumb opposition movements used in this study did not really represent piano hand movements though they can be perceived as a closed piano-related task by the professional pianists. The former movement is performed in a supine position and involved making contacts between fingers whereas the latter is performed in a prone position and is characterized by up and down movements of the fingers when striking keys. In consequence, it can be suggested that if the present task had been a piano hand movement, the central synchronization under the condition for replica would have been weaker and close to the zero level since piano movements are

more familiar and meaningful to the pianists than finger opposition movements. This hypothesis has yet to be tested.

Second, the differences between the two conditions within the parietal and right temporal areas are the consequences of near zero synchronization values under the condition for replica and negative values of synchronization under the condition for recognition. These negative values express synchronization decreases to below the level of the control condition which is a resting/an idling state. It can be suggested that a negative pattern of synchronization may be interpreted as an inhibitory state. Inhibition may be used: (i) to inhibit information which is irrelevant to the task to be performed, and/or (ii) to block information related to previous trials to prevent interference during the retention of new information. This suggestion has yet to be verified.

Expertise

The third hypothesis is partially validated. First, a functional connectivity difference between musically naïve subjects and professional pianists was observed within the central area when subjects maintained movement information in memory with the purpose of later reproduction. Synchronization in professional pianists is two times less than synchronization in musically naïve subjects. This synchronization difference may be due to mechanisms related to visuomotor transformation and response preparation (Passingham & Sakai, 2004) which display differences according to the (musical) expertise of the subjects. It can be suggested that the neuronal system of musically naïve subjects is not as efficient or, "economic" as that of professional pianists. From very early on, the latter are used to dealing with visuomotor transformations and response preparations from their earliest years.

Second, when subjects held movement information in memory with the purpose of later recognition, the lack of functional connectivity difference between the musically naïve subjects and the professional pianists may be explained by the low demand required to perform the recognition task. During the retention period and under the condition for recognition, the subjects maintained sensory information in memory. No operations in relation to motor response preparation or visuomotor transformation were required since the recognition task does not require motor output. No operations such as the mental rearrangement described by Sauseng et al. (2005), which was accompanied by stronger coupling, were involved in the present case. The musically naïve subjects and the professional pianists were not instructed to achieve a mental transformation on the viewed stimulus and did not need to perform this transformation since the viewed stimulus was displayed from an egocentric perspective. In summary, the mental operations performed under the condition for recognition could be characterized by the few memory processes that need to be achieved compared to under the condition for replica. Subsequently, it can be suggested that the low task demand, when the subjects have to maintain movement information in memory with the aim of subsequent recognition, makes

the task insensitive to differences such as the level of expertise. This suggestion is on line with the near zero synchronization values within the central, frontal, and left temporal areas and the negative patterns of synchronization within the occipital, parietal, and right temporal areas observed in both groups. These values and patterns may have reflected the easiness of the performed tasks. For example, the use of longer movement sequences, perhaps even several levels of difficulty, may have better involved working memory processes. This issue warrants further investigation.

Conclusion

In conclusion, this study presents strengths, such as the use of a non-linear measure to assess functional connectivity or the choice of the goal of the study, which, to our knowledge, has not yet been investigated. The results showed modifications in functional connectivity in the 20–30 Hz frequency band. More specifically, functional connectivity, within the occipital, parietal, central, frontal, right, and left temporal areas, was greater when musically naïve subjects were required to retain a movement in order to subsequently reproduce it compared to the condition in which they were asked to recognize it. In professional pianists, incomplete connectivity equivalence was detected between the two conditions. A difference in functional connectivity, between musically naïve subjects and professional pianists, was also observed within the central area when subjects maintained movement information in memory with the purpose of later reproduction. This was not the case when these subjects held movement information in memory with the purpose of later recognition. In summary, the findings indicate that instructions and expertise have an influence on functional connectivity during the retention stage and that task demand could also explain some of the results of the present study. These results have allowed some light to be shed on working memory processes. More specifically, the 20–30 Hz functional connectivity increase in the central area may be related to a stronger involvement of visuomotor transformation and response preparation in musically naïve subjects compared to professional pianists, suggesting that the SL index is a suitable tool to test the impact of expertise on some aspects of working memory.

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