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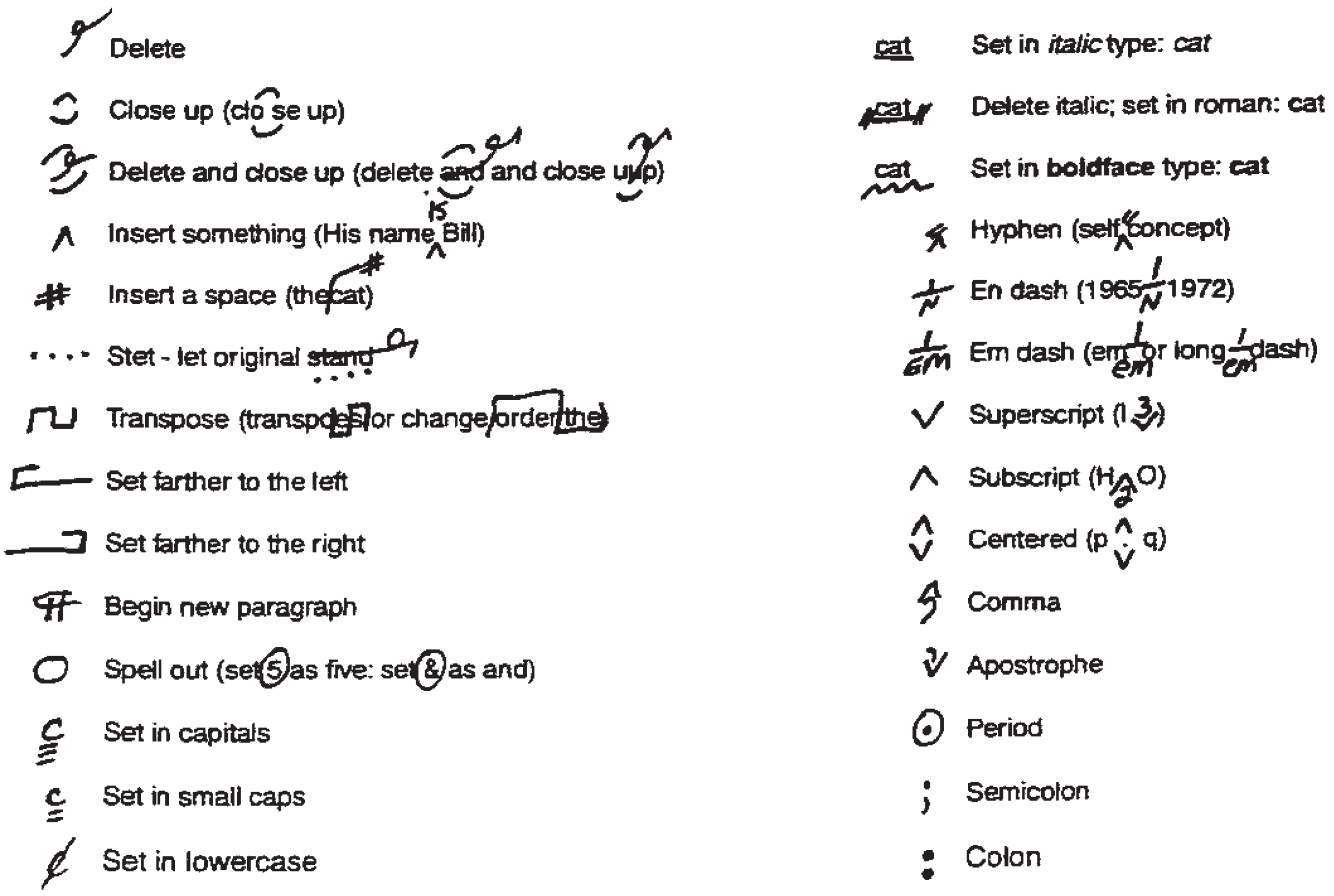

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Functional Frontoparietal Connectivity During Short-Term Memory as Revealed by High-Resolution EEG Coherence Analysis

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In this electroencephalographic study, the authors modeled the functional connectivity between frontal and parietal areas during short-term memory (STM) processes by spectral coherence analysis and the directed transfer function, that is, for the estimation of coherence “direction.” A no-STM task was used as a reference. STM was characterized by an increased frontoparietal electroencephalograph coherence at high frequencies (beta and gamma, 14–45 Hz). In the control task, parietal-to-frontal flow prevailed at those frequencies. However, the STM task showed a bidirectional frontoparietal flow at the gamma band. In conclusion, frontoparietal connectivity would optimize “representational” memory during STM. In this context, the frontal areas would increase their influence on parietal areas for memory retention.

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Language comprehension, reasoning, and decision making are all based on short-term memory (STM) processes. These can be easily investigated by delayed reaction time tasks (Goldman-Rakic, 1987), in which the subject is asked to retain a rapidly disappearing cue stimulus, which is necessary to give a correct motor response after a delayed go signal. In the "proper STM variant" of the task, the cue stimulus rapidly disappears, whereas in the control variant, the cue stimulus is delivered along the whole delay period, so that no STM load is present but motor responses are similar. Neurobiological correlates of the delayed reaction time tasks have been extensively investigated in nonhuman primates (Funahashi, Bruce, & Goldman-Rakic, 1989, 1990; Funahashi, Inoue, & Kubota, 1993; Mishkin, 1957). Both prefrontal and posterior parietal areas play a key role in the maintenance of the "representational memory" during the delay period (Butters & Pandya, 1969; Goldman-Rakic, 1988; Funahashi et al., 1989, 1990, 1993; Fuster, 1995; Kessels, Postma, Wijnalda, & de Haan, 2000; Mishkin, 1957). In addition, lesion studies in rats have shown that the delayed reaction time tasks rely on complex loops encompassing cortex, thalamus, and basal ganglia (Burk & Mair, 1998; Mair, Burk, & Porter, 1998).

In humans, functional magnetic resonance imaging and positron emission tomography scans during spatial STM disclosed activity in inferior and middle frontal areas, as well as in premotor, posterior parietal, and occipital ones (Berman & Weinberger, 1990; Grasby, Frith, Friston, Frackowiak, & Dolan, 1993; Jonides et al., 1993; McCarthy et al., 1994, 1996; Nagahama et al., 1996). Recently, thalamocortical activity during delayed reaction time tasks was also investigated by electroencephalographic (EEG) studies (Bastiaansen, Posthuma, Groot, & De Geus, 2002; Filipovic, Jahanshahi, & Rothwell, 2001) based on event-related changes in brain rhythmicity (Basar, 1998, 1999). It has been postulated that brain electromagnetic oscillations, especially in the alpha band (around 10 Hz), express the efficiency (i.e., gating) of information transfer through the thalamus toward the cortex (Brunia, 1999). The reduction in power density of "idling" alpha rhythms (or event-related desynchronization; ERD) is proportional to neuronal resources allocated in task-related processing (Pfurtscheller & Lopes da Silva, 1999).

A recent EEG study (C. Babiloni et al., 2004) on young adults showed that frontoparietal theta and alpha ERD and event-related synchronization (ERS) appear even during a very simple STM load (one bit), such as the one induced by a delayed-choice reaction time task. During STM, the theta power (4–6 Hz) decreased in left frontal and bilateral parietal areas compared with the control condition. Furthermore, the low alpha power (6–8 Hz) decreased in bilateral frontal and left parietal areas, whereas the high alpha power (10–12 Hz) decreased in the left frontoparietal areas. According to the current interpretation of brain rhythms, the decrement of theta power would reflect the inhibition of (para)hippocampal–cortical circuits' focus on selective memorization processes. These processes might be revealed by the concomitant decrement of the alpha power as an expression of an efficient information transfer within thalamocortical pathways.

It is noteworthy that the EEG analysis of the mentioned ERD–ERS study (C. Babiloni et al., 2004) did not allow the formation of any mechanistic hypotheses about the functional coupling between frontal and parietal activities during the memorization process. Indeed, no evidence has yet been provided that, once activations have been found in two (or more) cortical areas, they work in a coordinated manner or that one area is functionally more relevant than the others within the whole network. These are important issues, as cognitive functions are based on the activation of specific networks in which cortical regions are engaged in a hierarchical manner.

The present EEG study, therefore, addressed the working hypothesis of whether frontal and parietal areas are involved in a coordinated mode, even in the case of a very simple memorization process. Furthermore, because prefrontal cortex plays a major role both in STM and delayed reaction time tasks (Funahashi et al., 1989, 1990, 1993; Mishkin, 1957), a second aim was to investigate the possible leading role of frontal areas in the memorization, rather than control, process. The EEG data set on which spectral coherence and directed transfer function (DTF) were computed was the same one previously used to model the functional connectivity between frontal and parietal areas during STM processes (C. Babiloni et al., 2004). Indeed, significant coherence between EEG electrodes overlying two brain regions has been previously interpreted as evidence of functional coupling (Gerloff et al., 1998; Thatcher, Krause, & Hrybyk, 1986), mutual information exchange (Rappelsberger & Petsche, 1988), functional coordination (Gevins et al., 1998), and integrity of connection pathways (Locatelli, Cursi, Liberati, Franceschi, & Comi, 1998). On the other hand, DTF has been recently used to estimate the "direction" of the information flow between electrodes (C. Babiloni et al., 2003; Mima, Matsuoka, & Hallett, 2000). The DTF method is a multichannel parametric method of EEG analysis suitable to the aim of the present study, given that its validity relies on data from several experimental conditions. For instance, this approach, applied to intracerebral EEG data, provided an accurate reconstruction of the temporal propagation of epileptic activity in humans (Franaszczuk, Bergey, & Kaminski, 1994). Furthermore, reliable solutions of the DTF method have been reported on the basis of surface EEG data related to voluntary movements (C. Babiloni et al., 2003; Mima et al., 2000). Finally, the DTF method has been applied to the study of the functional relationships among hippocampus, entorhinal–piriform area, subiculum, and lateral septum in the rat (Korzeniewska, Kasicki, Kaminski, & Blinowska, 1997). It has been shown that the pattern of EEG intracranial activity propagation depended on the type of behavior and on the difficulty of the task performed by the animal, thus confirming and extending previous notions on the functional properties of the abovementioned cognitive neural network (Korzeniewska et al., 1997).

Method

Subjects, EEG Recordings, and Preliminary Data Analysis

The present EEG data were recorded during a previous study focused on the theta and alpha ERD during the STM processes (C. Babiloni et al., 2004). For the readers' convenience, procedures of subject selection, EEG recordings, and preliminary data analysis are reported in the following paragraphs. Experiments were performed in 14 healthy, right-handed adult volunteers. The mean age was 30.1 years (± 1.4 *SE*), the mean education level 12.6 years (± 1.1 *SE*), and the mean handedness score 92.5% (± 0.9% *SE*). Subjects were seated in a comfortable reclining armchair placed in a dimly lit, sound-damped, and electrically shielded room. They kept their forearms resting on the armchair, with the right index finger resting between two buttons spaced 6 cm apart. A computer monitor was placed in front of them (approximately 100 cm). The experiment included the STM and no-STM (NSTM) tasks performed in pseudorandom separate recording blocks. The STM task included a sequence consisting of baseline stimulus (0.7° cross placed at the center of the monitor), visual warning stimulus (the cross was surrounded by a circle for 1 s), visual cue stimulus (two vertical bars beside the fixation point; each vertical bar was approximately 2° wide and 2.5–7.0° high and was displayed for 2 s), delay period (blank screen for 3.5–5.5 s), go stimulus (a circle appearing for 1 s), and right finger movement to press the proper button. Subjects were instructed to click the left mouse button if the taller bar (cue stimulus) appeared at the left side of the monitor, and the right mouse button if the taller bar was at the right side of the monitor. In the NSTM condition, the visual cue stimulus was presented until the go stimulus appeared. Two blocks for each condition were pseudorandomly intermingled (block = 50 single trials; 2-min pause). Subjects were told in advance whether the block was NSTM or STM. The global luminance of the monitor was kept constant across the two conditions (i.e., the changes of the scene were limited to the bars' shape) and was measured directly on the monitor by a Tektronic J17 & J1800 Series LumaColor photometer.

Before the recording session, subjects underwent a training period of approximately 10 min to familiarize them with both the experimental apparatus and the tasks.

EEG data were recorded in continuous mode (0.1–60.0-Hz bandpass, 256-Hz sampling frequency) with a 46 tin electrode cap referenced to linked ears. Electrooculogram (0.1–60.0-Hz bandpass, 256-Hz sampling frequency) and surface electromyographic activity of bilateral extensor digitorum muscles (0.1–60.0-Hz bandpass, 256-Hz sampling frequency) were also collected. The EEG single trials associated with incorrect cognitive performance and artifacts (eye movement, etc.) were discarded. Spatial resolution of artifact-free EEG data was enhanced by surface Laplacian estimation (F. Babiloni, Carducci, Babiloni, & Urbano, 1998; F. Babiloni et al., 1996).

The EEG epochs were automatically and manually rejected. The computerized automatic procedure was based on a software package that included automatic procedures for (a) electrooculogram artifact detection and correction, (b) electromyogram analysis, (c) EEG artifact analysis, and (d) optimization of the ratio between artifact-free EEG channels and trials to be rejected. Rejection criteria were based on a threshold method and on a statistical method that evaluated the nonstationarity of the EEG signal (Moretti et al., 2003). Then, two expert electroencephalographists manually confirmed the automatic selections (interrater reliability higher than 95%). The EEG epochs contaminated by these artifacts were removed. Spatial resolution of artifact-free EEG data was enhanced by surface Laplacian estimation (regularized 3-D spline function; F. Babiloni et al., 1996, 1998). It should be noted that the surface Laplacian estimation acts as a spatial filter that reduces head-volume conductor effects and annuls electrode reference influence (F. Babiloni et al., 1996; Nunez, 1995). In some cases, the Laplacian values at the border electrodes were set to zero as a result of the unreliability of the spline Laplacian estimate at these sites.

The single-trial analysis was carefully repeated on the Laplacian-transformed EEG data in order to discard those trials contaminated by any residual computational artifacts. In 2 out of 14 subjects, the number of artifact-free EEG single trials was very low (i.e., less than 30% of the individual data set). Consequently, the EEG data of the remaining 12 subjects were further considered for the final data analysis. The mean of the artifact-free EEG data was 82 (± 12 *SE*) single trials for the STM task and 68 (± 10 *SE*) single trials for the NSTM task: no statistical difference, $F(1, 11) = 2.75$, $p = .15$. Motor reaction times after the go stimulus were computed for all the artifact-free EEG single trials.

Estimation of Functional Connectivity: Between-Electrode Coherence Analysis

EEG coherence is a normalized measure of the coupling between two EEG signals at any given frequency (Leocani & Comi, 1999; Pfurtscheller & Andrew, 1999; Rappelsberger & Petsche, 1988). The coherence values were calculated for each frequency bin by Equation 1

$$Coh_{xy}(\lambda) = |R_{xy}(\lambda)|^2 = \frac{|f_{xy}(\lambda)|^2}{f_{xx}(\lambda)f_{yy}(\lambda)}. \tag{1}$$

Equation 1 is the extension of the Pearson's correlation coefficient to complex number pairs. In this equation, *f* denotes the spectral estimate of two EEG signals *x* and *y* for a given frequency bin (λ). The numerator contains the cross-spectrum for *x* and *y* (f_{xy}), and the denominator contains the respective autospectra for *x* (f_{xx}) and *y* (f_{yy}). For each frequency bin (λ), the coherence value (Coh_{xy}) is obtained by squaring the magnitude of the complex correlation coefficient *R*. This procedure returns a real number between 0 (no coherence) and 1 (maximum coherence).

The EEG coherence between electrodes was computed only from electrodes of a 10–10 system montage overlaying dorsolateral prefrontal (F3, F4) and posterior parietal (P3, P4) cortical areas. At these internal electrodes, the spline surface Laplacian estimate from the spatial information content of 46 electrodes can be considered as highly reliable (Nunez, 1995; Perrin, Pernier, Bertrand, & Echallier, 1989). In particular, the between-electrode EEG coherence for the evaluation of functional frontoparietal connectivity was computed from F3 to P3 and F4 to P4. As a control, EEG coherence between F3 and F4 and between P3 and P4 was computed. The between-electrode EEG coherence was calculated at the "rest" period (from −2 to −1 s) and during two contiguous 1-s periods of the retention period for STM: T1 (from +2 to +3 s) and T2 (from +3 to +4 s). Corresponding periods were considered for the NSTM task. For the sake of simplicity, we referred to *retention period* as both the delay period of STM and the 2-s period beginning after the cue stimulus for NSTM.

Coherence was computed at the theta (4–7 Hz), alpha (8–13 Hz), beta (14–30 Hz), and gamma (30–45 Hz) bands, as previous studies have shown that the functional connectivity, as revealed by EEG coherence, can be observed over a wide frequency range (Sarnthein, Petsche, Rappelsberger, Shaw, & von Stein, 1998; von Stein, Rappelsberger, Sarnthein, & Petsche, 1999; von Stein & Sarnthein, 2000). A visual inspection of the individual coherence spectra confirmed the presence of substantial EEG coherence values in all subjects except 1. However, the low values of this subject's coherence were not against the direction of the group results, thus the statistical analysis was performed on coherence data of all the subjects.

Estimation of the Direction of the Functional Connectivity: Mvar Model

The so-called Mvar model was used to estimate the direction of the information flow between frontoparietal electrodes (F3–P3, F4–P4). This model was applied to the frequency bands in which significant event-related coherence (ERCoh) values were found for NSTM versus STM conditions (retention periods). The mathematical core of the algorithm was based on the ARfit programs running on the Matlab platform (Matlab 5.3, The Mathworks, Natick, MA). The model order was 7, and the goodness of fit was indicated by the values of Noise Matrix V of the Mvar model. In previous experiments, the Mvar model has been successfully used to estimate the direction of the information flow from cortical to spinal neurons as revealed by spectral coherence of EEG data (C. Babiloni et al., 2003; Mima, Matsuoka, & Hallett, 2001).

The Mvar model is defined as

$$\sum_{j=0}^{p} A_j X_{t-j} = E_t,$$

EQ: 1

where X_t is the L-dimensional vector representing the L-channel signal at time t, E_t is the white noise, A_j is the L × L matrix of model coefficients, and p is the number of time points considered in the model. From the identified coefficients of the model A_j, spectral properties of the signals can be obtained by the following z-transformation of the above equation: $X(z) = H(z)\ E(z)$, where $H(z)$ is a transfer function of the system and

$$H(z) = \left(\sum_{j=0}^{p} A_j Z^{-j} \right)^{-1}$$

$$z^{-i} = \exp(-i2\pi f dt)$$

The spectral matrix $S(f)$ can be obtained as $S(f) = X(f)\ X(F)^* = H(F)V\ H(f)^*$, where V is the residual white noise.

Because the transfer function $H(f)$ is not a symmetric matrix, the information transmission from the jth to the ith channel is different from that from the ith to the jth channel. The DTF from the jth channel to the ith channel is defined as the square of the element of $H(f)$ divided by the squared sum of all elements of the relevant row.

$$DTF_{ij}(F) = \frac{|H_{ij}|^2}{\sum_{m=1}^{L} |H_{im}(f)|^2}.$$

Before computing DTF, EEG data were preliminarily normalized by subtracting the mean value and dividing by the variance, according to requirements by Kaminski and Blinowska (1991). Therefore, DTF can be considered as a normalized value ranging from 0 to 1. A substantial difference between $DTF(f)_{ij}$ and $DTF(F)_{ji}$ may suggest an asymmetric information flow from the Electrode i to Electrode j. When $DTF(f)_{ij}$ is greater in magnitude than $DTF(F)_{ji}$, the direction of the information flow would be from Electrode j to Electrode i. Conversely, when $DTF(F)_{ji}$ is greater in magnitude than $DTF(f)_{ij}$ information flow would be from Electrode i to Electrode j.

Statistical Analysis

Statistical NSTM and STM comparisons were performed by analysis of variance (ANOVA) for repeated measures. Mauchley's test, evaluating the sphericity assumption and correction of the degrees of freedom, was performed by means of the Greenhouse–Geisser procedure. Duncan's test was used for post hoc comparisons ($p < .05$).

Dependent variables for the evaluation of behavioral aspects were the percentage of correct responses and the type of errors. For errors, the ANOVA included the variables condition (NSTM, STM) and error type (wrong responses, no response, delayed response), whereas for the evaluation of movement reaction time, only condition (NSTM, STM) was used. In the parallel study (C. Babiloni et al., 2004), no statistical differences ($p = .45$) in correct responses emerged between conditions (95% and 93% for the NSTM and STM tasks, respectively), nor were there statistical differences in the error type ($p = .47$). Finally, reaction times were shorter ($p < .007$) during the NSTM (604 ms) than the STM (650 ms) condition.

Statistical analysis of the event-related EEG coherence was carried out by means of two four-way ANOVAs focused on the comparison of the coherence values between the NSTM and STM conditions with the same extension as frequency bands. Of note, the comparison of the coherence values at different frequencies within a certain condition would have been biased by the differences in extension of the bands of interest. The first ANOVA design included the variables condition (NSTM, STM), side (taller bar on the left, taller bar on the right), band (theta, alpha, beta, gamma), electrode pair (F4–P4, F3–P3), and time (T1, T2), to test the functional frontoparietal connectivity. The second ANOVA design evaluated the specificity of results obtained with the first ANOVA. As a control, the second ANOVA included the variables condition (STM, NSTM), side (taller bar on the left, taller bar on the right), band (theta, alpha, beta, gamma), electrode pair (F3–F4, P3–P4), and time (T1, T2), to test the functional connectivity between the two hemispheres.

Statistical analysis of the DTF values (direction of the information flow) was performed by applying a four-way ANOVA for each frequency band showing significant coherence values. The ANOVA design included the variables condition (NSTM, STM), direction (frontal to parietal, parietal to frontal), electrode pair (F3–P3, F4–P4), and time (T1, T2).

Results

Power Density Spectra

F1 For illustrative purposes, Figure 1 plots the grand average power density spectra computed by standard fast Fourier transform methods from frontal and parietal (F3, F4, P3, P4) electrodes for the NSTM and STM conditions, at rest period and during the two retention-period intervals (T1, T2). During the rest period, these spectra showed an evident alpha peak, which was reduced in power during the retention periods. During those periods, beta frequency values also decreased in power. These results provided support to the reliability of the present EEG Laplacian estimates.

Functional Connectivity as Revealed by Spectral Coherence Between Electrodes

F2 Figure 2 illustrates the grand average of ERCoh spectra computed from laterolateral (F3–F4, P3–P4) and frontoparietal (F3–P3, F4–P4) electrode pairs during T1 and T2 periods of the NSTM and STM conditions. The event-related coherence, computed in T1 and T2, resulted from the difference of T1 and T2 coherences with respect to the coherence at rest period. The functional frontoparietal connectivity prevailed for STM rather than NSTM during the late phase (T2) of the retention period, when the target stimulus was presumably being rehearsed. These activities disappeared in the control condition (NSTM), when no memory engagement was required. This occurred at the higher frequencies, such as beta (14–30 Hz) and gamma (30–45 Hz).

T1 Table 1 shows the individual EEG coherence frequencies (alpha, beta, and gamma) relative to F3–F4, P3–P4, F3–P3, F4–P4 electrode pairs for the NSTM and STM conditions. The table also reports the mean and the standard error across subjects. These frequencies showed the maximal coherence values observed within alpha, beta, and gamma bands of interest during the T1 and T2 periods. Of note, the theta band was too narrow in frequency (4–7 Hz) for an individual selection of the peak coherence values. No statistical difference ($p > .05$) was observed among individual coherence frequencies for frontoparietal electrodes (F3–P3, F4–P4) in the NSTM and STM conditions.

F3 Figure 3 illustrates the results of the ANOVA analysis that compared ERCoh of the variables condition (NSTM, STM), side (taller bar at left, taller bar at right), band (theta, alpha, beta, gamma), electrode pair (F3–P3, F4–P4), and time (T1, T2), to test the functional frontoparietal connectivity, $F(3, 33) = 3.09$, $p < .04$. Duncan's post hoc testing indicated that, for the T2 period, ERCoh between left frontoparietal electrodes (F3–P3) was stronger for the STM condition than for the NSTM condition at beta ($p < .05$) and gamma ($p < .001$) bands. Meanwhile, the ERCoh between right frontoparietal electrodes (F4–P4) was stronger for

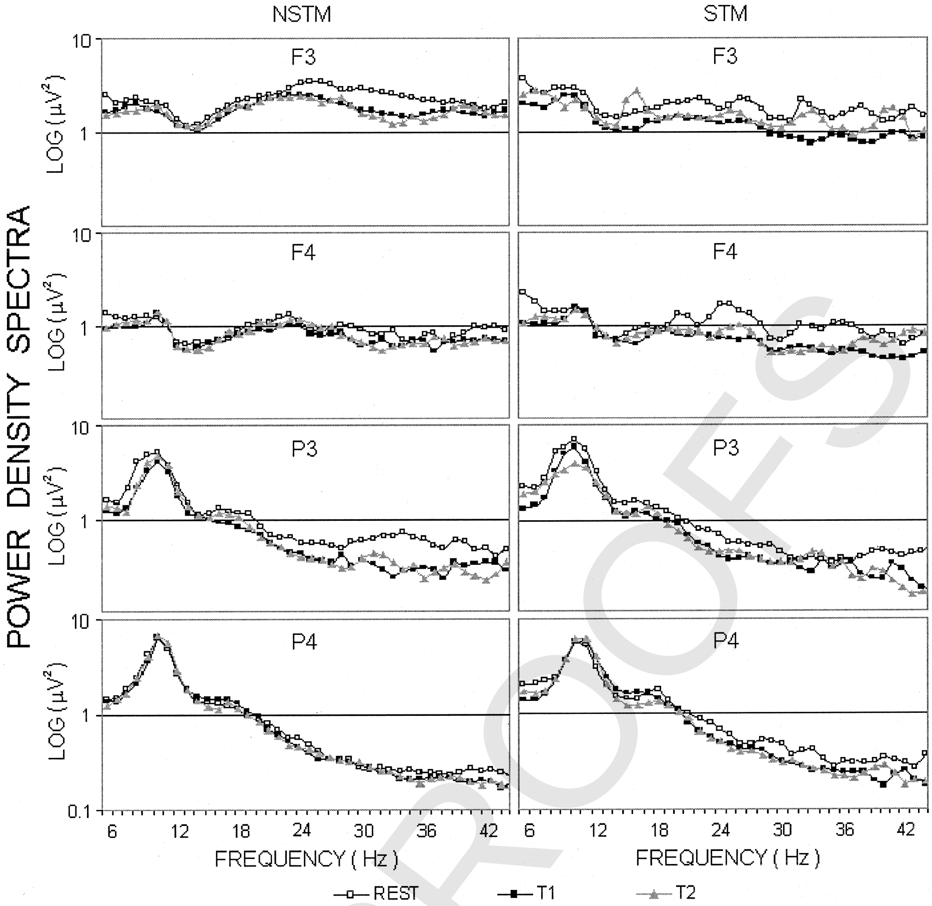

Figure 1. Grand average power density spectra computed from frontoparietal (F3–P3, F4–P4) and laterolateral (F3–F4, P3–P4) electrodes for no short-term memory (NSTM) and short-term memory (STM) conditions, at rest period and during the two time intervals of the retention period (T1, T2)

the STM condition than for the NSTM condition only at the gamma band ($p < .05$). These findings appeared to be specific for pairs of frontoparietal electrodes, given that ANOVA analysis testing ERCoh for control electrode pairs (F3–F4, P3–P4) was not significant ($p > .05$).

Of note, the focus of the analysis was the comparison of the coherence (DTF) values between the NSTM and STM conditions with the same extension as the frequency bands.

Direction of Functional Connectivity as Revealed by DTF

Statistical analysis of the DTF values (direction of the functional connectivity) for the beta band showed a main effect of direction, indicating a prominent parietal-to-frontal direction, $F(1, 10) = 6.09$, $MSe = 0.0067$, $p < .03$, irrespective of condition (NSTM, STM). Duncan's post hoc testing indicated that, for both conditions, parietal-to-frontal direction was significantly predominant compared with frontal-to-parietal direction for all the considered variables (electrode pairs and time).

The results of the second ANOVA analysis computed for the gamma band are illustrated in Figure 4. There was a significant four-way interaction, $F(1, 10) = 4.70$, $MSe = 0.002$, $p < .05$, among the variables condition (NSTM, STM), direction (frontal to parietal, parietal to frontal), electrode pair (F3–P3, F4–P4), and time (T1, T2). Duncan's post hoc testing indicated that parietal to frontal direction was significantly predominant compared with frontal to parietal direction for NSTM ($p < .02$–.002), but not for STM. The only exception for STM was observed in DTF values computed for the left hemisphere (F3–P3) during the T2 period ($p < .002$).

F4

Discussion

Methodological Remarks

The present experimental design did not permit the dissociation of frontoparietal connectivity related to memorization of the cue stimulus versus movement preparation (after the go stimulus). Indeed, subjects already knew the movement target during the retention period, so that memorization and motor preparation could run together. However, that motor preparation does not confound effects of retention processes is likely for at least two reasons: First, the motor preparation was paired for the NSTM and STM conditions; therefore, time intervals, go stimulus, and motor demands were identical. Second, the period between cue and go stimuli varied on a trial-by-trial basis (5.5–7.5 s); this discouraged

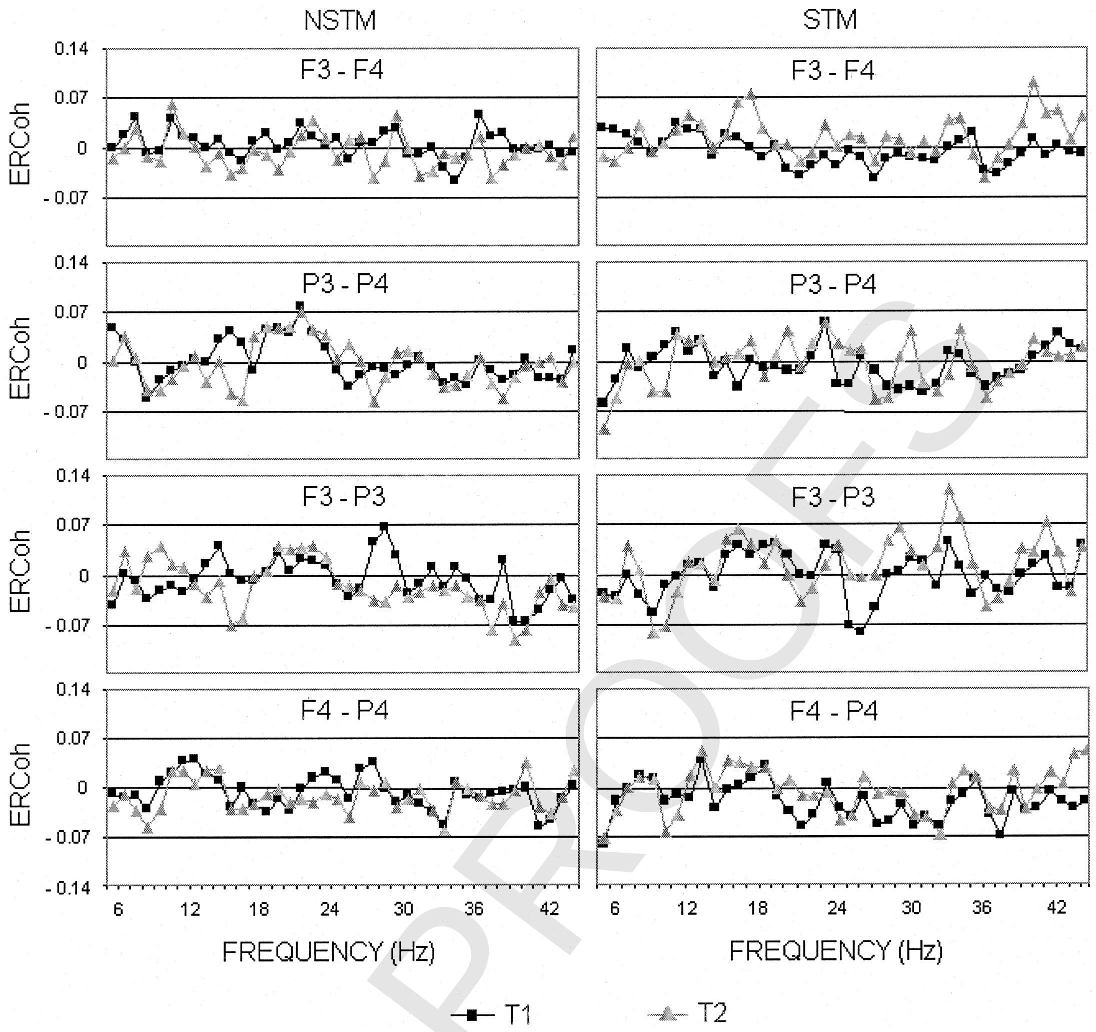

Figure 2. Grand average of event-related coherence (ERCoh) spectra computed from frontoparietal (F3–P3, F4–P4) and laterolateral (F3–F4, P3–P4) electrode pairs during the two time intervals of the retention period (T1 and T2) of the no short-term memory (NSTM) and short-term memory (STM) conditions.

a fixed, early-leaned predetermined motor preparation before the go signal.

Surface Laplacian estimation minimizes volume conduction and removes electrode reference effects (Nunez, 1995). It is noteworthy that DTF (but not coherence analysis) between a pair of electrodes is indifferent to common signals applied to both of them for volume conduction. However, it is affected by volume conductor when this effect impinges only, or mainly, on one of the two electrodes. For this reason, we used DTF analysis on surface Laplacian estimates.

Frontoparietal Connectivity During STM

Functional frontoparietal connectivity, as revealed by EEG coherence between electrodes, prevailed for the STM condition rather than the NSTM condition during the late phase (T2) of the retention period, that is, when the target stimulus was presumably being rehearsed. These activities disappeared in the control condition (NSTM), when no memory load was required. This effect occurred at the higher frequencies such as the beta (14–30 Hz) and gamma (30–45 Hz) bands. Therefore, these findings extend previous evidence of high-frequency synchronization of neural oscillatory responses occurring in properly stimulated cortical visual areas (Gray, Konig, Engel, & Singer, 1989; Konig, Engel, & Singer, 1995). Indeed, high-frequency oscillations are thought to reflect mainly the elaboration of complex sensory stimuli over primary and nonprimary sensory areas, and may bind the cooperative processing of nodes within a brain neural network (Engel, Fries, & Singer, 2001; Keil, Muller, Ray, Gruber, & Elbert, 1999; Tallon-Baudry, Bertrand, Delpuech, & Permier, 1997, 1999; von Stein & Sarnthein 2000). Furthermore, it has been shown that high-frequency oscillations over parietal areas mediate the interaction of the coherent visual representation with the experience-based perception of objects (Engel et al., 2001; Keil et al., 1999; Sarnthein et al., 1998; Tallon-Baudry et al., 1997; von Stein et al., 1999). Finally, synchronization of gamma oscillations has been shown to affect long-lasting (> 1 hr) excitatory characteristic of

Table 1
Individual Electroencephalogram Coherence Frequencies

	Electrodes and frequency bands															
	F3–F4				P3–P4				F3–P3				F4–P4			
Subjects	Theta	Alpha	Beta	Gamma	Theta	Alpha	Beta	Gamma	Theta	Alpha	Beta	Gamma	Theta	Alpha	Beta	Gamma
No short-term memory																
B.A.	4–7	10	23	39	4–7	10	18	34	4–7	10	28	38	4–7	11	23	33
B.O.	4–7	9	17	41	4–7	9	24	40	4–7	12	26	39	4–7	9	22	39
C.B.	4–7	11	18	41	4–7	14	25	35	4–7	13	30	38	4–7	14	30	40
F.B.	4–7	10	19	33	4–7	13	24	36	4–7	13	21	35	4–7	14	30	35
F.P.	4–7	10	19	33	4–7	13	24	41	4–7	11	24	40	4–7	11	23	42
M.I.	4–7	9	22	37	4–7	9	17	35	4–7	10	16	32	4–7	9	17	33
N.O.	4–7	9	25	37	4–7	14	24	40	4–7	14	27	37	4–7	10	25	36
P.A.	4–7	12	20	40	4–7	10	28	38	4–7	10	19	38	4–7	11	21	40
P.O.	4–7	10	27	40	4–7	11	26	40	4–7	12	24	38	4–7	13	20	36
S.I.	4–7	8	27	42	4–7	8	18	33	4–7	10	25	43	4–7	10	32	40
S.O.	4–7	13	24	33	4–7	9	27	41	4–7	13	32	41	4–7	10	27	38
M	4–7	10.091	21.909	37.818	4–7	10.909	23.182	37.545	4–7	11.636	24.727	38.091	4–7	11.091	24.545	37.455
SD	—	1.446	3.562	3.459	—	2.212	3.790	3.012	—	1.502	4.714	2.914	—	1.814	4.719	3.045
SE	—	0.436	1.074	1.043	—	0.667	1.143	0.908	—	0.453	1.421	0.879	—	0.547	1.423	0.918
Short-term memory																
B.A.	4–7	10	24	35	4–7	10	27	37	4–7	11	24	37	4–7	11	28	40
B.O.	4–7	9	24	35	4–7	9	27	36	4–7	12	28	41	4–7	10	24	39
C.B.	4–7	10	17	39	4–7	14	27	35	4–7	13	30	40	4–7	14	25	39
F.B.	4–7	10	21	33	4–7	12	24	34	4–7	13	23	33	4–7	14	31	39
F.P.	4–7	11	23	26	4–7	9	27	41	4–7	9	23	40	4–7	9	23	41
M.I.	4–7	9	27	38	4–7	9	18	35	4–7	9	17	34	4–7	9	18	34
N.O.	4–7	10	30	40	4–7	14	28	41	4–7	10	25	39	4–7	10	23	37
P.A.	4–7	12	26	38	4–7	9	27	38	4–7	10	20	38	4–7	11	21	40
P.O.	4–7	10	30	41	4–7	10	30	37	4–7	11	21	36	4–7	11	20	38
S.I.	4–7	9	26	39	4–7	12	18	39	4–7	10	21	41	4–7	10	32	41
S.O.	4–7	10	26	39	4–7	10	39	41	4–7	10	26	33	4–7	10	25	42
M	4–7	10	24.909	36.636	4–7	10.727	26.545	37.636	4–7	10.727	23.455	37.455	4–7	10.818	24.545	39.091
SD	—	0.894	3.780	4.273	—	1.954	5.681	2.580	—	1.421	3.725	3.078	—	1.722	4.367	2.212
SE	—	0.270	1.140	1.288	—	0.589	1.713	0.778	—	0.428	1.123	0.928	—	0.519	1.317	0.667

AQ: 1 *Note.* Dashes indicate______________________________.

the involved cortical regions. (Whittington, Traub, Faulkner, Stanford, & Jefferys, 1997). In particular, spectral coherence points to a larger number of synchronized firing neurons (Hari et al., 1998; Manganotti et al., 1998, Pfurtscheller & Andrew 1999), whereas high frequencies (beta-gamma) possibly represent the "binding" code for neuronal populations involved in specific task-related information processing. Taking into account these assumptions, we can speculate that, in our experimental conditions, the coherence of frontoparietal high-frequency oscillations may link single neurons with similar functional properties within neural assemblies, using the maintenance of sensory traces for short-term memorization (Basar, Basar-Eroglu, Karakas, & Schurmann, 2000; Engel et al., 2001; von Stein & Sarnthein, 2000).

The present results showed a lack of statistical modulation of coherence at low EEG frequencies (i.e., theta–alpha) during the delay period of the STM condition compared with the NSTM condition. This is apparently at odds with previous EEG coherence studies (Sarnthein et al., 1998; von Stein & Sarnthein, 2000) indicating an increase in EEG coherence at the theta band during working memory tasks. However, it should be stressed that, in those studies, the memory load was heavier than in the present investigation, in which only one bit of visuospatial information (i.e., right or left position of the taller bar) had to be retained for few seconds. Indeed, the bulk of previous reports indicate that theta rhythmicity is especially modulated by heavy mental efforts in cognitive tasks (Gevins & Smith, 2000; McEvoy, Pellouchoud, Smith, & Gevins, 2001; McEvoy, Smith, & Gevins, 2000; Pellouchoud, Smith, McEvoy, & Gevins, 1999).

The present results complement the evidence of previous magnetoencephalographic (Okada & Salenius, 1998), EEG (Gevins & Smith, 2000; Gevins, Smith, McEvoy, & Yu, 1997), and neuroimaging (Courtney, Ungerleider, Keil, & Haxby, 1996) studies, which modeled the involvement of prefrontal, dorsolateral occipital, inferior posterior parietal, and premotor areas during visuospatial STM. Indeed, representational memory would impinge on not only frontal, but also posterior (mainly parietal) regions (Amorim et al., 2000; Gevins et al., 1997; Gevins & Smith, 2000; Krause et al., 2000; McEvoy et al., 2001; McEvoy, Smith, & Gevins, 1998).

The analysis of the information flow between electrodes (i.e., DTF computation) for both beta and gamma frequencies showed a predominance of parietal-to-frontal direction during the retention

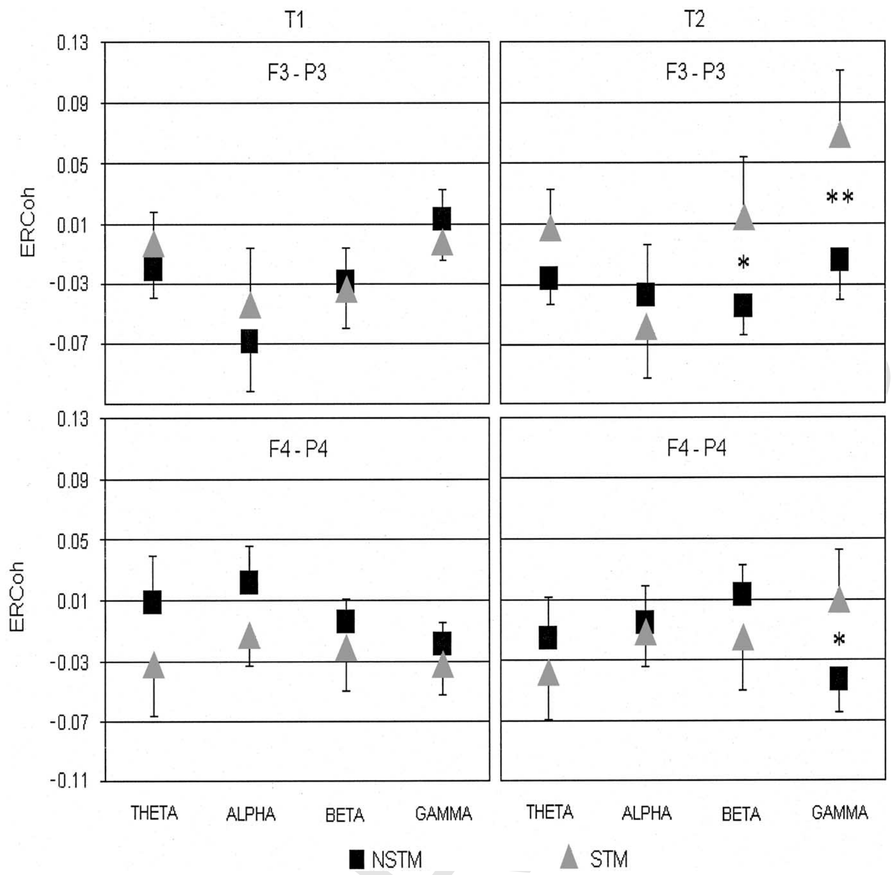

Figure 3. Across-subject means (± *SEM*) of frontoparietal electroencephalograph event-related coherence (ERCoh) as provided by the analysis of variance (ANOVA) design. The ANOVA analysis compared ERCoh of the variables condition (no short-term memory [NSTM], short-term memory [STM]), frequency band (theta, alpha, beta, gamma), electrode pair (F3–P3, F4–P4), and retention interval (T1, T2) to test the functional frontoparietal connectivity. A statistical interaction was computed among all variables, $F(3, 33) = 3.09$, $p < .04$. $^{*}p < .05$, $^{**}p < .001$, Duncan's post hoc test.

period of the NSTM condition. This is in line with the fact that posterior parietal cortex receives visual information from primary visual areas; somatosensory information from the primary somatosensory area (Area 2); and motor information from primary motor, supplementary motor, and premotor areas (Wise, Boussaoud, Johnson, & Caminiti, 1997). Posterior parietal cortex is also a crucial node of the cortical neural network subserving integration of information regarding the intra- and extrapersonal space for coordinated limb movements (Haaland, Harrington, & Knight, 1999).

Compared with the NSTM condition, the STM condition changed the pattern of the information flow between electrodes. At gamma frequencies, there was a globally balanced direction of the information flow between frontal and parietal areas during the retention period. It can be speculated that the prevalence of the parietal-to-frontal direction may be contrasted by an opposite "top-down" flow of information from frontal to posterior parietal areas. This speculation is in accordance with the well-known role of this cortical area in spatial representational memory, as revealed by animal studies including single-neuron recordings (Funahashi et al., 1989, 1990, 1991, 1993; Funahashi & Kubota, 1994; Fuster, 1973; Gnadt & Andersen, 1988; Goldman-Rakic, 1987, 1995, 1996; Kubota & Niki, 1971; Levy & Goldman-Rakic, 2000). Converging evidence has been obtained in human subjects by clinical (Squire, 1987; Strauss, Prescott, & Tune, 1986) and neuroimaging (reviewed by Kessels et al., 2000; Krause et al., 2000) studies.

As a final point, it should be noted that a conclusive interpretation of the statistical EEG effects, in terms of memory load, is challenged by the fact that both perceptual and memory differences were present during the delay period, according to the characteristics of the delay response task (Goldman-Rakic, 1987). In this regard, two important pieces of evidence are in favor of a memory, rather than a perceptual, effect on the present coherence and DTF results. First, we used long warning (1 s) and cue (2 s) stimuli in order to avoid or minimize the effects of visual processing during the delay period. Furthermore, it was shown in the previously mentioned companion paper (C. Babiloni et al., 2004; Figure 3) that the visual evoked potentials, reflecting visual processing, characterized the first part of the cue period and were completely absent during the delay period. Therefore, it is unlikely that visual processing can account for the concomitant coherence

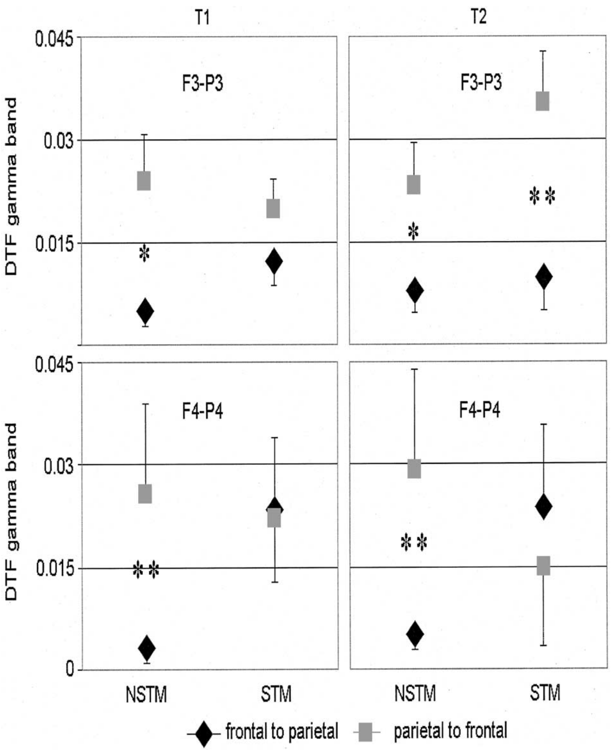

Figure 4. Across-subject means (± *SEM*) of frontoparietal gamma band directed transfer function (DTF) as provided by the analysis of variance (ANOVA) design. The ANOVA design included the variables condition (no short-term memory [NSTM], short-term memory [STM]), direction (frontal to parietal, parietal to frontal), electrode pair (F3–P3, F4–P4), and retention interval (T1, T2). There was a statistical interaction, $F(1, 10) = 4.70$, $MSe = 0.002$, $p < .05$, among the variables. $^{*}p < .02$, $^{**}p < .002$, Duncan's post hoc test.

differences between the NSTM and STM conditions across the delay period. Second, the coherence values were computed in two consecutive periods lasting 1 s during the delay period (i.e., T1, T2). The present results showed that the statistical coherence and DTF differences between the two conditions were greater in the second period than in the first period, in line with an increase of the memory load across the delay period and against the hypothesis of a major perceptual influence (i.e., it would have been stronger at the beginning of the delay period).

Conclusions

In the present EEG study, we modeled the functional connectivity between frontal and parietal areas during STM processes, as revealed by the spectral coherence between electrodes and by a mathematical approach (DTF computation) recently used to estimate the direction of the information flow between electrodes (C. Babiloni et al, 2003; Mima et al., 2000). Results showed that the functional frontoparietal connectivity, as revealed by beta (14–30 Hz) and gamma (30–45 Hz) coherence, prevailed in the STM condition rather than the NSTM condition. Moreover, DTF findings indicated a prevalence of the parietal-to-frontal information flow at the beta and gamma bands during the NSTM condition and at the beta band during the STM condition. This agrees with a prevalence of visual processes from visual (parietal) to associative and motor (frontal) areas with an NSTM task based on visuomotor transformations. In contrast, parietal-to-frontal and frontal-to-parietal information flows were balanced at the gamma band during the STM condition. These results suggest that coordinated high-frequency oscillations (beta, gamma) within a frontoparietal network would optimize representational memory during STM. In this context, the frontal areas would increase their influence on the parietal areas for the maintenance of that memory during STM retention. It is noteworthy that the present memory task was designed to be very simple, in view of its application in forthcoming neuroimaging studies on healthy aging, mild cognitive impairment, and Alzheimer's disease. The influence of so simple a memory requirement on the frontoparietal coupling encourages such a perspective.

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