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Time-course of motor inhibition during hypnotic paralysis: EEG topographical and source analysis

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\textbf{Abstract}

Cognitive hypotheses of hypnotic phenomena have proposed that executive attentional systems may be either inhibited or overactivated to produce a selective alteration or disconnection of some mental operations. Recent brain imaging studies have reported changes in activity in both medial (anterior cingulate) and lateral (inferior) prefrontal areas during hypnotically induced paralysis, overlapping with areas associated with attentional control as well as inhibitory processes. To compare motor inhibition mechanisms responsible for paralysis during hypnosis and those recruited by voluntary inhibition, we used electroencephalography (EEG) to record brain activity during a modified bimanual Go-Nogo task, which was performed either in a normal baseline condition or during unilateral paralysis caused by hypnotic suggestion or by simulation (in two groups of participants, each tested once with both hands valid and once with unilateral paralysis). This paradigm allowed us to identify patterns of neural activity specifically associated with hypnotically induced paralysis, relative to voluntary inhibition during simulation or Nogo trials. We used a topographical EEG analysis technique to investigate both the spatial organization and the temporal sequence of neural processes activated in these different conditions, and to localize the underlying anatomical generators through minimum-norm methods. We found that preparatory activations were similar in all conditions, despite left hypnotic paralysis, indicating preserved motor intentions. A large P3-like activity was generated by voluntary inhibition during voluntary inhibition (Nogo), with neural sources in medial prefrontal areas, while hypnotic paralysis was associated with a distinctive topography activity during the same time-range and specific sources in right inferior frontal cortex. These results add support to the view that hypnosis might act by enhancing executive control systems mediated by right prefrontal areas, but does not produce paralysis via direct motor inhibition processes normally used for the voluntary suppression of actions.

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1. Introduction

Hypnosis can induce striking changes in perception and behaviour under the influence of specific suggestions, such as being paralyzed, blind, or hearing sounds – yet the cognitive and neural underpinnings of these phenomena are still poorly understood. From the perspective of neuroscience, hypnosis is generally defined as a modified state of consciousness (Gruzelier, 2005), characterized by changes in attention and reduced awareness to the peripheral world (Cojan et al., 2009; Crawford, 1994; Raz and Shapiro, 2002; Spiegel and Spiegel, 1978). Because these effects imply a dissociation between the phenomenal experience of the hypnotized subject and the actual state or stimulation from the outside world, a better understanding of hypnosis would provide invaluable insights on the ways by which top-down mechanisms can affect awareness and goal-directed behaviour (Egner and Raz, 2007).

In the current study, we specifically focussed on unilateral hypnotic paralysis. We examined the neural substrates and time-course of motor control processes underlying movement inhibition during hypnotic paralysis, by recording event-related potentials (ERPs) during a Go/Nogo motor paradigm in conditions with and without hypnosis. Our aim was to test for the similarity in neural activity and the possible temporal overlap between inhibitory control mechanisms responsible for hypnotically induced paralysis and those normally recruited by voluntary suppression of motor action.

Several theoretical accounts of hypnotic phenomena have invoked a crucial role of “cognitive control” and “supervisory attentional systems” (Gruzelier, 1998; Hilgard, 1977; Oakley, 1999). However, these accounts diverge in terms of the exact type of effects of hypnosis on attention, and even propose changes in opposite directions. According to a first view, hypnotic phenomena might result from a weakening of attentional control, while lower-level automatic routines are still operating freely without normal supervisory control (Egner and Raz, 2007; Woody and Bowers, 1994; Woody and Farvolden, 1998). For example, in a classic model proposed by Gruzelier (1998), the influence of hypnosis on top-down processes was divided into three distinct levels, corresponding to a gradual inhibition of activity in frontal cortex during the course of induction. While the first step of hypnotic induction in this model may recruit executive control systems in order to produce “sensory fixation”, the second step of induction is thought to involve an activation of fronto-limbic inhibitory systems under suggestions of relaxation and tiredness, which will in turn inhibit more anterior frontal executive functions in the critical third step. In this model, therefore, the attenuation of frontal activity and reduced attentional control constitute an essential component of hypnotic phenomena, necessary for the subsequent effects of suggestion.

Kaiser et al. (1997) specifically tested this hypothesis of reduced executive functions by recording ERPs during a Stroop task in subjects under hypnosis, without specific suggestion. These authors hypothesized that an inhibition of frontal functions should be reflected by a reduction of ERPs typically elicited by error processing in Stroop tasks: the Error Negativity (Ne) reflecting error detection, and the Error-related late Positivity (Pe) reflecting error evaluation or adjustment. Their results showed a significant reduction for the Pe, during hypnosis relative to normal state, but no reduction for the Ne. This was interpreted as a failure of controlled “context updating” processes with a preservation of unconscious error detection, and taken as evidence for an inhibition of frontal executive functions during hypnosis (Kaiser et al., 1997). However, it should be noted that this study did not use a hypnotic suggestion concerning the task but rather investigated the effect of hypnotic state per se. Changes in performance and error processing in hypnotized (or highly susceptible) subjects during a Stroop task might potentially be related to several different processes, other than inhibition of frontal monitoring functions, including a disconnection between conflict-monitoring and executive control systems, a failure in the maintenance of task sets, as well as an alteration in motivational state (see Egner and Raz, 2007). Therefore, the exact mechanisms responsible for the inhibition of frontal lobe function by hypnosis were not directly tested in this study.

In contrast, a second view of hypnotic phenomena is that these imply an increase in executive control and frontal activity, allowing greater focussing of attention and attenuation of peripheral distractors. Thus, hypnotic suggestions would modulate or override the activation of habitual responses or behaviours through heightened cognitive control (Cojan et al., 2009; Crawford, 1994; Oakley, 1999) – quite contrary to popular beliefs that conceive hypnosis as a “loss of control” leading to involuntary acts. In support of this view, Egner et al. (2005) reported a distinctive pattern of frontal activation during Stroop task performance (Egner et al., 2005). Using functional magnetic resonance imaging (fMRI), these authors found increased activation in anterior cingulate cortex (ACC) during hypnosis in susceptible subjects as compared with baseline, as well as with respect to subjects with low susceptibility. No difference was observed in other prefrontal areas. These findings were interpreted as reflecting greater monitoring of interference-related information during the Stroop task, mediated by ACC, but functional decoupling with dorsolateral prefrontal cortex (DLPFC) areas normally involved in selective attention. Again, however, this study used no specific hypnotic suggestion. Different results showing reduced ACC activation during a word-colour Stroop task were obtained in another study where subjects received a hypnotic suggestion that the words had lost their meaning (Raz et al., 2005), such that the Stroop interference was actually abolished. Therefore, it remains unclear where changes in ACC activity may reflect a cause or rather a consequence of hypnotic inhibition. Increases or decreases in ACC are also found to parallel changes in pain perception during hypnotic suggestion of hyperalgesia or analgesia, respectively (Rainville et al., 1997). This modulation might be driven by top-down influences from other brain regions, but their neural sources remain to be determined.

Along the same line, hypnotic suggestion of limb paralysis has been explained by an active inhibition of motor processes by executive control systems implemented by the frontal lobe (Halligan et al., 2000; Oakley, 1999). Oakley (1999) suggested that this active inhibition may act to suppress the initiation of
voluntary movement or exclude the corresponding experience of volition from the field of conscious awareness. Moreover, two neuroimaging studies by Halligan et al. (Halligan et al., 2000; Ward et al., 2003) reported that a hypnotically induced paralysis of the leg was associated with increased activation in ACC and right orbito frontal cortex (OFC) when participants were asked to attempt a movement with their paralyzed limb, concomitant with a lack of motor cortex activation. The authors concluded that the activation in ACC and OFC was probably responsible for an active inhibition of the motor cortex during attempts to move, under the influence of hypnotic suggestion. However, such increases could also reflect enhanced monitoring and conflict processing given the simultaneous suggestion of paralysis. In an experiment where subjects were instructed to imitate hand movement shown on a screen, similar results were found: increased activation in ACC, together with frontal gyrus and insula (Burgmer et al., 2012). Interestingly, this effect did not depend on the hand side, suggesting that these hyper-activations might reflect attention middle frontal gyrus (MFG), conflict detection (ACC), and self-representation processes (insula) during hypnotic paralysis rather than only motor inhibition processes. However, no modulation of ACC was found in another recent study on hypnotic paralysis (Cojan et al., 2009).

A related hypothesis put forward that hypnotic paralysis might arise through a modified representation of the self that is characterized by (hypnotically) impaired motor abilities. Two recent fMRI studies using a resting state approach have provided some support to this idea. In a first study where high and low susceptible subjects were compared after a hypnotic induction, only the highs showed a reduction in anterior, superior, medial frontal portion of the default mode networks (McGeown et al., 2009). A second study on paralysis induction revealed an increased connectivity of the precuneus with the right DLPFC, angular gyrus, and a dorsal part of the precuneus, all areas that could mediate a modified representation of the self (Pyka et al., 2011).

Interestingly, Oakley (1999) proposed that limb paralysis induced by hypnosis might be "the product of inhibition after the intention to move has been generated within self-awareness so that only the final stage of carrying out that intention is missing". Hence, in this view, the intention to move and mental imagery of movement might still remain intact despite hypnotic paralysis, again contrasting with the popular view that the hypnotized subject lacks volition. This would actually accord with neuroimaging data showing preserved activation of primary motor cortex during mental preparation of movement with a hypnotically paralyzed hand (Cojan et al., 2009). Furthermore, Burgmer et al. (2012) did not find any effect of hypnosis on brain activity during movement observation, suggesting that early motor processes and motor mirror systems are not altered by the hypnotic suggestion.

However, the neural mechanisms underlying the inhibition of motor execution by hypnotic suggestion are still unclear, and their overlap with those responsible for inhibition of motor or cognitive responses in other tasks (outside hypnotic situations) has not been systematically investigated. In fact, ACC has only rarely been associated with inhibitory control functions (Braver et al., 2001; Swick and Turken, 2002; Wenderoth et al., 2005), whereas the voluntary suppression of motor or cognitive responses has consistently been shown to depend on the right inferior frontal gyrus (rIFG) and pre-SMA across a range of different tasks (Aron et al., 2004a, 2004b; Chevrier et al., 2007; Rubia et al., 2003; Sharp et al., 2010; Xue et al., 2008).

To determine whether similar prefrontal areas would be responsible for motor inhibition during hypnotic paralysis and intentional response withholding, Cojan et al. (2009) used fMRI in a response inhibition paradigm to compare the effect of hypnotic suggestion with voluntary inhibition in normal conditions and with respect to simulated paralysis. A Go/Nogo task combined with motor preparation was given to participants who either responded normally with both hands or received a suggestion of unilateral paralysis (either via hypnosis or simulation instruction). This study could thus directly test whether specific inhibitory processes are activated during induced paralysis on Go trials, and whether these inhibitory processes are similar to those employed for voluntary inhibition on Nogo trials in a normal context and/or for feigned paralysis. While the results confirmed a selective implication of the right IFG in both voluntary motor inhibition on Nogo trials and simulated paralysis on Go trials, right prefrontal areas showed an increased activation in all response conditions during hypnosis, suggesting different inhibitory mechanisms and a key role of right IFG in selective attention control beyond motor inhibition only (Cojan et al., 2009).

In the present study, we used ERP in the same Go/Nogo paradigm to further elucidate the time-course of the recruitment of inhibitory cortical mechanisms across different conditions, with and without hypnosis. Several electrophysiological investigations of Go/Nogo or Stop signal paradigms have reported that two main ERP components are typically associated with motor inhibition: the N2 and the P3 (Bokura et al., 2001; Donkers and van Boxtel, 2004; Smith et al., 2007; van Boxtel et al., 2001). The N2 wave consists of a negative shift at a latency of 150 msec, with maximal amplitude over the Fz electrode, whereas the P3 is a positive shift at a latency of 300 msec, with a maximum at Pz and Cz electrode on the scalp (Falkenstein et al., 1999). Recent work suggested that N2 and P3 may reflect distinct aspects of cognitive control and inhibition. For instance, one study found that the N2 and the P3 were differentially modulated by the amount of response conflict and response withholding, respectively (Enriquez-Geppert et al., 2010). Another study (Smith et al., 2007) compared these ERPs in a Go/Nogo paradigm where the participants had either to count (covert task) or to press a button (overt motor task) in response to frequent tones (Go stimuli) and not to the infrequent ones (Nogo stimuli) (Smith et al., 2007). The N2 amplitude on Nogo trials did not differ between the two tasks but the P3 amplitude on Nogo stimuli was stronger for inhibiting the overt motor response in the button-press task, compared to the covert counting task. The authors concluded that only the P3 activity might directly reflect motor inhibition, while the N2 potential could reflect a "non-motoric" stage of inhibition control. However, even if a consensus on the functional significance of the N2/P3 complex in inhibition task seems to emerge from these recent data, it has also been shown that the P3 may encompass a wide range of other cognitive control processes, such as...
context updating, decision making, attentional processes, in addition to response inhibition (Bekker et al., 2004; Bruin et al., 2001; Karch et al., 2010; Polich and Kok, 1995). It is unknown whether this component would also be generated when motor inhibition is induced by hypnotic suggestion, or whether it is specific to voluntary inhibition.

The aim of our study was therefore to determine the topographical patterns and time-course of brain activity associated with motor execution and inhibition processes during a Go/Nogo task, under a hypnotic suggestion of paralysis, in comparison with normal conditions and simulated paralysis. Our paradigm allowed us to directly test for any commonality or specificity in ERPs generated by voluntary motor inhibition on Nogo trials and inhibition caused by hypnotic or simulated paralysis, in the same participants.

2. Methods

2.1. Participants

We recruited 24 healthy volunteers who were divided in two different groups: Hypnosis and Simulation (eight women and four men in each group, two left-handed in each). All gave their written consent to participate according to the Geneva University Hospital Ethics Committee. They were mainly students from the medical university, matched for age (20–35 years old) and gender across the two groups. None had a history of neurological or psychiatry disease, or took medication or drugs. Participants in the Hypnosis group were taken from a pool of pre-tested subjects who were screened for hypnotic suggestibility with the Harvard Group Scale of Hypnotic Susceptibility, Form A (Shor and Orne, 1963), and reached a minimum score of 9 positive items. Then, they were also individually tested on the Stanford Hypnotic Susceptibility Scale, Form C (Weitzenhoffer and Hilgard, 1962) by an experienced clinician (L.W.), and also reached a score of 9 on this scale.

Paralysis was produced by hypnosis in one group and by voluntary simulation in the other group. In the hypnosis condition, subjects received a suggestion that their left hand was unable to move, prior to performing the Go/Nogo task. The hypnotic induction was given by an experienced clinician (N.C.). Induction was produced by a standard eye roll procedure alongside with relaxation instructions (Maldonado and Spiegel, 2008), followed by a suggestion describing that the left hand progressively became heavy, stiff, and eventually unable to move, while the right hand could still continue to respond normally. In the simulation condition, participants were asked to perform the Go/Nogo task while feigning a paralysis of the left hand, and thus act “as if” they suffered from motor weakness and “tried” to move their left hand but were unable to do so. Subjects in the Simulation group were not tested for hypnotisusceptibility and recruited on their willingness to participate in an experiment investigating motor paralysis.

2.2. Data acquisition

We used a Go/Nogo task similar to a previous study by Cojan et al. (Cojan et al., 2009). Participants were presented with pictures showing the dorsal view of a left or a right hand, which could be of three different colours: grey, green, or red. Each trial started with a fixation cross (duration from 1000 to 2000 msec), followed by a preparation cue (Prep) which depicted either the left or the right hand in grey colour (600–1000 msec) and instructed the participant to prepare a movement (to press a button) with the corresponding hand. This grey hand could turn either green (Go stimulus) or red (Nogo stimulus), both with a fixed duration of 750 msec. Participants had to press the button as quickly as possible when hand turned green (75%), and to withhold the prepared response if the hand turned red (25%). After each imperative stimulus (Go or Nogo), a visual feedback was presented during 1000 msec, signalling correct, incorrect, or no response detected. The order of presentation of left or right hands was randomized. Stimulus display and behavioural response recording were controlled by E-prime v.2 (Psychology Software Tools, http://www.pstnet.com).

Four blocks of 120 trials (half right hand, half left hand) were recorded with a 64-channel Biosemi ActiveTwo system, with electrodes positioned according to the extended 10/20 system. Four supplementary electrodes (electro-oculogram) were used to record the eyes movements and blinks. The EEG signal was continuously recorded with a sampling frequency of 512 Hz and the electrodes offset potential was kept below 20 kΩ.

Both groups were tested in the normal or paralysis condition (simulated or hypnotically induced) in successive order, counterbalanced across participants.

2.3. Data processing and analysis

Evoked related potentials were computed offline using BrainVision Analyzer V.2. (Brain Products GmbH) after filtering between .5 and 35 Hz. Epochs were selected from 100 msec prior to onset of the stimulus to 750 msec after the onset of the imperative stimulus (Go or Nogo), with a baseline correction using the 100 msec pre-stimulus recording period. Only correct responses (to Go/Nogo cues) were analyzed and data were down-sampled to 512 Hz for analysis.

In addition to standard averaging approach to compute ERP peaks at selected electrodes (see Picton et al., 2000), we employed a topographical analysis to determine time-windows with distinct configurations of electric field corresponding to successive “microstates” in the evoked EEG response (Lehmann et al., 2010). This topographical analysis allows the identification of stable configurations of electric field (topographical maps) associated with different stages of information processing from perception to motor response (Michel et al., 2009). Unlike the classic waveform analysis that concentrates on a few electrodes of interest, the topographic approach takes into account all the electrodes to explain the data at each time point (Michel et al., 2004; Pourtois et al., 2008). Thus, this segmentation approach can isolate periods with systematic changes in distribution of the global electric field over the scalp, which are presumably generated by different sources of activity, and identified in a data-driven manner without any a priori on specific time point or scalp sites for effects of interest (Michel et al., 2004).

The topographical segmentation analyses were conducted with Cartool software (Brunet et al., 2011; freely available at...
This topographical analysis used a k-mean cluster analysis based on the spatial correlation between maps which group together all EEG maps with a high spatial similarity in the topographical distribution of activity (Pascual-Marqui et al., 1995). Two segmentations were computed on the group-averaged data: one for the motor preparation phase (time-locked to the grey hand cue), the other for imperative phase (time-locked to the green/Go or red/Nogo hand cue). For the preparation phase, the threshold of correlation for merging maps was set to 90% and we rejected maps shorter than four time frames. For the imperative phase, the threshold of correlation above which the maps were merged in the same cluster was set to 92%, and we rejected maps shorter than three time frames. Different parameters were chosen because of the different duration of each phase (600 msec for preparation and 750 msec for imperative phase) and the different distribution of map data in the two conditions. Indeed, as the duration of the preparation phase was shorter, it was reasonable to allow fewer maps to explain the data, by decreasing the threshold of the correlation and increasing the minimum duration of a map.

The reliability of this segmentation in successive topographies, which corresponds to the solution with the optimal number of maps explaining the whole EEG data, was assessed by two criteria: the Cross Validation (CV) criterion and the Krzanowski-Lai (KL) criterion. The best ratio between these values was chosen to select the most robust segmentation (Brunet et al., 2011; Michel et al., 2004, 2009; Murray et al., 2008). The results of the cluster analysis are shown with colour-coded segments under the Global Field Power (GFP) curves (see Fig. 2). As the dominant scalp topographies are identified in the group-average data, the segmentation analysis is then verified statistically at the individual level in order to assess which map remain significantly present at the individual level in different experimental conditions (Brunet et al., 2011). The statistical analysis applies a fitting procedure based on the comparison between single-subject ERP data from each participant and topographical maps identified by the cluster analysis on the group-averaged data (Murray et al., 2008).

Finally, we performed an analysis of the plausible neural sources for topographies of interest. We then used the Brainstorm software (Tadel et al., 2011) (freely available for download online under the GNU general public license http://neuroimage.usc.edu/brainstorm) and a minimum-norm estimation (MNE) to reconstruct the source and analyze their time-course of activity, across our different experimental conditions and specific periods of topographical modulations. The MNE assumes that the 3D current distribution should have minimum overall intensity (Michel et al., 2004). The solution space was based on three-sphere head model with a matrix of 15 000 solutions points, distributed throughout the MNI152 brain template.

3. Results

3.1. Behavioural results

For Go trials in the normal context, both groups responded with high level of accuracy with both the left and right hand (95.1% and 99.3% respectively for the Hypnosis group, 89.5% and 98.3% for the Simulators group). By contrast, in the paralysis context (due to hypnosis or simulation), no responses were recorded for the left “affected” hand, indicating a successful compliance with our instructions of paralysis. However, in the paralysis context, both groups showed a decrease in the accuracy with the right hand (94.6% and 95.3% for hypnosis and simulator respectively). A repeated-measures analyse of variane (ANOVA) on the percentage of correct responses (in normal context only) revealed a main effect of the hand (p < .001, with higher accuracy for the right hand) and a main effect of the group (p = .03, simulators being slightly less accurate). Furthermore, a second ANOVA comparing performance of the right hand across experimental conditions showed a main effect of the context (p = .003), with a higher number of errors during paralysis than during the normal context. Similar analyses on reaction times (RT) showed a main effect of Hand (p < .001), with longer RTs for the left hand. This lower performance of the left hand is consistent with normal right-handedness and thus independent of the paralysis context.

3.2. ERP results

We first examined ERPs evoked by the preparation cues (grey hands). A large P1-N1 waveform was observed for each hand condition and each context, as typically elicited by a visual stimulus onset, but without any modulation as a function of paralysis (present or absent) in the two participant groups (hypnosis or simulation). No difference was observed between the right and left hand.

Our main goal was to examine electrophysiological activity associated with the inhibition of motor action in the different experimental conditions. Voluntary motor inhibition was probed by correct responses to Nogo stimuli in the normal condition, which required an interruption of the prepared action. These trials generated a positive waveform with maximum amplitude at Cz electrode and a peak around 370 msec after cue onset (Fig. 1A), which was not seen on Go trials. This Nogo effect is consistent with a P3 component as commonly reported in other studies on inhibition (Bokura et al., 2001; Falkenstein et al., 1999; Polich and Kok, 1995; Smith et al., 2008). In the paralysis context, however, the positive P3 deflection still occurred on Nogo trials for the right hand, but this effect was no longer present for the left paralyzed hand, for both groups (Fig. 1B). In addition, ERPs on Go trials were similar in the normal and paralysis contexts, with no evidence for an extra P3 or any other additional activity associated with movement inhibition in this condition (Fig. 1B).

3.3. Topographical segmentation results

We performed two separate cluster analyses of ERP topographies for the preparation and the imperative phases, respectively, across all trial conditions in each phase. These data yielded a solution with four stable map configurations (microstates) over time for the preparation phase (Fig. 2), and 17 maps for the imperative phase (Fig. 3). These two sequences of maps explained respectively 94.36% (preparation phase) and 92.25%
Fig. 1 — ERPs in response to Go and Nogo cues. Data are shown for a) the normal context and b) paralysis context, displayed in microvolts as a function of time post-cue onset, for electrodes Fz, Cz, and Pz (Go in green, Nogo in red, Left hand in dark, Right hand in light, Hypnosis group in solid line, Simulation group in dash).

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(imperative phase) of the variance in ERPs. For clarity, we present the detailed results for each phase in separate sections.

3.3.1. Motor preparation phase

The spatial topographical analysis revealed that preparation cues elicited a succession of four distinct maps over time (Fig. 2), which appeared identical across the eight experimental conditions. Statistical analyses on the number of time frames during which these maps were present across conditions did not show any significant effect, suggesting a similar sequence of processing stages during motor preparation for the Hypnosis group and the Simulation group, for both the left and right hands (see Fig. 2 for details). No lateralization differentiating left versus right hand preparation was observed in these maps.

3.3.2. Imperative phase

Results from the spatial cluster analysis on ERPs time-locked to the imperative cue (Go or Nogo) revealed a series of 17 dominant scalp maps explaining the changes in EEG activity across time and conditions. Topographies were clearly different between Go and Nogo conditions in the normal context (Fig. 3A and B); green- vs red-coloured hands, respectively), and such differences overlapped with the peak of the P3 component observed during inhibition in the waveform analysis above (Fig. 3A and B). In both groups (Hypnosis and Simulation), two topographies (maps #8 and #10) were specifically associated with Go conditions, whereas a unique topography (map #7) characterized the Nogo conditions. In both groups also, these topographies were clearly present and similar for the two hands in the normal context (Fig. 3A), but they were abolished or modified for the left hand in the paralysis context (Fig. 3B).

Statistical analyses were performed to formally compare the number of time frames during which these maps were present in each condition and each group. A mixed repeated-measure ANOVA was first performed for maps #8 and #10 on all trials from the normal context, using Instruction cue (Nogo vs Go) as within-factor and Group (Hypnosis vs Simulation) as between-factor. This revealed a significant main effect of Instruction cue \((p < .001)\), confirming a selective expression of these two maps in the Go condition (Fig. 3A, two top rows), but there was no other main effect, nor any interaction. Conversely, a similar analysis for map #7 revealed a main effect of Imperative cue \((p < .001)\), reflecting a specifically longer expression of this topographical configuration in the Nogo condition instead (Fig. 3A, two bottom rows). Again, there was no other effect.

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Fig. 2 – Topographical segmentation analysis during the preparation phase. a) The topographical segmentation results is shown under GFP curves for the eight different conditions during motor preparation (the two top rows represent left and right hands in the normal context, the two bottom rows represent the paralysis context). Each colour labels a period of distinct and stable electric field topography. b) The four topographic maps identified by the segmentation analysis during a 600 msec post-cue period during preparation are shown with the nasion upward and left scalp leftward, in colours corresponding to the segmentation.
We then tested for changes due to the paralysis by conducting a repeated-measure ANOVA on the same maps with Context (normal vs paralysis) and Hand (right vs left) as within-factors and Group (Hypnosis vs Simulation) as between-factor. For maps #8 and #10 on Go trials only, this ANOVA revealed no main effect but a significant interaction of Hand \(\times\) Context \((p = .01)\), which confirmed a selective disappearance of these maps for the Left-Go trials during the paralysis context (Fig. 3B, first top row), in keeping with the absence of movement in this condition. However, this loss of the Go-related maps did not differ between hypnotic and simulated paralysis (no main effect nor interaction involving Group; see Fig. 3A, top row in right vs left column).

The same analysis yielded similar results for map #7 on Nogo trials, with a significant interaction of Hand \(\times\) Context \((p = .04)\) as well as a marginal effect of Group \((p = .08)\), but no other effect or interaction. This again reflected a selective loss of this Nogo-related map in the paralysis context, during both hypnosis and simulation.

Most remarkably, the critical Left-Go condition under hypnotic paralysis revealed a specific map (#11), which appeared from 344 to 406 msec post-cue onset (GFP peak at 375 msec), and overlapped with the P3 time-window (Fig. 3B, first row in left column). This topographical activity did not appear in any other condition. In particular, it was clearly different in comparison with 1) Left-Go trials in the normal context and 2) Left-Go trials during hypnotic paralysis.
context, and 2) Left-Go trials for simulators in the paralysis context. Since this map was not present in all experimental conditions (zero time frames were found for several conditions in individual data), we restricted our statistical analysis to trials from the paralysis context, using an ANOVA with Instruction cue (Nogo vs Go) as within-factor and Group (Hypnosis vs Simulation) as between-factor. This showed no main effect, but a significant interaction between Group and Instruction cue ($p = .04$), indicating that this map #11 was selectively associated with the “paralyzed” Left-Go trials in the Hypnosis Group (Fig. 3B).

For completeness, we also tested for any modulation of the topographical organization of neural activity for the right hand in each group and each context, but this revealed that none of these different maps was significantly modified during the left-hand paralysis in comparison with the normal context.

In summary, our cluster analysis showed that in the normal context, conditions requiring motor inhibition were characterized by a unique topographical distribution (map #7), while conditions requiring motor execution were represented by two different maps arising in succession (maps #8 and #10) during the same time-window, in all groups. However, during induced paralysis, a unique topography (map #11) replaced these topographies in the Left-Go condition for the Hypnosis group specifically. This map #11 was not seen during simulated paralysis, suggesting that neither classical voluntary inhibition nor residual motor activity were present in this time-window corresponding to inhibition and motor execution processes in other conditions.

3.4. Source localization

We next performed a source localization analysis (minimum-norm BrainStorm) (Tadel et al., 2011) in order to test for the neural sources leading to the specific topography differences between conditions. First, we compared sources active in the Nogo condition (map #7) relative to Go (maps #8 and #10), during a time-window overlapping with these distinctive maps and the P3 effect observed in ERPs (304–445 after instruction cue onset). A t-test was applied on the intensity of sources activated during this interval in these two conditions, for the normal context and both groups. This revealed a significant enhancement of sources in medial prefrontal areas during the Nogo condition ($t > 5.0, p < .001$), with a peak between 380–390 msec (Fig. 4) corresponding to the P3 effect (375 msec, see Figs. 1 and 2).

More importantly, we then tested for neural sources underlying the critical difference in activity around 334–406 msec (map #11) in the Left-Go condition under hypnotic paralysis, relative to sources active in the Left-Go with a simulated paralysis in the same time interval. Again, a t-test was applied on the intensity of sources activated during this interval in each of these conditions. As illustrated in Fig. 5a, the rIFG was the only region exhibiting significantly high activity during left hypnotic paralysis ($t = 2.16, p < .008$), overlapping with the mean latency of the P3 peak (375 msec).

To further test the modulation of activity in this region across all experimental conditions, we defined a region of interest (ROI) in the rIFG with 20 vertices in source space. We then calculated the distributed inverse solution for each subject and each condition, and extracted the averaged intensity of activity in this ROI.

We then performed ANOVAs on these intensity values for each hand separately (left and right) with the within-factors Instruction cue (Go vs Nogo) and Context (Paralysis vs Normal), plus the between-factor Group (Hypnosis vs Simulation). For the right hand, there was a significant main effect of Instruction cue ($p < .003, F = 13.05$), reflecting greater activity in rIFG in Nogo than Go, for both contexts (paralysis and normal) and both group (Fig. 5B, right graph). For the left hand, however, this analysis revealed a significant three-way interaction of Group $\times$ Context $\times$ Instruction ($p = .037, F = 4.93$). This reflected the fact that, for this hand, a differential increase for Nogo versus Go arose for both groups in the normal context (as for the right hand), whereas activity was higher in the Hypnosis group than the Simulation group during the paralysis context (Fig. 5B, left graph).

Follow-up ANOVAs conducted for the left hand in each context separately confirmed a main effect of instruction cue during the normal state ($p < .001, F = 19.08$), but a main effect of Group ($p = .005, F = 9.75$) during paralysis. Thus, source activity in the rIFG appeared to be enhanced during both the Left-Go and Left-Nogo trials during the hypnotic paralysis context. Taken together, these data therefore indicate that while Left-Go under hypnosis was associated with a unique topography configuration (i.e., map #11) reflecting differential activity in rIFG, this increase was also present in other trial conditions involving the left hand during hypnotic paralysis.

4. Discussion

Our study provides new insights on the neural substrate and time-course of executive control mechanisms underlying motor inhibition induced by hypnosis, and also highlights functional differences with voluntary motor inhibition produced by simulation. The role of executive attentional control during hypnosis has remained unclear in the literature, with some researchers proposing that it may heighten monitoring and control functions, associated with increased activity in frontal regions (e.g., ACC; see Cojan et al., 2009; Egner and Raz, 2007; Halligan et al., 2000); but other researchers suggested that it may actually involve reduced control and hypoactivation of frontal areas, leading to more automatic behaviours instead (Egner et al., 2005; Gruzelier, 1998; Kaiser et al., 1997). Here, by using a motor Go-Nogo task which includes a motor inhibition component, we could directly compare two distinct sources of inhibition, that is, when required by task demands or when induced by hypnosis. Our new data dovetail nicely with recent fMRI work (Cojan et al., 2009) indicating that the right IFG may play a key role in executive control mechanisms associated with the induction of hypnotic paralysis.

The behavioural results during our task showed that participants complied well with instructions in all conditions and showed appropriate performance in each experimental context: no response was made with the left hand on any trial (Go or Nogo) during the paralysis state (in both the hypnosis and Simulation groups), while very few errors were made in
the normal state (97% correct overall). However, the paralysis context induced a slight decrease in performance with the non-paralyzed right hand for both groups. This may reflect a general effect of the context of paralysis and greater attentional demands of the task in this condition, which required a response to only half of the Go stimuli during the induced paralysis and thus implied a partly dual task set with different “rules” for left and right hand (see Cojan et al., 2009). In contrast, in the normal context, participants had to respond with both hands similarly, allowing for more concentration and better accuracy. Importantly, however, this effect did not differ between the Hypnosis and Simulation groups, and if anything, the simulators tended to perform worse (particularly in the normal context), ruling out any global effect of hypnosis on attention or vigilance during the paralysis context.

Our EEG measures allowed us to probe for the effect of induced paralysis on neural activity associated with distinct stages of motor preparation and motor inhibition. In particular, our modified Go/Nogo task enabled us to test whether paralysis produced any change in the covert motor intentional stages prior to actual movement execution, in addition to any active inhibition at the time of the execution command itself. For the preparation phase, both the ERP waveforms and topographical analysis converged to indicate no significant modulations in the sequence or amplitude of brain activity...
across all task conditions, suggesting similar steps of information processing during the covert preparatory period preceding the Go/Nogo imperative cue. The absence of modulation concerning the left hand in the paralysis context suggests that the participants were engaged in the motor preparation in the same way with both hands. These data thus also indirectly indicate that the hypnotic paralysis does not imply a suppression of motor intention for the affected hand, although we could not observe any positive marker of motor preparation in this paradigm. Indeed, comparing right versus left motor preparation in our task did not disclose a reliable measure of asymmetrical preparatory activation such as the lateralized readiness potential (Cui et al., 1999; Muller-Gethmann et al., 2003), presumably due to the short interval between preparation and execution in this task (600–1000 msec). In any case, the lack of significant change or asymmetry in ERP activity during preparation in the paralysis context is broadly consistent with previous models postulating a persevered motor intention in hypnotic paralysis (Oakley, 1999), and to add previous findings showing intact preparatory activation in right motor cortex for a left paralyzed hand under hypnosis (Burgmer et al., 2012; Cojan et al., 2009). Thus, Burgmer et al. (2012) observed normal increases in the mirror motor system during movement observation after hypnotic paralysis of the left hand.

We note, however, that in our previous fMRI study using a similar Go/Nogo paradigm (Cojan et al., 2009), we found a specific increase in precuneus activity during the preparation of a left hand movement under the hypnotic suggestion of paralysis. This effect was attributed to a possible role of imagery and mnemonic processes associated with this region in relation to the hypnotic suggestion (Rainville et al., 2002). No correlate of this effect was found in the current ERP data. Differences in sensitivity between methods (EEG vs fMRI) and/or differences in the timing of the presentation of PREP cues in both studies could explain this discrepancy between the results of both studies. In our previous fMRI study, the PREP cues were presented with a longer duration (between 1000 msec and 5000 msec), while the present study focused on a shorter time-window of 600 msec after the onset of the cue. Even if temporal information is not readily accessible with fMRI, we can assume that different, additional or stronger, cognitive processes might take place within a longer time-window. Therefore, our fMRI results could presumably highlight later or more sustained processes that were not accessible in the time-range of our analysis in the current ERP study. This would accord with the view that activity in the precuneus might reflect slow cognitive processes implicated in motor imagery, memory, and self-representation (Cojan et al., 2009) appearing after 600 msec.

The second important result of our study was the finding that a specific succession of maps (map #8 and map #10) characterized motor execution on Go trials (in normal conditions), whereas a clearly distinct topography (map #7) arose for motor inhibition on Nogo trials (in normal conditions). These distinct maps for execution and inhibition were not only present for both hands in the normal context but also present for the normal (right) hand in the paralysis context (see Fig. 3). Notably, the map associated with inhibition was characterized by a specific voltage configuration over the scalp, with a typical central positivity and high amplitude (strong GFP) peaking 350–400 msec after the instruction cue onset. Moreover, this map overlapped with the positive component that was also selectively observed during Nogo trials in our waveform analysis. Both the topography and time-range of this inhibitory activity therefore accord with a P3 effect that has frequently been reported in previous EEG investigations of motor inhibition (e.g., Fallgatter et al., 1997; Bokura et al., 2001; Polich, 2007; Enriquez-Geppert et al., 2010). In contrast, with found no evidence for N2-like activity associated with inhibition (see Bokura et al., 2001), but recent research suggests that increases in N2 may not represent response inhibition but rather response conflict processing (Donkers and van Bokel, 2004; Randall and Smith, 2011). As there was no direct conflict between successive cues (preparation followed by instruction) in our paradigm, the current findings seem consistent with the view that this positive P3-like ERP configuration provides a reliable marker of neural activity specifically associated with inhibitory processes rather than conflict-monitoring (Enriquez-Geppert et al., 2010; Smith et al., 2008). Furthermore, our source localization analysis suggested that the distinctive topographical activity associated with inhibition (map #7) was accompanied with increased activity in medial prefrontal areas, consistent with an important role of these areas (particularly supplementary motor areas) in action inhibition (Coxon et al., 2009; Sagaspe et al., 2011; Sharp et al., 2010; Tabu et al., 2012). Most critically, however, our EEG results showed that these inhibitory processes active during the P3 time-range (map #7) were similarly recruited during Nogo trials for both hands in the normal context, but also during Nogo trials for the right hand in the paralysis context. These findings indicate that the induced paralysis did not impair information processing mechanisms underlying motor inhibition for the right hand. In addition, the absence of this specific EEG topography during paralysis on the Left-Go trials (in both contexts) also suggests that paralysis was not produced through the recruitment of the same inhibitory mechanisms (see also Cojan et al., 2009).

Finally, a third important result concerned a distinctive pattern of brain activity associated with hypnotic paralysis. Indeed, we were able to demonstrate that one specific configuration (map #11) was uniquely observed during the hypnotic suggestion of paralysis on the critical Left-Go trials (i.e., with the affected hand). This map was not identified by the ERP segmentation analysis in any time point during any of the other experimental conditions, including for the simulated paralysis on Left-Go trials (see Fig. 3). Moreover, this activity clearly differed from those seen during motor execution (maps #8 and #10) or voluntary inhibition (map #7). This observation again highlights a functional difference in the neural processes involved when a subject subjectively experienced a paralysis induced by hypnosis and has to execute a movement, relative to when a subject fakes a paralysis intentionally. In addition, it is worth noting that the latency of map #11 also coincided with the latency of the P3 component, which was related to voluntary response inhibition in the present study (see above) and previous work (Enriquez-Geppert et al., 2010; Smith et al., 2007). However, the existence of distinct topographies implies that they must have been generated by different configuration of active sources in
the brain (Michel et al., 2004). Accordingly, our source localization analysis revealed a distinctive activation in the right inferior frontal cortex during the hypnotic paralysis, relative to the simulated paralysis. These findings therefore suggest a specific role of executive control mechanisms mediated by right prefrontal areas in the mechanisms of hypnosis, a result converging with recent data from fMRI (Cojan et al., 2009) which also demonstrated a unique pattern of increased activity in the right inferior and middle frontal gyri during left hypnotic paralysis. The rIFG activates in various conditions requiring a suppression or change in motor or cognitive programs, including Nogo or Stop (Aron et al., 2003; Rubia et al., 2003; Swick et al., 2011), whereas the rMFG is linked with high-level executive functions (Talati and Hirsch, 2005), such as attentional effort (Demeter et al., 2011) and adjustment to novel stimulus-response contingencies (Brass et al., 2005). More generally, therefore, our data provide new support to the notion that the frontal cortex is not inhibited by hypnosis, neither due to the specific suggestion of paralysis, nor due the more general context of hypnosis. This adds to the growing evidence that hypnosis may involve specific attentional processes and thus corroborates neurocognitive models linking hypnosis with attentional control (Cojan et al., 2009; Crawford, 1994; Oakley, 1999; Oakley and Halligan, 2009).

Remarkably, when further inspecting the intensity of source activity in the rIFG across conditions, we found that it was also significantly increased by voluntary inhibition on Nogo trials (relative to motor execution on Go trials) for both hands in the normal context, and for the right hand in the paralysis context. This pattern nicely dovetails with functional neuroimaging (Aron et al., 2004a, 2004b; Garavan et al., 1999; Hampshire et al., 2010; Konishi et al., 1999) and neuropsychology studies (for review see Aron et al., 2003; Chikazoe, 2010) that consistently reported that the rIFG is implicated in tasks requiring response inhibition or executive control, in concert with other fronto-parietal areas more generally involved in top-down attention, orienting, or shifting (Corbetta et al., 2008; Raz, 2004). However, this pattern of activity in rIFG was markedly (and selectively) modified for the left hand in the paralysis context: this source showed a relative increase in intensity for all left conditions (Go and Nogo) during hypnosis, whereas a relative decrease was seen in the same conditions during simulation. Taken together, these data suggest that, even though map #11 was selectively expressed during the Left-Go trials under hypnosis, the rIFG might not only be recruited for inhibiting movement with the paralyzed hand in this condition, but rather be more generally engaged for controlling actions with the left hand during hypnosis (unlike during simulation where it appeared disengaged instead). Moreover, since map #11 was not seen in our segmentation analysis for other conditions, it is likely that the rIFG activity reflected by this map might have been mixed with (and thus masked by) additional sources in fronto-parietal networks during Nogo trials in the normal conditions, with stronger field power, therefore resulting in a distinct topography during these trials (i.e., map #7). In keeping with the latter conjecture, our previous fMRI results indicated that the right inferior frontal cortex may show a sustained increase in activity during hypnosis as compared with the normal state, irrespective of task conditions, which was interpreted as reflecting a state of globally enhanced monitoring or “hypercontrol” allowing external stimuli to be effectively filtered out and internal representations to override instead. Therefore, our current finding that hypnotic paralysis was associated with a unique configuration of brain activity, as revealed by the specific appearance of map #11 in Left-Go trials in this context, provides striking and converging evidence across different methods and different populations that the right inferior frontal areas may play a key role in attentional mechanisms mediating hypnotic phenomena.

It remains to be clarified however whether this right-hemispheric laterality, typically observed for both hands during motor inhibition tasks (Aron et al., 2004a, 2004b; Garavan et al., 1999; Hampshire et al., 2010; Konishi et al., 1999), would also hold when hypnotic paralysis is induced on the right side. Like many previous studies, we focused on motor function of the left hand only (see also Blakemore et al., 2003; Cardena et al., 2012; Cojan et al., 2009; Halligan et al., 2000; Marshall et al., 1997), which could potentially bias the laterality of our findings. However, our results are thus comparable with these previous studies, and unlikely to differ for right-sided motor changes since the most critical brain areas were not related to elementary motor or sensory functions. Nonetheless, future work should definitely address this issue by comparing both arms. We also note that a recent EEG study (Cardena et al., 2012) during hypnotically induced levitation of the left arm reported changes in fast rhythmic frequencies over the left frontal regions, rather than changes in the right hemisphere. This difference between this study and ours could reflect the difference in paradigm and lack of inhibition during levitation (as opposed to paralysis), and might accord with fMRI results showing more sustained activation in left prefrontal cortex attributed to task-set maintenance during hypnotic suggestion (Cojan et al., 2009). In any case, the role of each hemisphere and the laterality of hypnotic effects remain to be more fully clarified. Future research also needs to better integrate the current modulation of prefrontal control processes observed during an active motor task with changes induced by hypnosis in the default mode network at rest (McGeown et al., 2009, Pyka et al., 2011).

In sum, our EEG study adds novel support to previous hypotheses that the prefrontal cortex is not hypoactive during hypnosis but rather exhibits significant increases in activity within brain regions intimately connected to executive control and attention (Cojan et al., 2009; Ward et al., 2003). Our data also confirm an involvement of specific control processes during hypnotic paralysis, distinct from those implicated in voluntary inhibition under normal conditions (see Cojan et al., 2009) and reflected by a P3 component in ERPs, but seemingly operating in the same time-window as voluntary inhibition. It remains to be seen whether similar patterns are observed in other hypnotic phenomena characterized by the inhibition of different motor or sensory modalities.

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