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Effect of gravity on human spontaneous 10-Hz electroencephalographic oscillations during the arrest reaction

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ABSTRACT

Electroencephalographic oscillations at 10 Hz (alpha and mu rhythms) are the most prominent rhythms observed in awake, relaxed (eye-closed) subjects. These oscillations may be considered as a marker of cortical inactivity or an index of the active inhibition of the sensory information. Different cortical sources may participate in the 10-Hz oscillation and appear to be modulated by the sensory context and functional demands. In microgravity, the marked reduction in multimodal graviceptive inputs to cortical networks participating in the representation of space could be expected to affect the 10-Hz activity. The effect of microgravity on this basic oscillation has heretofore not been studied quantitatively. Because the alpha rhythm has a functional role in the regulation of network properties of the visual areas, we hypothesised that the absence of gravity would affect its strength. Here, we report the results of an experiment conducted over the course of 3 space flights, in which we quantified the power of the 10-Hz activity in relation to the arrest reaction (i.e., in 2 distinct physiological states: eyes open and eyes closed). We observed that the power of the spontaneous 10-Hz oscillation recorded in the eyes-closed state in the parieto-occipital (alpha rhythm) and sensorimotor areas (mu rhythm) increased in the absence of gravity. The suppression coefficient during the arrest reaction and the related spectral perturbations produced by eye-opening/closure state transition also increased in on orbit. These results are discussed in terms of current theories on the source and the importance of the alpha rhythm for cognitive function.

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1. Introduction

In the last few years, electroencephalography (EEG) applied in the emerging field of 'neuronal oscillations' (Buzsaki and Draguhn, 2004) has provided new insights into the neurophy-

siological activity underlying perceptual processes in the brain. The EEG signal is considered as a macroscopic sum of local field potentials induced by synchronised dendritic depolarisation of the pyramidal cells in the cortex. Among the different activities extending from very slow to ultra-fast frequencies, the alpha

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rhythm around 10 Hz (range 8–12 Hz) is the most prominent rhythm observed in awake, relaxed subjects (Berger, 1929). It has classically been considered as a marker of cortical inactivity, i.e., 'cortical idling' (Pfurtscheller and Aranibar, 1977; Pfurtscheller et al., 1996). This dominant rhythm is most pronounced at occipital and parietal recording sites during eye closure, but can be recorded at other locations over the scalp, e.g., corresponding to the mu rhythm over the sensorimotor cortex (Gastaut, 1952; Pfurtscheller et al., 1996).

As scalp EEG signals are produced by partial synchronisation of neuronal-scale field potentials across a cm^2-scale, each scalp electrode records a weighted mixture of different cortical sources that may be concurrently modulated by different processes (Makeig et al., 2000). For example, the alpha activity in the lower (8–10 Hz) and upper (10–12 Hz) frequency ranges appear to be modulated differently depending on the functional demand. Lower frequency alpha activity (8–10 Hz) has been suggested to indicate the state of arousal, whereas the upper frequency alpha activity (10–12 Hz) seems to be related to specific cognitive functions such as memory encoding (Klimesch, 1996). It has been proposed that alpha rhythm may indicate the active inhibition of sensory information during internally directed tasks involving imagination. A large upper alpha power in a reference interval preceding a task is related to both large suppression of upper alpha power during the task and good performance (Klimesch et al., 1990; Hanslmayr et al., 2005). Repetitive transcranial magnetic stimulation (TMS) given at the individual's alpha rhythm frequency improves cognitive performance (Klimesch et al., 2003).

The arrest reaction of the alpha rhythm on eye opening, first described by Berger (1929), is highly stable. It occurs over a large part of the brain and provides two distinct physiological states induced by opening or closure the eyes. It could thus serve as a prototypical and experimentally practical model system for studying the effects of microgravity on the background spontaneous alpha dynamics.

When performing day-to-day activities, the brain must deal with the effects that gravity has on the human body and environment. A number of different sensors related to the visual, vestibular and proprioceptive systems convey specific information about gravity (for a review, see Berthoz and Güell, 1998). Previous experiments conducted in microgravity (Lipshits et al., 2001, 2005; McIntyre et al., 1998, 2001) have shown that subjects acquire and store visual information in a multimodal reference frame that combines proprioceptive (egocentric) and gravitational (allocentric) information when both are available. The dynamic interaction of the brain with the physical world is thus moulded within the gravitational constraints.

The gravito-inertial forces acting on the otolith organs and the interaction between these receptors and the semicircular canals provide a fundamental reference about the orientation of the head and body relative to the gravity vector. These vestibular signals are not only combined with visual cues, which play a dominant role (Clement et al., 1987), but also with somatosensory information (Maurer et al., 2000). Proprioceptors along the trunk and lower extremities, such as tactile mechanoreceptors, muscle spindles and Golgi tendon organs, provide neural information on the relative position of segments (Dietz and Duysens, 2000; Mergner et al., 1998). These

proprioreceptors may also serve as indicators of the subjective vertical (Bronstein, 1999), which is an essential component of the egocentric representation of the 3D space, especially in the absence of visual guidance (Lestienne and Gurfinkel, 1988). Furthermore, as already proposed by Mittelstaedt (1996), recent experiments (Jarchow et al., 2003) have demonstrated the existence of non-otolithic graviceptors located in the neck and in the lower chest. Movement of the abdominal mass, sensed by visceral receptors, could be another source of extravestibular graviception. Baroreceptors have also been found in the human body at the aortic output of the heart as well as on the outside of the kidneys (Mittelstaedt, 1996).

Gravity plays a particularly crucial role in the perception of the vertical axis and in building of the neural representation of space. This representation results in fine from integration of the various signals related to gravity that are processed in different areas of the posterior parietal and vestibular cortex. These different cortical areas combine signals with different modalities into a common spatial frame (Berthoz, 1991; Andersen et al., 1997). The electrical stimulation of the lateral temporo-parietal area induces pitch or yaw plane illusions (Kahane et al., 2003), demonstrating a high level of spatial plane integration in the brain. This region participates in a network that is activated by visual motion or vestibular stimulation. This "vestibular network" is composed of the temporo-parietal junction, the cingulate cortex, the ventral premotor area, the supplementary motor area, the middle and post-central gyrus, the posterior thalamus and the putamen. It was recently demonstrated (Indovina et al., 2005) that the vestibular network is involved in processing visual motion when it is coherent with natural gravity, supporting the hypothesis that the fundamental physical constraint of Earth's gravity is internalised in human brain processing.

In spite of the importance of graviception on Earth for visuomotor and other aspects of motor control, performance of cosmonauts remains relatively good in microgravity (for a review, see Berthoz and Güell, 1998; Vidal et al., 2003; White et al., 2005). For example, the performance of a mental rotation task in which cosmonauts judged whether two 3D objects presented in different orientations were the same is identical in microgravity and in normal gravity (Leone et al., 1995). This suggests the existence of a strong regulatory process exerted on the different inputs of the cortex.

Because alpha rhythm has a functional role in the regulation of network properties of the visual areas (e.g., in gain regulation, Lopes da Silva et al., 1974), microgravity can be expected to modify the strength of this regulation in order to preserve the functionality of the network in a novel environment. Although the presence of alpha rhythm has been documented in microgravity (Maulsby, 1966; Elliott et al., 2001), no quantified analysis of the arrest reaction was performed. A major hypothesis of the present study is that the marked reduction all these multimodal graviceptive inputs to the vestibular network, and more generally to cortical representation of space and body in space could be expected to affect the background EEG activity and in particular during the arrest reaction. Previous EEG studies have been conducted in microgravity, pioneering with early flights in the 1960s (Maulsby, 1966). The focus was essentially placed on sleep EEG. Recent studies also addressed sleep EEG

during space flights (Elliott et al., 2001). However, the effect of microgravity on EEG has not been studied systematically in perception or navigation tasks.

2. Results

2.1. Variations of 10-Hz oscillations during the arrest reaction

Fig. 1 illustrates the raw EEG recorded in the ISS in one cosmonaut during the arrest reaction. In the eyes-closed state, the alpha rhythm appears as spindle-shaped episodes of oscillation peaking around 10 Hz that dominate the spontaneous activity of the brain. In all 14 channels, 10-Hz oscillations are well recognisable, showing higher amplitude over the parieto-occipital region. The arrest reaction reveals some functional differences between the 10-Hz activity recorded in the posterior versus anterior loci. Just after the order to open the eyes, the 10-Hz rhythm recorded at the frontal and sensorimotor loci (corresponding to the mu rhythm) is suppressed whereas the parieto-occipital alpha remains unchanged. The latter is only suppressed after the eyes actually open. FFT analysis performed throughout the 14 channels during the eye-closed, relaxation state confirmed the prevalence of the 10-Hz activity (peak range between 9.5 and 10.5 Hz, Fig. 2A). The power spectrum of this dominant rhythm greatly decreased in the eyes-opened state (Fig. 2B).

2.2. Comparison between earth and microgravity conditions

We compared statistically the measurements performed before the flight (EB), in flight (W) and after the flight (EA) with a single-factor ANOVA test with 3 levels. Fig. 3 illustrates the main effect of microgravity in a grand average pool of data (all 5 cosmonauts). A small but significant shift ($p < 0.00002$) of the mean alpha peak frequency was noted (9.9 ± 0.5 Hz on Earth vs. 10.4 ± 0.4 Hz in the ISS). The base-to-peak amplitude of the power spectrum of the alpha rhythm (illustrated for the P3 channel) in the eyes-closed state is significantly increased in microgravity compared to that measured on Earth before or after the flight ($p < 0.001$). In contrast, the base-to-peak amplitude of the power spectrum in the eyes-open state was not significantly different in microgravity (Fig. 3A) ($p = 0.48$). We defined a suppression coefficient (SC) as the peak value resulting from the subtraction of the power spectrum recorded in the eyes-closed state (continuous lines in Fig. 3A) from that recorded in the eyes-opened state (pointed lines in Fig. 3A). SC significantly increased in microgravity (Fig. 3B). In order to test the effect of postural constraints in the ISS (somatosensory stimulations provided by the foot and thigh straps in the attached condition), we performed the same set of recordings in a free-floating condition. No difference in the alpha rhythm power and SC was found between these two conditions. Fig. 3C illustrates the stability of SC on Earth in both cosmonauts and non-cosmonauts (EB vs. EA, n.s.) and their significant increase in cosmonauts in microgravity (W vs. EB and EA). The mean values and SD are very close for both control group and cosmonauts on Earth before and after the flight. Statistical analysis confirms the absence of difference between cosmonauts on Earth and the control group.

The head figurines of Fig. 4 illustrated the difference between the SC measured in the ISS and on Earth (with data recorded before and after flight pooled together) for cosmonauts (A) and between the EDF vs. EB and EA combined periods for the control subjects (B). Statistical analysis revealed that the SC values recorded in parieto-occipital (O1, O2, Pz, P3, P4) and central (C3, C4, Cz) loci were significantly increased in
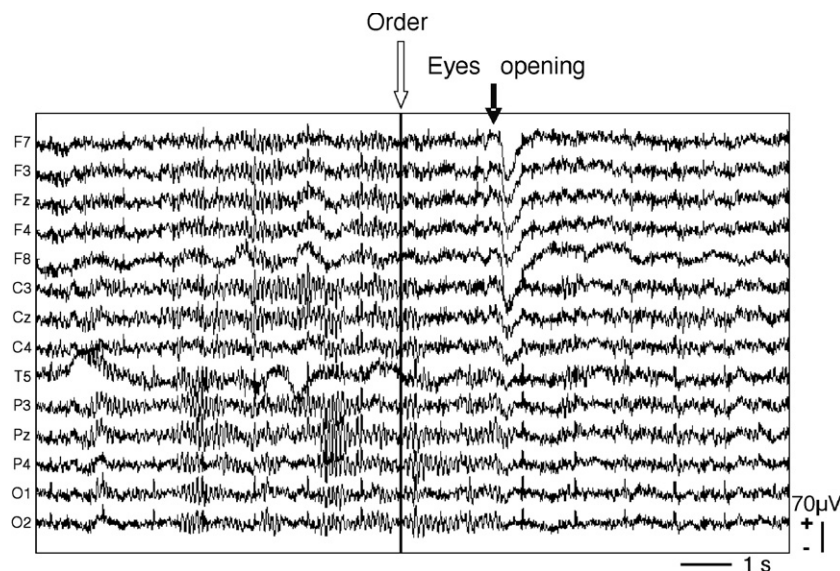

Fig. 1 – Raw EEG recordings during the arrest reaction in weightlessness. Fourteen EEG channels referenced to linked mastoid (from F7 top) to O2 (bottom). The white arrow indexes to the order to open the eyes. The black arrow points to the onset of the eye movement artefact related to eye opening, mainly recorded by frontal electrodes (F7, F3, FZ, F4, F8). Note that the amplitude of mu rhythm (recorded by central electrodes (C3, CZ, C4)) is reduced before eye opening whereas alpha rhythm (P3, P4, PZ, O1, O2) is only reduced after this movement.
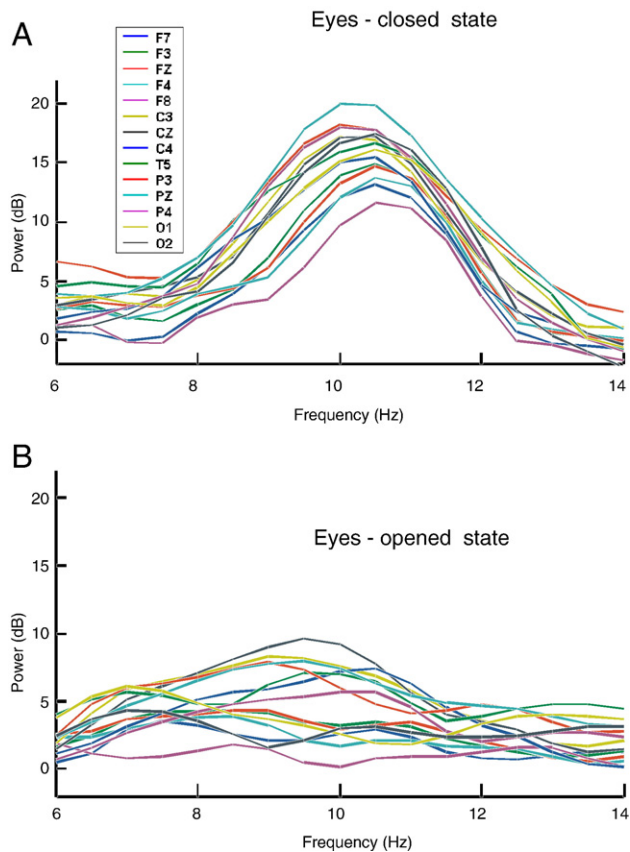
Fig. 2 – Power spectral analysis in eyes-closed and eyes-opened states. Fast Fourier transform analysis in one cosmonaut of all recorded channels in eyes-closed (A) and in eyes-opened (B) states.

microgravity. The three latter electrodes are situated over the sensorimotor cortex, which is the site of mu rhythm. In contrast, the SC values of the frontal recordings (Fz, F3, F4, F7, F8) remained unchanged in microgravity (Fig. 4A). The same analysis performed in the control subjects showed a great stability of the SC values throughout the same period of time in all recorded channels (Fig. 4B).

2.3. Dynamic analysis of the alpha rhythm during the arrest reaction

Dynamic analysis of EEG signals was performed during the transition between the eyes-open and eyes-closed states. ERSP method was applied as illustrated in Figs. 5 and 6. The same set of recorded data as that treated by classical (static) FFT analysis (see Fig. 2) was used for this ERSP approach. In order to visualise power changes across the frequency range (extending here from 1 to 50 Hz), we subtracted the mean baseline log power spectrum from each spectral estimate using the EEGLAB software. The baseline-normalised ERSP that preceded the eyes-opening (Fig. 5) or the eyes-closing (Fig. 6) events were settled for all the frequencies for ERSP values around 0 dB. Time 0 corresponds to the order for opening (Fig. 5) or closing (Fig. 6) the eyes. After the order was given, a relatively thin band of spectral perturbation occurred in the alpha rhythm as an ERD

(blue) after eyes-opening (Fig. 5) or an ERS (red) after eyes-closure (Fig. 6). The frequency peak of these ERSP bands remained relatively stable during all the eyes-open period in spite of the presence of some band clustering. When the same procedure was applied on the EEG recorded in the ISS, the same phenomenon was observed but with a greater strength. The spectral perturbations remained centred on the alpha rhythm band but were stronger and the frequency band widths were slightly larger (Figs. 5B and 6B). In order to quantify the amplitude of this dynamic behaviour, we measured the difference between maximal values of the ERD and ERS and we compared the resulting values obtained on Earth with those recorded in the ISS. The mean amplitude was 22.9±2.3 dB on Earth, and 32.0±3.1 in the ISS. This increase was highly significant ($p < 0.003$) and confirmed the previous FFT analysis. Fig. 7 illustrates the grand average of both transitions. The rate of rise of the alpha rhythm emergence was significantly higher in the ISS (slope=19.6±7.3 dB/s) when compared with Earth recordings before (slope=6.5±1.9 dB/s) and after (slope=4.5±1.8 dB/s) the flight (Fig. 7A). Conversely, the rate of alpha suppression was not significantly steeper in ISS (Fig. 7B).

3. Discussion

Our findings demonstrate that the power of the spontaneous 10-Hz EEG alpha rhythm recorded in the parieto-occipital regions and those recorded in the sensorimotor areas (mu rhythm) are increased, and that the spectral perturbations of these rhythmic activities produced by eye-opening/closure state transition are potentiated, in microgravity.

3.1. Gravity signals as a regulator of the 10-Hz rhythm: neuronal hypotheses

Neuronal networks of the human brain can display different states of synchrony characterised by their EEG oscillation frequencies (Steriade, 2000). These oscillations play a broad role in the nervous system and form the basis for sensorimotor functions (Baker and Baker, 2003), cognition (Llinas and Pare, 1991; Fries et al., 2001), consciousness (Crick and Koch, 1990; Llinas and Ribary, 1993; Varela et al., 2001) and emotions (Hinrichs and Machleidt, 1992).

Berger (1929) first described that the alpha rhythm is stronger in a state of relaxed wakefulness when the eyes are closed and that opening the eyes can block the occipital alpha rhythm. This arrest reaction or alpha blocking was interpreted as desynchronisation of the spontaneous cortical oscillatory background activity by the massive visual afferent input (Adrian and Matthews, 1934). However, its amplitude is not simply a reflection of the amount of visual stimulation. For example, even intentional 'looking' with the eyes closed can decrease alpha rhythm amplitude (unpublished observations). Conversely, profound relaxation in the eyes-open state may increase alpha amplitude. Alpha rhythm generators have been localised by multichannel magnetoencephalography and electroencephalography within the primary and secondary visual areas of the occipital and in the parieto-occipital cortex (Hari et al., 1997; Manshanden et al., 2002). However, the cortical and subcortical brain regions participating in the

state-related fluctuations of the alpha rhythm as well as their functional role in the arrest reaction are not yet conclusively described (Steriade, 2000). Subcortical nuclei such as the thalamus are involved in the active gating of different sensory influx (Steriade et al., 1997) and contribute to the alpha rhythm change recorded during visual attention (Babiloni et al., 2004), vigilance (Lopes da Silva et al., 1997) and arrest reaction (Feige et al., 2005). At least two different types of processes might be involved in the regulation of the alpha rhythm. One is related to intracortical synchronisation (Lopes da Silva et al., 1997), the other to feedback loops between inhibitory cells in the thalamic reticular nucleus and thalamocortical neurons, such as those described during sleep spindle oscillations (Steriade and Llinás, 1988). In this latter case, the large amplitude of the alpha rhythm would result from a coherent cortical drive from the thalamus coincident with a lack of other input. The appearance of a high-amplitude 10-Hz rhythm on the scalp

may be viewed as the expression of a default oscillatory state driven by rhythmic input compatible to their resonant frequency (Narici and Romani, 1989). In this theoretical framework, microgravity could facilitate the expression of a single-peak 10-Hz dominant rhythm at rest resulting in an increase of the 10-Hz power in microgravity.

Mu rhythm most often occurs during a pre-movement period and ceases around movement onset (Donoghue et al., 1998; Pfurtscheller et al., 2003). The decrease in mu rhythm roughly coincides with the increase in gamma oscillation above 30 Hz (Pfurtscheller et al., 2003) and with the appearance of firing rate modulation of cortical neurons coupled to the motor action (Donoghue et al., 1998; Wolpaw and McFarland, 2004). In the present study mu rhythm was dissociated from the posterior alpha rhythm by its early desynchronisation occurring well before eye opening. The significant increase in its power in microgravity indicates physiological similarity with the parieto-occipital alpha rhythm but not with the frontal alpha rhythm, which remained unchanged in micro-gravity. This may indicate that the sensorimotor and the parieto-occipital cortex are linked through a common network that is affected by gravity, possibly because these cortical areas rely on a common reference frame that is influenced by gravity. The posterior parietal cortex, one of the sources of the alpha rhythm, is situated at a transition between the sensory and the motor cortex. It is implicated in transforming sensory signals into plans for action and it is involved in the integration of space representation (Andersen et al., 1997, 1999). Record-ings of the local field potential in this part of the cortex in the monkey have demonstrated a temporal structure of the signal that varies with the type of planned or executed motor behaviour (Scherberger et al., 2005). Moreover, a vestibular network has been identified in the parietal cortex involving the temporo-parietal junction (Bottini et al., 2001; Lobel et al., 1998; Brandt and Dieterich, 1999; Kahane et al., 2003; Indovina et al., 2005) which is involved in the processing of gravity. It may therefore be expected that the background oscillating activities of these regions are influenced by the different signals related to gravity. By comparing the eyes-closed and eyes-opened states in complete darkness using fMRI, Marx et al. (2004) have defined an 'interoceptive' (eyes-closed) state, characterised by
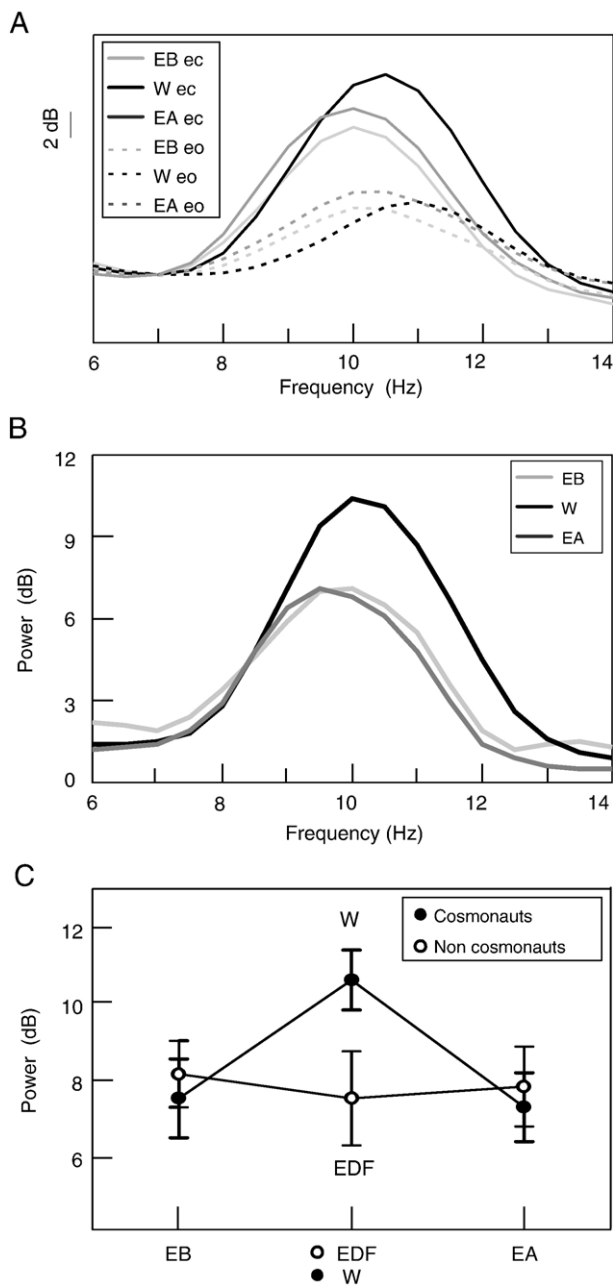

Fig. 3 – Power spectrum recorded at P3 and the suppression coefficient during the arrest reaction. (A) Superimposition of grand averaged power spectrum of the EEG recorded from the P3 channel in the eyes-closed state (ec) and in the eyes-opened state (eo) on Earth before the flight (EB), in weightlessness (W) and on Earth after the flight (EA). (B) Superimposition of the curve representing the difference between the power spectrums recorded in the eyes-closed and eyes-opened states. The peak value represents the suppression coefficient of the alpha rhythm during the arrest reaction. (C) Comparison of the suppression coefficient of the alpha rhythm (mean values and SD) recorded in the non-cosmonauts (○) and cosmonauts (●) on Earth before the flight (EB), in weightlessness (W), on Earth during the flight (EDF) period and on Earth after the flight (EA). Note the stability of the suppression coefficient on Earth in both control subjects and cosmonauts and their significant increase in cosmonauts in weightlessness.
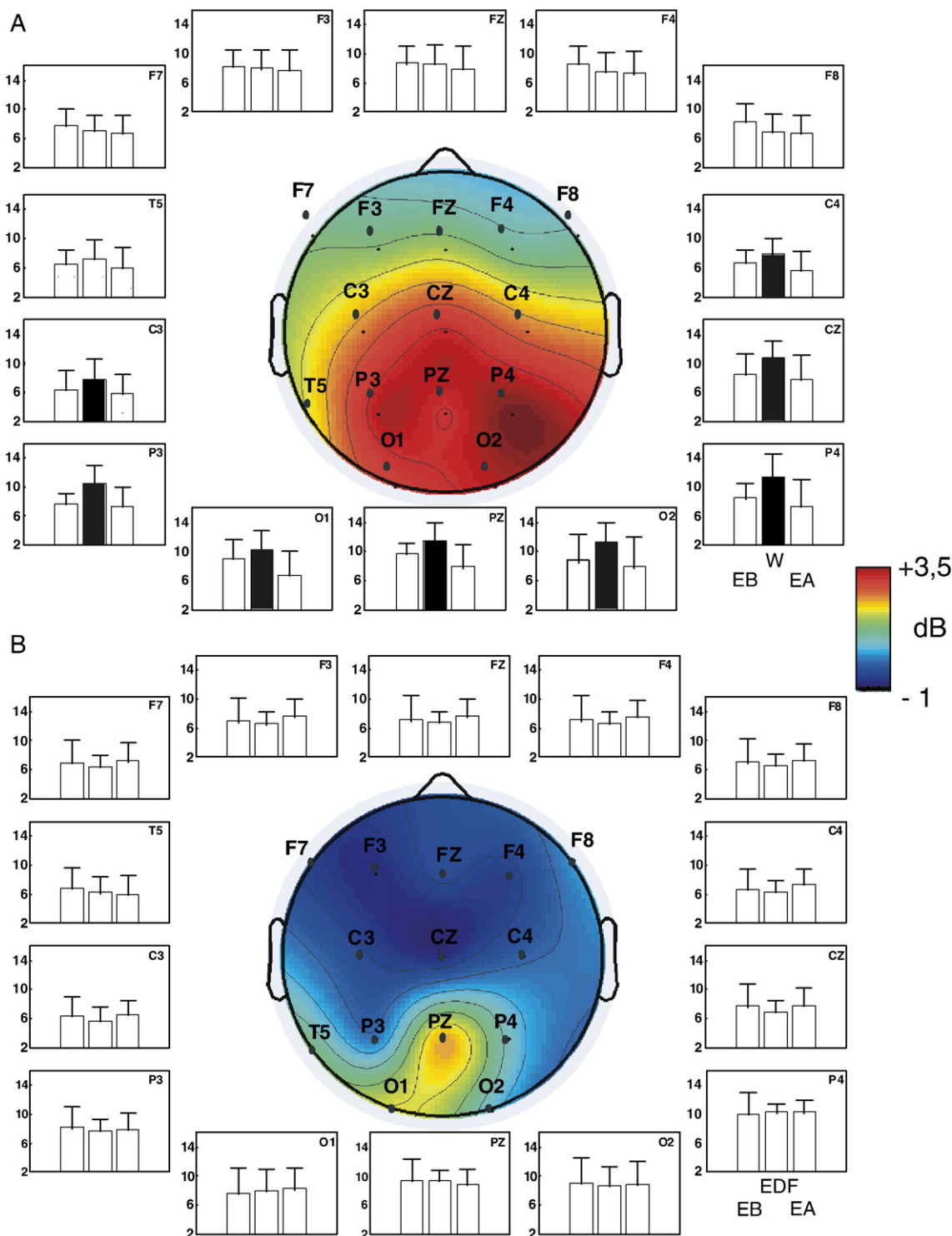
Fig. 4 – Topography of the effect of weightlessness on the 10-Hz 'suppression'. Topographical histograms of the 10-Hz suppression (arrest reaction) recorded in cosmonauts ($n=5$) (A) on Earth before the flight (EB), in weightlessness (W) (for the) and on Earth after the flight (EA) and in non-cosmonauts on Earth during the same period of flight ($n=5$) (B). The scalp maps summarise in a grand averaged mode the topographical difference in the 10-Hz 'suppression' coefficient (SC) between the recordings performed in weightlessness and on Earth. The differences in SC values are expressed in a colour scale in dB. The black bars in the histograms correspond to significant SC values ($p<0.05$).

imagination and multisensory activation, and an 'exterocep- tive' (eyes-opened) state, largely dominated by attention and ocular motricity. The increase of the alpha and mu rhythm in

microgravity in the eye-closed state but not in the eye-opened state may be viewed as the expression of a new level of the 'interoceptive' state reached by the cosmonauts. On Earth, in
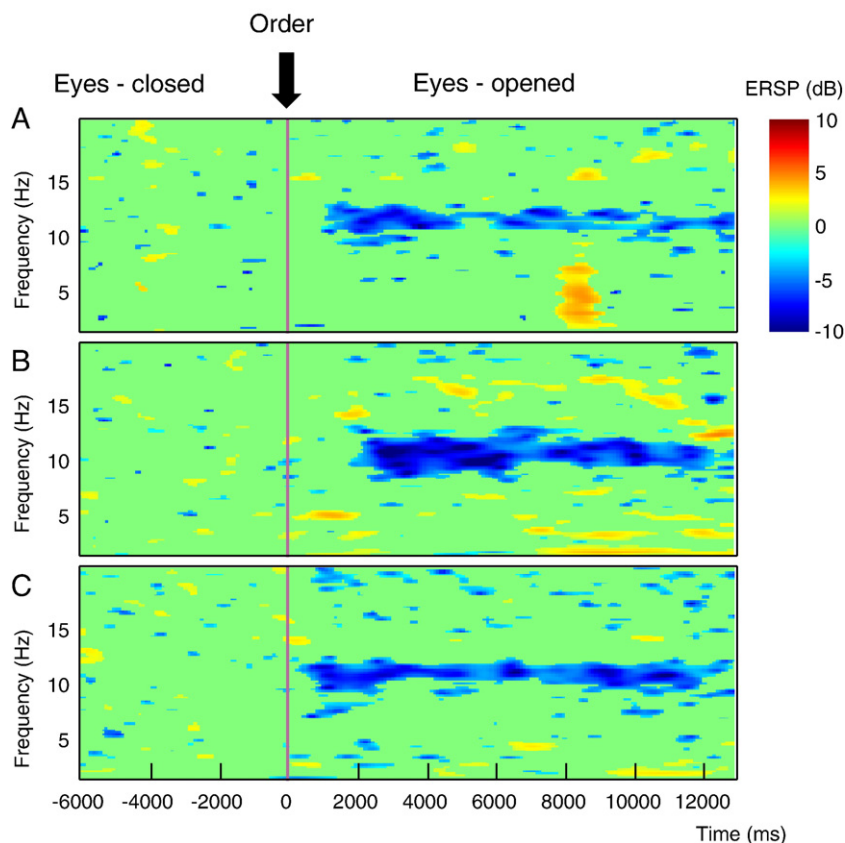
Fig. 5 – Event-related spectral perturbation (ERSP) time-locked to the order of eyes opening. (A–C) ERSP-image plot of the colour-coded single trials of the EEG spectrum recorded in P3 channel in one cosmonaut (C1) on Earth before the flight (A), in weightlessness (B) and on Earth after the flight (C). The trials are time-locked to the order to open the eyes (stripped line). Blue colour indicates a decrease in power.

the eye-closed state all the graviceptor inputs are actively conserved and contribute to keep the neural representation of space relatively constant in spite of the absence of vision. In this 'interoceptive' state, excitatory inputs related to gravity can be expected to modulate (decrease) the power of the dominant 10-Hz oscillation. Conversely, the reduction of these gravity-related signals in the ISS can induce an increase of the alpha and mu power only in the absence of visual information. In the eye-open state the same amount of visual information is able to suppress the higher 10-Hz oscillation as on Earth, indicating the maintenance of the prevalence given to visual inputs in microgravity (Clement et al., 1987).

The alpha rhythm has also been considered as a mechanism for increasing signal-to-noise ratios within the cortex by means of inhibition of unnecessary or conflicting processes to the current task (Klimesch, 1999; Klimesch et al., 2000). In this framework, that is compatible with Crick's spotlight-of-attention hypothesis (Crick, 1984), alpha rhythm synchronisation acts as a surrounding inhibition mechanism regulating the sensitivity of a focally active cortical network: the greater the task demands within this network, the more inhibition is needed and the greater the synchronisation. The perturbation of the reference frame and the sensory conflicts produced by microgravity could necessitate such a type of regulation. Indeed, the detection and amplification of weak signals are facilitated by coherent summation of oscillators. The augmenting

properties of resonators-oscillators (Buzsaki and Draguhn, 2004) probably implicated in the increase of the alpha and mu power may also induce some cortical plasticity that is necessary for adaptation of the reference frame to microgravity. In this context, reverberation in cortico-thalamic loops is able to produce self-sustained rhythmic activities indicative of "memory" events (Steriade and Timofeev, 2003).

Although the results of cognitive testing in microgravity are varied, there are many examples in which cognitive processes are unaffected by the absence of gravity. For instance, cognitive processing involved in visual discrimination test of the oblique effect was conserved in microgravity; the relative advantage of vertical and horizontal stimuli over oblique orientations was maintained, both in free-floating and in attached position (Lipshits et al., 2005). Speed and accuracy of short-term memory retrieval and logical reasoning functions have also been observed to be unimpaired in weightlessness (Manzey et al., 1993; Manzey and Lorenz, 1998). It is unlikely therefore that the increase of the resting state of alpha and mu rhythms in weightlessness is indicative of global cognitive impairments in 0 g.

3.2. Influence of parameters unrelated to gravity

Most alpha activity parameters are known to be stable over time (Salinsky et al., 1991; Pollock et al., 1991), facilitating
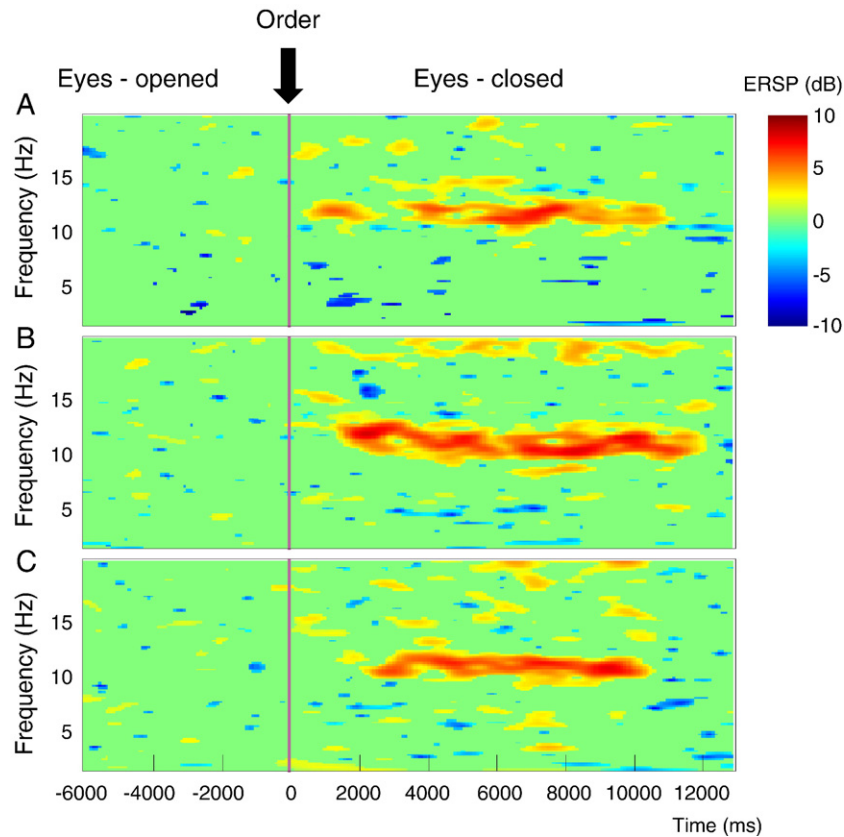
Fig. 6 – Event-related spectral perturbation (ERSP) time-locked to the order of eyes closing. (A–C) ERSP-image plot of the colour-coded single trials of the EEG spectrum recorded in P3 channel in one cosmonaut (C1) on Earth before the flight (A), in weightlessness (B) and on Earth after the flight (C). The trials are time-locked to the order to close the eyes (stripped line). Red colour indicates an increase in power.

longitudinal studies. This stability was further confirmed in our control subjects. However, a number of parameters have been demonstrated to have an effect on alpha rhythm. Auditory stimulation was shown to be able to trigger an increase in alpha rhythm amplitude in the eyes-opened state (Feige et al., 2005). This cross-modal influence can be interpreted as a gating effect exerted by the auditory stimulation on the visual system, unmasking the resting alpha oscillation (Pfurtscheller, 1992). However, the background noise inherent to the ISS environment (90 dB) cannot explain the increase in the alpha power that we found in microgravity, as alpha power was not increased in the eyes-open state, even though the auditory stimuli were the same. Other uncontrolled parameters that could interfere with the EEG, such as medication or major sleep alterations were ruled out.

3.3. Influence of cortical arousal and emotion

Increases in lower frequency alpha power have been recorded in conjunction with positive emotional reactions such as joy in adults (Hinrichs and Machleidt, 1992; Petsche et al., 1997) mimicking the hedonic hypersynchrony of the theta rhythm recorded in infants (Lehtonen et al., 2002). In this context, microgravity could perhaps be viewed as a pleasant situation (as reported by the cosmonauts), perhaps leading to an alpha power increase. However, reproducible change in power was found throughout the experiments conducted in space, arguing against an emotional effect. As noted by Cervantes et al. (1975), EEG synchronisation in response to pleasant stimulation requires a concomitant decrease in afferent inflow from some of the muscles involved in postural control including head, neck and trunk muscles. This requirement may be fulfilled in the ISS. However, the two different postures (*attached* or *free-floating*) did not influence the increase in alpha power, further confirming the dominant and stable character of the alpha power increase in microgravity. Therefore, the absence of graviception seems to be the main factor associated with the enhancement of alpha and mu rhythm in the ISS.

3.4. Haemodynamic effects on alpha rhythm

In line with previous studies showing negative correlations between alpha rhythm and brain metabolic markers (Sadato et al., 1998; Goldman et al., 2002; Moosmann et al., 2003), Feige et al. (2005) demonstrated an inverse relationship between the alpha power amplitude and blood oxygen level-dependent (BOLD) signal change during the arrest reaction. BOLD signals are significantly increased in primary and secondary visual areas after eye opening when the alpha rhythm power is the lowest. Conversely, primary visual areas and the thalamic lateral geniculate nuclei were deactivated when the eyes are
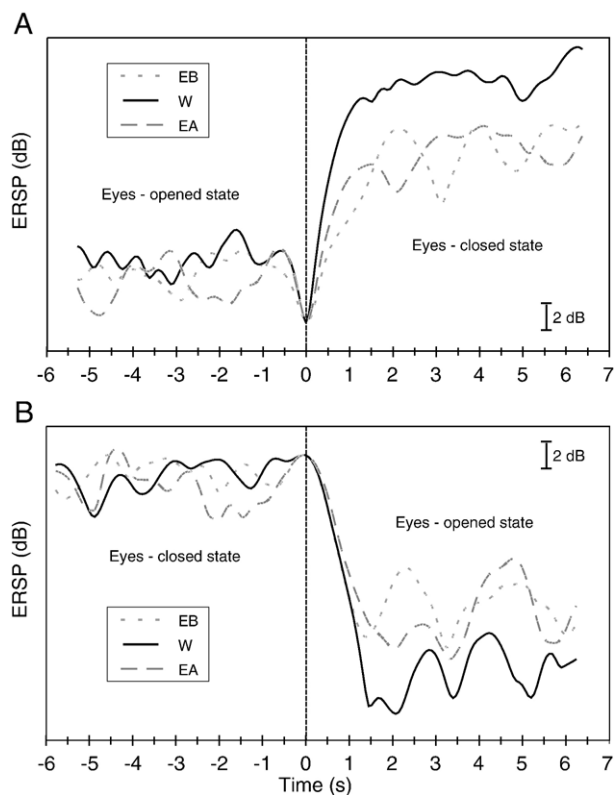
Fig. 7 – Transition between the two states of the arrest reaction. Superimposition of grand average curve of maximal event-related synchronisation power during eye-opened to eye-closed state transition (A) and of maximal event related desynchronisation power during eye-closed to eye-opened state transition (B). The continuous, the dotted and the stripped line correspond, respectively, to recordings performed in weightlessness, on Earth before the flight and on Earth after the flight.

closed. It was also demonstrated that the changes in metabolic activity were coincident with the changes in alpha rhythm amplitude (Feige et al., 2005). It might therefore be hypothesised that the alpha power increase in the ISS is due to a general lowering of brain blood oxygenation of the cosmonauts. However, the increase in alpha power in microgravity only appeared during the eyes-closed state, and not during the eyes-open state. By this fact it seems that the alpha power increase can be attributed to a change in brain blood oxygenation in microgravity. Moreover, previous spaceflight experiments failed to demonstrate impairments in cerebral blood flow autoregulation (Fu et al., 2002).

3.5. Conclusion

The present study demonstrates a modification of alpha and mu rhythms in microgravity, which could be linked to gravity-related sensory inputs. Alpha and mu rhythm represent "arrest rhythms" that may have a role in the maintenance of network coherence in the absence of visual and sensorimotor information, respectively. They may also participate in memory and cognitive processing. In this context, our finding of enhanced

alpha and mu rhythm in microgravity suggests their implication in general mechanisms of multi sensorimotor conflict solving and integration.

4. Experimental procedures

4.1. Subjects

Five male cosmonauts (C1–C5) participated in this investigation. The mean age (±SD) of the cosmonauts was 42±3 years. Four cosmonauts had previous experience of space flights; whereas one cosmonaut (C2) had no such experience. All cosmonauts were in excellent health, as regularly determined by a special medical commission during all periods of the investigation. Following the stay on orbit, cosmonauts reported on eventual medication use and sleep quality aboard the ISS.

Subjects may be divided into two groups, depending on the duration of their space flights, those who participated in the short-duration Russian–Belgian (ODISSEA) and Russian–Spanish (CERVANTES) so-called "taxi" missions and those who participated in the long-duration ISS INCREMENT 9 mission. The duration of these missions was 10 days for the former and 6 months for the latter. Each cosmonaut was tested on the ground before flight, during space flight aboard the ISS and on the ground after return to Earth. Details of the testing schedules for each cosmonaut are shown in Fig. 8A. Prior to flight, cosmonauts were tested in 2 pairs of sessions over the 2 months preceding lift-off, except for one of those (cosmonaut C4) tested in 3 pairs of sessions over the 3 months preceding lift-off. Sessions within each pair were separated by at least one day. In flight, subjects were tested on two or more days over the course of their space flight, with at least one day between pairs of test sessions. The cosmonauts were tested on at least two days during the week immediately following the landing and two more times one to three weeks later. Cosmonauts' recordings on Earth before and after the flight were thus used as their own control, to be compared with inflight 0-g measurements. In order to control the stability along time of the alpha rhythm on Earth, EEG recordings were also performed in five other male age-matched non-cosmonauts in excellent health. They were recorded on Earth following the same mean time schedule as the cosmonauts. All gave informed consent prior to starting the experiment and were free to stop the procedure at any time. The protocol was approved by the Human Research Multilateral Review Board in compliance with the Multinational Space Station Human Research Informed Consent procedures.

4.2. Experimental set-up

Subjects looked straight ahead at the laptop screen through a form-fitting face-mask and cylindrical tube (Figs. 8B, C). The screen was centred on the line of gaze at a distance of ~30 cm from the eyes. The mask and tube removed any external visual references. Auditory orders "close" or "open" were given at intervals of 10 s. Each session consisted of 3 transitions from the opened to closed eyes-states and 3 transitions from the closed to opened eyes-states. During this test, a grey page with a central coloured square was displayed on the computer screen.
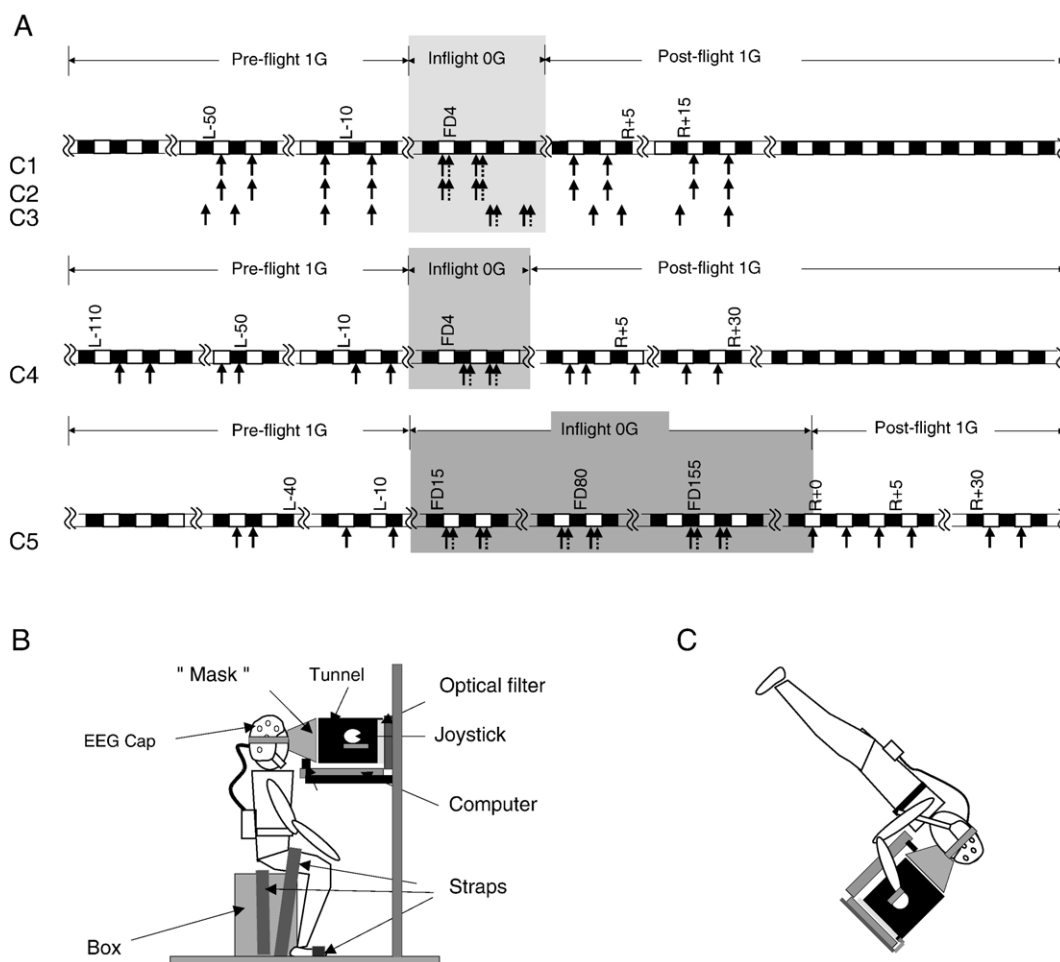
Fig. 8 – Testing schedule and recording conditions. (A) Testing schedule for cosmonauts (C1–C5) who performed the experiment during the *Odissea* (C1, C2 and C3), *Cervantes* (C4) and *Increment 9* (C5) space flights to the International Space Station. Testing on Earth before the flight (Pre-flight 1G) started 110 days prior to launch (L-110 for *Increment 9*) and 50 days prior to launch for *Odissea* and *Cervantes* (L-50), and continued up to 30 days after return to Earth (R+30). Cosmonauts C1, C2, C3 and C4 performed the experiments at 0g on two different days around the 4th day (FD4) during a ten-day mission whereas cosmonauts C5 performed the same testing around the 15th (FD15), the 80th (FD80) and the 155th day (FD155). (B) Schematic view of the experimental set-up in the *attached* condition, where the cosmonauts used belts, foot straps and a tabletop to reproduce the same seated posture as on Earth. (C) Schematic view of the *free-floating* condition, where subjects held the experimental apparatus (laptop computer and tunnel) in their hands with an elastic band used to hold the mask against the face.

On Earth, subjects performed the experiment while seated upright in front of the computer. During space flight, they performed the experiment in two conditions. In the *attached* condition, the cosmonauts used belts, foot straps and a table-top to reproduce essentially the same seated posture as that used on Earth (Fig. 8B). In the *free-floating* condition, subjects held the experimental apparatus (laptop computer and tunnel) in their hands with an elastic band used to hold the mask against the face (Fig. 8C). An assisting cosmonaut then positioned the subject in the centre of the free-working volume within one of the space station modules. The subject was then released and both subject and apparatus floated free from any contact with the station. The assisting cosmonaut ensured that no contact with the walls of the station occurred. To accomplish this, the assistant applied short tugs on the clothing of the subject to adjust the position without giving

strong directional cues. Very few such corrections (1–2 per session per subject) were required.

EEG was measured using an electrode-cap (Electro-Cap adapted for the ISS), in which 14 Ag–AgCl electrodes were placed at positions F7, F3, Fz, F4, F8, C3, Cz, C4, T5, P3, Pz, P4, O1, O2, according to the International 10–20 System. All the electrodes were referenced to the combined potential measured by adhesive electrodes applied to the mastoids. Blinks and horizontal eye movements were monitored with electrodes placed at the lateral canthi of the eyes (horizontal electro-oculogram, EOG). Scalp electrode impedances were checked and electrode placement in the receptacle was adjusted in order to achieve the lowest possible values. The EEGs were filtered with an analogue band pass of 0.01–120 Hz and sampled at 256 Hz. EEG treatments were performed off-line with the EEGLAB software (Delorme and Makeig, 2004). A standard thresholding method

was used for the detection of gross eye blinks or movement artefacts. Data trials were recognised as artefactual if the absolute value of any point in the trial exceeded a fixed threshold. Transient periods of current drift were also rejected.

4.3. Chronology of experimental sessions

A total of fifty-one recording sessions were performed on Earth (22 before and 29 after the flight) and 38 sessions in the ISS. This gave for final analysis a total of 114 eye-state transitions during, 66 before and 87 after the flight. All the cosmonauts and all control subjects were able to complete the experiment. No cosmonaut reported drug consumption or sleep disturbance in the ISS.

The arrest reaction was quantified by means of static and dynamic analysis. In order to exclude the possibility that EEG modifications were due to eye movement artefacts or other transient effects related to opening and closing the eyes, in this first quantification of alpha power we excluded the transition periods between the steady state sections of eyes opened and eyes closed. In this static analysis, EEG epochs of 7s during steady states (avoiding the 1 s before and the 2 s after the occurrence of the order) of both eyes-closed and eyes-opened condition were analysed by means of fast Fourier transform (FFT) performed on 512 points. The peak frequency and the maximal power at this peak were measured in each state (eyes opened or closed) and in each gravitational condition (on Earth and in the ISS). The conditions in microgravity *attached* or *free-floating were* also compared.

4.4. Data analysis

Dynamic analysis was also performed with the EEGLAB software. This software allows one to analyse the event-related dynamics (Makeig et al., 2002; Delorme and Makeig, 2004) by quantifying the event-related spectral perturbation (ERSP). This allows detection of event-related desynchronisation (ERD) or synchronisation (ERS) over a narrow-band (Pfurtscheller and Aranibar, 1977). For ERSP calculation, the power spectrum was computed over a sliding 50ms window and then averaged across trials. Power (in dB) at a given frequency and latency relative to the time locking event was indicated by the colour of each point. Typically, for n trials, if $Fk(f, t)$ is the spectral estimate of trial k at frequency f and time, then

$$\mathrm{ERSP}(f, t) = \frac{1}{n}\sum_{k-1}^{n} |F_k(f, t)|^2. \tag{1}$$

We used a sinusoidal wavelet transform to compute $F_k(f, t)$, providing a specified time and frequency resolution (Delorme and Makeig, 2004). The bootstrap method (option in the EEGlab analysis software) was used to provide a measure of the significance of ERSP deviations from baseline power using surrogate data by randomly shuffling the single-trial spectral estimates from different latency windows during the baseline period. The transition between the two physiological states was also quantified by the rate of rise (eyes-opened to eyes-closed) and the rate of decrease (eyes-closed to eyes-opened) of the alpha power measured by the ERSP procedure. For this, the corresponding slopes were measured by performing linear regression of the data between the onset of the ERS or the ERD

and the respective level of the mean reached plateau. Finally, the grand average of these curves was obtained after their realignment along time.

For each subject and each trial, we computed (i) the base-to-peak alpha power during the eyes-closed state, (ii) the difference between the alpha power peaks measured during the eyes-closed and the eyes-opened state, (iii) the mean ERD and ERS values measured 2s after the transition between eye-closed and opened states over a time period of 7s and (iv) the slopes of the regression line of the ERS and ERD transition towards the respective plateau. The ANOVA test for repeated measures was used to compare within the same subject those values at different times before, during and after the flight. Results are expressed and illustrated as mean±SD and are considered significant if $p<0.05$. All statistical analyses were performed using Statistica 6.0.

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