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Mu and alpha EEG rhythms during the arrest reaction in microgravity

Mu and alpha oscillations (8-12 Hz) are the most prominent electroencephalographic rhythms observed in awake, relaxed subjects. Different cortical sources may participate in these oscillations and appear to be modulated by the sensorimotor 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 these spontaneous rhythms. Here, we report the results of an experiment conducted over the course of 3 space flights, in which we quantified the power of the mu and alpha rhythms 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 mu and alpha rhythms recorded in the eyes-closed state in the sensorimotor areas (mu rhythm) and in the parieto-occipital cortex (alpha rhythm) increased in microgravity. The suppression coefficient produced by eye-opening/closure state transition also increased in microgravity. These results are discussed in terms of current theories on the source and the physiological significance of these EEG rhythms.

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1. Introduction

Neuronal networks of the human brain can display different states of synchrony characterised by their electroencephalographic (EEG) oscillation frequencies [1]. These oscillations play an important role in the nervous system and form the basis for sensorimotor functions [2], cognition [3,4], consciousness [5,6,7] and emotions [8]. Human sensorimotor cortex at rest generates an 8–12 Hz EEG rhythm referred to as the rolandic mu rhythm [9]. Mu rhythm most often occurs during a premovement period and ceases around movement onset [10,11]. The decrease in mu rhythm roughly coincides with the increase in gamma oscillation above 30 Hz [11] and with the appearance of firing rate modulation of cortical neurons coupled to the motor action [10,12]. This rhythm is also attenuated when subjects are observing, but not executing a movement [13]. In the same frequency range, the alpha rhythm is observed in awake, relaxed subjects [14] and classically considered as a marker of cortical inactivity i.e. 'cortical idling' [11]. This dominant rhythm is most pronounced at occipital and parietal recording sites during eye closure. As scalp EEG signals are produced by partial synchronisation of neuronal-scale field potentials across a cm2 -scale, each scalp electrode records a weighted mixture of different cortical sources that may be concurrently modulated by different processes [15]. Here we used the arrest reaction produced by eye opening [14] as a prototypical and experimentally practical model system for studying the effects of microgravity on the mu and alpha rhythm dynamics. Since these rhythms have functional roles in the regulation of their respective network properties, microgravity can be expected to modify the strength of these neural regulations in weightlessness.

Methods

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; while 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. 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 0g 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.

Subjects looked straight ahead at the laptop screen through a form-fitting face-mask and cylindrical tube. 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. 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 tabletop to reproduce essentially the same seated posture as that used on Earth. 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. 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.

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 [16]. A standard thresholding method was used for the detection of gross eye blinks or movement artefacts. Data trials were recognized as artefactual if the absolute value of any point in the trial exceeded a fixed threshold. Transient periods of current drift were also rejected. Five cosmonauts performed 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. No cosmonaut reported drug consumption or sleep disturbance in the ISS. EEG epochs of 7 s 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 Fourrier 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). We defined a ‘*suppression’ coefficient* (SC) as the peak value resulting from the subtraction of the power spectrum recorded in the eyes-closed state from that recorded in the eyes-opened state. The conditions in microgravity *attached* or *free-floating* were also compared. For each subject and each trial, we computed the difference between the alpha power during the eyes-closed and the eyes opened state. As each subject performed a different number of trials before, during and after their flight, we conducted two statistical analyses as follows. First, we computed an ANOVA analysis on data from each subject individually, grouping trials according to a single factor with three levels: before (EB), during (W and EDF) and after the flight (EA). Then, to compare across subjects we computed the mean SC for each subject from the multiple recordings taken during each of the three different phases of the mission. A single factor ANOVA analysis with repeated measures was then applied on the three values for each subject

(N = 5). These analyses were computed on the SC from each of the following electrodes: C3, CZ, C4, P3, PZ, P4, F3, FZ, F4. 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.

Results

Figure 1 illustrates the raw EEG recorded in the ISS in one cosmonaut during the arrest reaction. In the eyes-closed state, the mu and alpha rhythms appear as spindle-shaped episodes of oscillation peaking around 10 Hz. The arrest reaction reveals some functional differences between the mu rhythm recorded over the sensorimotor areas (C3, CZ and C4) and the alpha rhythm recorded in the parietal areas (P3, PZ and P4). Just after the order to open the eyes, the mu rhythm is suppressed whereas the alpha rhythm remains unchanged. The latter is only suppressed after the eyes actually open. We compared statistically the measurements performed before the flight (EB), in flight (W) and after the flight (EA). Figure 2A shows the *'suppression' coefficient* (SC) of both mu (illustrated for C3, CZ, C4) and alpha (illustrated for P3, PZ, P4) rhythms. All subjects showed a significant increase in SC for each of these channels for statistical analyses performed subject by subject ($p < 0.05$ in all cases, see Table 1). Furthermore, the ANOVA analysis with repeated measures carried out across subjects also revealed a significant increase in SC in the microgravity condition ($p < 0.01$ in all cases, see Table 2). A post-hoc analysis (Scheffé test) confirmed that the two ground conditions each differed from the microgravity condition ($p < 0.01$) in all cases while there was no significant differences between the ground measures taken before and after the flight ($p > 0.4$). In contrast, the SC values corresponding to the 10 Hz oscillation recorded at the frontal loci (illustrated for F3, Fz, F4) remained unchanged in microgravity (Fig 2A). No difference in the mu and alpha rhythms power and SC were found between *attached* and *free-floating* conditions. The stability of mu and alpha 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) is also illustrated in Fig. 2. 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.

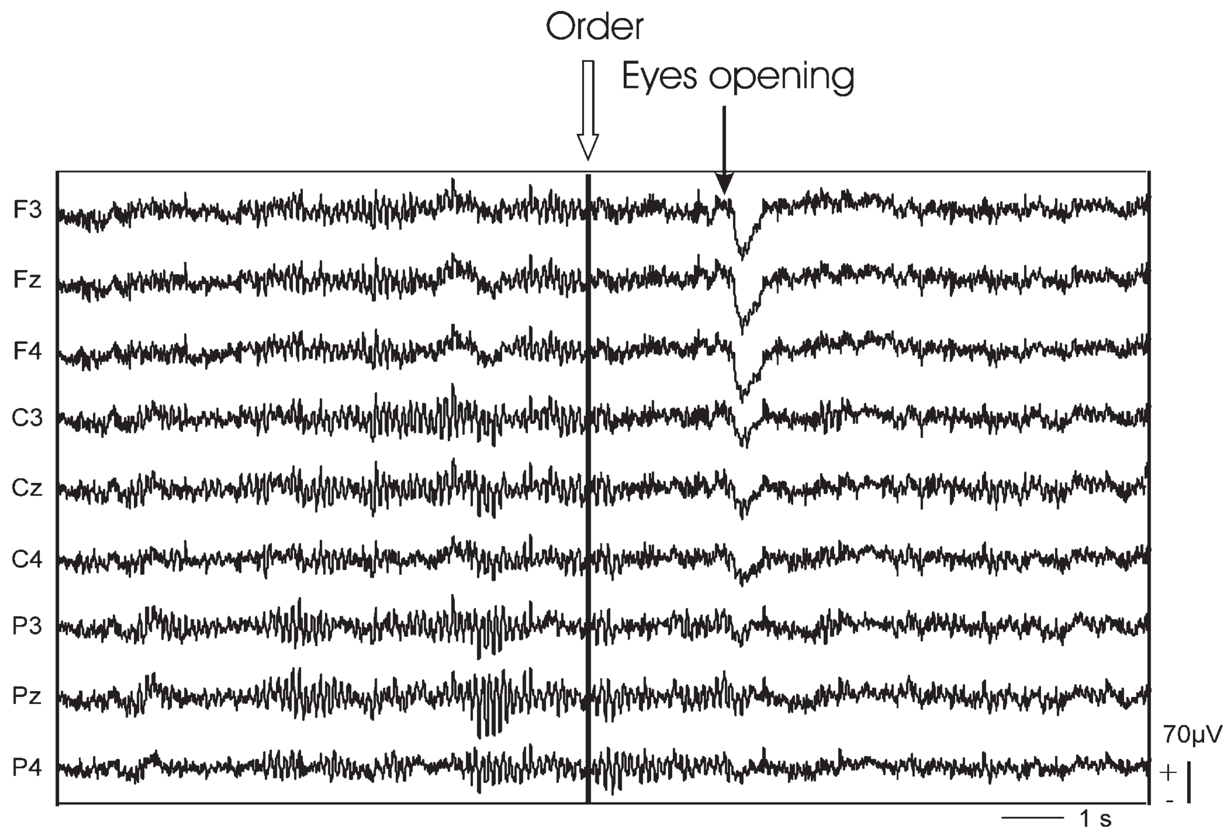

Fig. 1: Raw EEG recordings during the arrest reaction in weightlessness. Nine EEG channels referenced to linked mastoid (from F3 (top) to P4 (bottom)). The white arrow indexes to the order to open the eyes. The black arrow points to the onset of the eye movement artefact related to eye opening, mainly recorded by frontal electrodes (F3, FZ, F4). Note that the amplitude of mu rhythm (recorded by central electrodes (C3, CZ, C4)) is reduced before eye opening while alpha rhythm (P3, PZ, P4) is only reduced after this movement.

Discussion

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

Most alpha activity parameters are known to be stable over time [30], facilitating longitudinal studies. This stability was further confirmed in our control subjects. However, a number of parameters have been demonstrated to have an effect on 10 Hz oscillation. Auditory stimulation was shown to be able to trigger an increase of 10 Hz oscillation in the eyes-opened state [28]. 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 [29]. However, the background noise inherent to the ISS environment (90 dB) cannot explain the increase in the alpha-mu power that we found in microgravity, as it was not increased in the eyes-opened state.

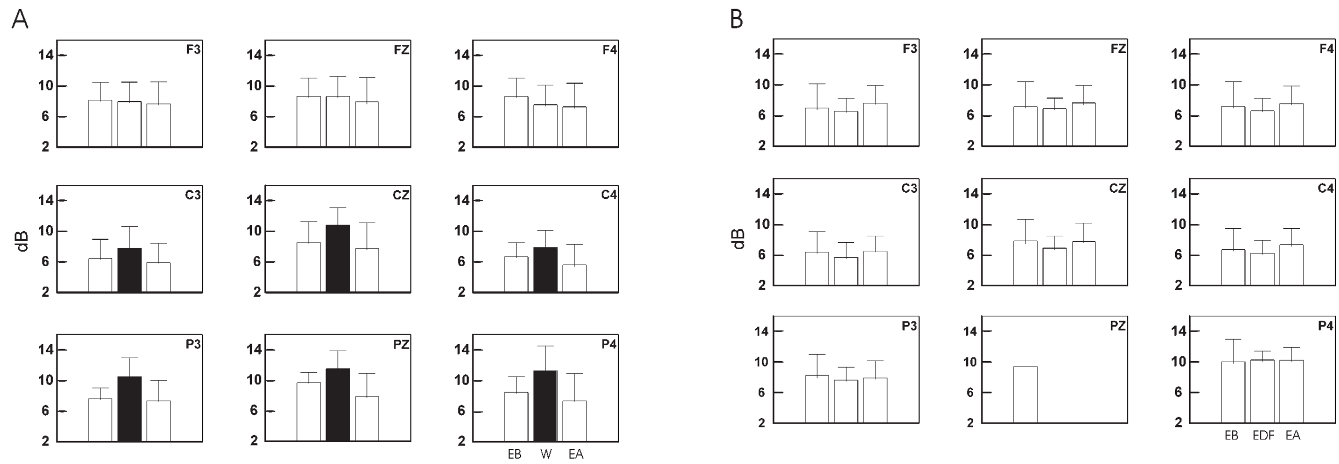

Fig. 2: Histograms of the effect of weightlessness on the 10 Hz 'suppression' coefficient. Histograms of the 10 Hz suppression (arrest reaction) recorded in cosmonauts (n=5) (A) on Earth before the flight (EB), in weightlessness (W) and on Earth after the flight (EA), and in non cosmonauts on Earth during the same period of flight (EDF) (n=5) (B). The black bars in the histograms correspond to significant SC values (p< 0.05).

*Table 1: Results of the one-way ANOVA analysis for each subject with mission phase (Earth Before, Weightlessness, Earth After) as the independent factor. *p < 0.05, **p< 0.01*

	C3	Cz	C4	P3	Pz	P4	F3	Fz	F4
Crew 1	F(2, 8) 8,78**	F(2, 5) 14,14**	F(2, 7) 5,43*	F(2, 8) 5,34*	F(2, 8) 9,91**	F(2, 8) 6,82*	F(2, 8) 2,55	F(2, 8) 3,39	F(2, 9) 1,57
Crew 2	F(2, 7) 6,13*	F(2, 7) 8,71*	F(2, 7) 13,71**	F(2, 7) 32,95**	F(2, 7) 23,99**	F(2, 7) 18,12**	F(2, 7) 2,24	F(2, 7) 3,76	F(2, 7) 4,11
Crew 3	F(2, 6) 26,45**	F(2, 6) 6,55*	F(2, 6) 13,29**	F(2, 6) 4,90*	F(2, 7) 5,54*	F(2, 7) 7,21*	F(2, 7) 1,26	F(2, 7) 1,29	F(2, 7) 1,67
Crew 4	F(2, 22) 9,45**	F(2, 20) 4,14*	F(2, 20) 7,14**	F(2, 22) 4,72*	F(2, 23) 8,13**	F(2, 22) 7,68**	F(2, 23) 2,75	F(2, 19) 3,34	F(2, 20) 2,42
Crew 5	F(2, 30) 3,30*	F(2, 29) 3,32*	F(2, 31) 3,90*	F(2, 30) 3,28*	F(2, 34) 4,97*	F(2, 30) 3,65*	F(2, 28) 1,19	F(2, 30) 0,46	F(2, 31) 1,49

*Table 2: Results of the one-way ANOVA analysis with repeated measures conducted on data from 5 cosmonautes with mission phase (Earth Before, Weightlessness, Earth After) as a within-subjects factor. *p < 0.05, **p < 0.01*

	C3	Cz	C4	P3	Pz	P4	F3	Fz	F4
F (2,8)	(9.41**	12.70**	19.87**	10.58**	11.69**	16.77**	1,09	1,53	0,76

Other uncontrolled parameters that could interfere with the EEG, such as medication or major sleep alterations were ruled out.

One of processes involved in the regulation of 10 Hz rhythms is related to feedback loops between inhibitory cells in the thalamic reticular nucleus and thalamocortical neurons [31]. In this case, the large amplitude of the 10 Hz oscillation (mu and alpha rhythms) 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 [17]. In this theoretical framework, microgravity could facilitate the expression of a single-peak 10-Hz dominant rhythm at rest resulting in a power increase of 10 Hz oscillation in microgravity.

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 microgravity. 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 [18,19]. Recordings 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 [20]. Moreover, a vestibular network has been identified in the parietal cortex involving the temporo-parietal junction [21,22,23,24,25] 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.

The increase of the mu and alpha rhythms 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 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 produce by sensorimotor (mu rhythm) and parietal areas (alpha rhythm). Conversely, the reduction of these gravity-related signals in the ISS can induce an increase of the mu and alpha power only in the absence of visual information. The augmenting properties of resonators-oscillators [26] probably implicated in the power increase of these rhythms 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 [27].

In conclusion, the present study demonstrates a modification of mu and alpha rhythms in microgravity, which could be linked to gravity-related sensory inputs. In this context, our finding of enhanced mu and alpha rhythm in microgravity suggests their implication in general mechanisms of multimodal sensorimotor conflict solving and integration.

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