Neural activity in the brain at the onset of odor detection and during periods of sensory deprivation.

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Abstract

The perception of olfactory stimuli is a complex, system-level process that activates cognitive and emotional mechanisms while simultaneously shaping their development through the morpho-functional properties of the cerebral olfactory cortex. This process is closely linked to cognitive functions such as emotion, memory, semantic processing, and other internal mental activities, engaging virtually all rhythmogenic neural networks (theta, alpha, and beta bands). Guided by a three-factor model of perception (attention, hedonic value, and gender), we conducted a comprehensive comparative neurophysiological study to examine neocortical mechanisms underlying the effects of olfactory sensation on brain function. The study involved three everyday-life conditions: directed analytical odor detection (Experiment 1), passive odor perception (Experiment 2), and temporary nasal obstruction (Experiment 3). Our findings demonstrate that both passive and analytical odor perception are associated with the activation of cortical neural networks. This activation stimulates the cortical-hippocampal loop (reflected in theta-wave activity), leading to enhanced cortical-cortical and cortical-subcortical coherence, and modulates mental, emotional, and verbal processes (theta1,2; alpha3; beta1,2; gamma bands). Notably, the initial moment of odor detection is marked by robust activation of cognitive memory circuits, emotional responses, and semantic analysis. Simultaneously, mechanisms for evaluating the familiarity and biological significance of incoming sensory information are engaged.

Introduction

Olfaction is a fundamental sensory system for emotional wellbeing, with unique neurobiological pathways that allow odors to directly and powerfully influence mood, memory, and social behavior. Olfactory dysfunction is a significant risk factor for emotional disorders, and restoration of olfactory function can improve psychological health. The emotional effects of odors are shaped by individual differences and context, making olfaction a rich area for therapeutic and clinical intervention (Bratman et al, 2024; Ni et al, 2025; Amirsadri, & Sedighi, 2026). Recent research has highlighted the involvement of second-order olfactory cortical centers in odor perception, suggesting that olfactory awareness is inherently a recognition of quality - a holistic mental phenomenon (Savic, 2005; Stevenson, 2009; Young, 2014; Keller, 2016; Freiherr, 2017). The ability to identify and discriminate odors relies heavily on past experiences (memory) and cognitive factors, which shape the perception of odor properties in conjunction with other sensory modalities (Stevenson, 2009). It is well established that emotional processes have privileged and robust access to olfactory information (Keller, 2016). Furthermore, some researchers propose that the pharmacological properties of volatile organic compounds and odorants can influence cognitive functions. This effect is thought to occur through mood alterations during odor perception, expectations of cognitive outcomes, and the roles of key neurotransmitters that mediate various behaviors via contextual associations with odors (i.e., contextual conditionality) (Johnson, 2011).

Tomographic studies demonstrate that olfactory processing unfolds from an initial, holistic evaluation of pleasantness and familiarity to advanced cognitive identification, with several intermediate stages

involving polymodal associations. Both odor discrimination and perception, similar to other sensory modalities, are mediated by distributed cortical networks (Illig & Haberly, 2003; Fjældstad et al., 2017; Freiherr, 2017; Pashkovski et al., 2020; Sagar et al., 2023). Tomographic imaging reveals that olfactory processing begins with activation in the olfactory bulb and primary olfactory cortex (piriform, entorhinal cortex, amygdala), reflecting the early holistic assessment of odor qualities. As processing advances, neural activity spreads to secondary and associative regions, including the orbitofrontal cortex, cingulate cortex, and insula, which are involved in higher-order cognitive identification and emotional appraisal. These spatial activation patterns allow imaging to distinguish between early sensory, intermediate associative, and advanced cognitive stages of olfactory processing (Lascano et al., 2010; Micarelli et al., 2014; Muir et al., 2019). Additionally, tomographic techniques capture the temporal progression of olfactory processing: initial responses occur in the ipsilateral temporal cortex (amygdala, parahippocampal gyrus, insula), followed by contralateral homologous regions and, finally, frontal areas. This temporal sequence mirrors the transition from basic sensory encoding to associative and cognitive processing, enabling differentiation of the timing and functional significance of each stage (Lascano et al., 2010).

Until recently, it was widely believed that the olfactory system was unique among sensory systems in lacking a morphological thalamic relay, a feature that set it apart. However, tomographic studies have now demonstrated that the thalamus becomes functionally engaged during the conscious analysis of odors (Tham et al, 2011). The mediodorsal thalamus forms connections with the primary olfactory (pyriform) cortex (Öngür & Price, 2000), and thus with olfactory projection areas in the orbitofrontal cortex. This suggests that the degree of attention directed toward odors can significantly influence neuronal integration along these indirect pathways, strengthening the connectivity between the mediodorsal thalamus and the orbitofrontal cortex - reflecting the dominance of olfactory salience over attentional tone (Plailly et al., 2008; Tham et al, 2011).

The sense of smell plays a vital role in quality of life, emotional experience and regulation, cognitive abilities, social relationships, dietary choices, stress management, and depressive symptoms (Bratman et al., 2024). Anosmia is consistently linked to an increased risk of depression, anxiety, reduced well-being, and cognitive deficits such as impaired memory, attention, and executive function. These effects are observed in both clinical and general populations, as well as in neurodegenerative diseases and post-infectious conditions like COVID-19 (Bratman et al., 2024; Oleszkiewicz et al., 2025). Sensory deprivation, including loss of smell, induces neurobiological changes that heighten vulnerability to depression, anxiety, and cognitive impairment, primarily through disrupted brain network integration (Marazziti et al., 2026). Anosmia frequently co-occurs with emotional disturbances, partly because the neural circuits involved in olfactory processing overlap with those responsible for emotional regulation (Lee et al., 2022). Neuroimaging studies demonstrate that anosmia leads to decreased functional connectivity within the olfactory network and between olfactory, cognitive, and emotional brain regions - including the amygdala, hippocampus, entorhinal cortex, and orbitofrontal cortex - resulting in diminished information integration and processing capacity (Iravani et al., 2021; Lee et al., 2022; Jarrahi, 2024; Lee et al., 2024).

Existing published data on EEG correlates of olfactory perception remain limited, with notable gaps in systematicity and consistency. In this study, we aim to perform a comprehensive neurophysiological investigation of neocortical mechanisms underlying the effects of olfactory stimulation on human brain activity (using EEG) across various conditions relevant to everyday life, including focused analytical detection, passive perception, as well as the blockage and restoration of nasal breathing.

Materials and Methods

Sample

A total of 567 healthy, right-handed volunteers (300 women and 267 men), aged 18 to 24 years (mean age = 18.95, SD = 1.12), participated in this study. All were first- to third-year students from the Taras Shevchenko National University of Kyiv, Educational and Scientific Centre “Institute of Biology and Medicine”, and Faculty of Psychology. Eligibility required the absence of clinical signs of mental or cognitive impairment and no documented rhinal pathologies. Exclusion criteria included use of psychoactive medications, drug or alcohol addiction, and any psychiatric or neurological complaints. In accordance with the guidelines of the Bioethics Committee of the Taras Shevchenko National University of Kyiv, Educational and Scientific Centre “Institute of Biology and Medicine” and the principles outlined in the Helsinki Declaration on Biomedical Research Involving Human Subjects (1975), all participants were fully informed in advance about the nature and procedures of the experiments and provided their written informed consent prior to participation. Participation was voluntary and credited toward course requirements.

EEG recordings

Participants underwent EEG recording while seated comfortably in a reclining position with their eyes closed, inside a soundproof and darkened shielded chamber, with a volume of 6 m^3. EEG signals were acquired using the EEG-16S system (MEDIKOR, Hungary). Silver/silver chloride electrodes were placed at symmetrical frontal (F3, F4), parietal (P3, P4), occipital (O1, O2), and temporal (T3, T4) sites according to the international 10–20 system, with all electrodes referenced to interconnected ear electrodes. Interelectrode impedance was kept below 5 kΩ. Analog EEG signals were digitized at a sampling rate of 100 Hz. Signal processing included a high-frequency filter with a 30 Hz cut-off, a 50 Hz power line filter, and an amplifier time constant of 0.3 seconds. For analysis, artefact-free 20-second EEG segments were selected from each 1-minute interval (resting state, odor exposure, and after-effect).

The most promising approach for examining interregional brain relationships is the simultaneous use of spectral analysis (for local synchronization) and coherence analysis (for long-range synchronization) of EEG data. This combined method allows for evaluating the coherence of electrical oscillations across different brain regions and enables the study of the brain’s integrated functioning and the systemic mechanisms underlying various central nervous system states. Spectral power (SP), normalized spectral

power (NSP), and both interhemispheric and intrahemispheric average coherence were calculated for all segments using specialized software based on the Fast Fourier Transformation (FFT) algorithm. The following frequency bands were analyzed: low θ1 (4.1–5.86 Hz), high θ2 (6.05–7.42 Hz), low α1 (7.62–9.38 Hz), middle α2 (9.57–10.74 Hz), upper α3 (10.94–12.89 Hz), low β1 (13.09–19.22 Hz), and upper β2 (20.12–25.0 Hz).

Experimental Design

Olfactory stimuli are used to investigate how the brain and behavior respond to different smells. Central processing of odors occurs via two primary pathways: the orthonasal and retronasal routes (Seo & Hummel, 2017). In this study, we examined EEG correlates of olfactory sensation under three everyday-life conditions: active odor perception through directed analytical detection (Experiment 1), passive odor perception or “passive smelling” (Experiment 2), and reverse temporal anosmia induced by temporary nasal obstruction (Experiment 3).

Olfactory stimuli

Odor administration involved the use of various essential oils, including lemon (Citrus limonium Risso) and lemon balm (Melissa officinalis L.) from Bergland-Pharma GmbH & Co, Austria; ylang-ylang (Cananga odorata), lavender (Lavandula officinalis), and rosemary (Rosmarinus officinalis) from The Body Shop, Great Britain; bergamot (Citrus bergamia) from AROMAFORCE, France; alpine pine (Pinus alpinum) from Brüder Unterweger GmbH, Austria; mint (Mentha piperita), anise (Pimpinella anisum), common wormwood (Artemisia absinthium L.), and an alcoholic tincture of common valerian (Valeriana officinalis) from the production association "Pharmacy," Ukraine; and rose (Rosa sp.) from Bulgarian Rose Oil, Bulgaria. All essential oils in the collection are crafted exclusively from top-quality natural ingredients, most of which are GMP and ISO certified and have undergone testing in medical facilities. They are guaranteed free from synthetic additives and are approved for use in body massage, bath inhalations, room scenting (odorization), and aromatherapy medallions.

All odorants (essential oils, EO) were used at concentrations several times lower than the maximum permissible limits: EO up to 1 mg/m³ (compared to 10 mg/m³). A measured amount of EO was applied to a glass slide using a micropipette, and the slide was placed in a directed airflow from a silent fan positioned outside the participant’s field of vision. The chamber temperature was maintained at 18–22°C, and the odor saturated the chamber within 1–2 minutes.

Experiment 1

In 1st experiment, 124 participants (53 women and 71 men) were asked to identify various odors and rate their hedonic valence (from unpleasant to pleasant) on a 10-point Likert scale ranging from − 5 to + 5. Odors were presented using standard glass tubes containing strips of filter paper (50 × 10 mm)

moistened with either distilled water or an odorant. Each odorant was administered in a single drop, ensuring a supraliminal stimulus sufficient for detection and identification. The tubes were placed in a mobile holder positioned 5 cm from the participant's nose, allowing them to adjust the odor source without direct contact. Participants were not informed about the contents of the tubes. EEG recordings were conducted during a 3-minute resting state and a 3-minute period of active odor perception.

Experiment 2

In the passive odor perception study, 320 participants (171 women and 149 men) were exposed to essential oils or distilled water, which were introduced into the chamber through the ventilation system. The odorant concentration was maintained at approximately 0.6 mg/m³, corresponding to the threshold for smell detection. Participants were not informed about the presence or possibility of odors. After a 2-minute adaptation period, EEG recordings were taken during a 3-minute resting state and an 8-minute odor exposure period.

Experiment 3

In the third series of studies, EEG activity was examined in 123 participants (76 women and 47 men) while systematically altering their breathing patterns (nose–mouth–nose) within a single session. After a 5-minute adaptation period and baseline EEG recording at rest, participants' nasal breathing was completely blocked using a specialized nostril occluder/nose clips to induce experimental temporal anosmia. Five minutes into this condition, the chamber was infused with lemon essential oil via the ventilation system, without informing participants. Lemon essential oil was chosen due to its familiarity and positive valence. Following 5 minutes of odor exposure, the nasal occluder/nose clips was removed, restoring nasal breathing. EEG recordings were obtained at each stage: during rest (5 min), artificial temporary anosmia (5 min), odor exposure (5 min), and after the resumption of nasal breathing (5 min).

Statistical Data Analysis

Statistical evaluation was carried out using the Wilcoxon signed-rank test and the Kolmogorov-Smirnov test (IBM SPSS Statistics for Windows version 15.0). Differences were deemed statistically significant when $P < 0.05$.

Results

Experiment 1

Analysis of EEG parameter changes during directed analytical odor detection revealed that attentional processes play a key role in shaping EEG responses at the onset of active odor perception, both in control (distilled water) and odor conditions. Notably, we observed increased long-range connectivity in

the β1 subband during the identification of distilled water (Fig. 1, B), reflecting external attention and the multimodal processing of sensory information (Engel & Fries, 2010). Concurrently, enhanced temporal interhemispheric connectivity in the α1,2 and β2 subbands indicated activation of top-down control system. The predominance of right-hemispheric changes in regions critical for olfactory processing - such as increased θ activity in F3-F4-T4 and strengthened distant frontotemporal interactions in the β1,2 range - suggests that the initiation of olfactory search is closely linked to thalamo-cortical attention networks, supporting efficient odor identification and discrimination (Tham, Stevenson & Miller, 2011).

The onset of genuine perceptual activity - specifically, odor identification during the first minute of exposure - was marked by attentional engagement, evidenced by a widespread reduction in normalized spectral power (NSP) within the α1 and α2 subbands. Simultaneously, mechanisms associated with short-term memory were activated, as indicated by increased θ-band synchronization and elevated NSP in the β and α3 bands within the central-posterior regions of the cortex. Notably, the spatial distribution of cognitive and emotional activation during real odor exposure closely resembled that observed with the olfactory "placebo" (distilled water) (Fig. 1, A).

Strengthened long-range connectivity across all EEG frequency bands - except for θ2 and α1 - indicates a marked increase in perceptual and cognitive activity. This encompasses the activation of short-term (working) memory mechanisms (θ1 subband) and semantic processing (α3 subband) (Klimesch, 1999; Klimesch et al., 2000), as well as heightened internal cognitive-emotional arousal (α3, β1,2 subbands, predominantly in the post-central cortex) (Fig. 1, C). It is well established that heightened synchronization in the theta and beta frequency bands across frontal and parietal brain regions during working memory tasks facilitates information transfer within fronto-posterior neural circuits, indicative of increased cognitive-emotional tension (Deiber et al., 2007). Additionally, activity in the alpha (α3) and beta (β1,2) EEG subbands is strongly associated with cognitive-emotional arousal in the post-central cortex and neighboring areas. Emotional arousal is generally characterized by a decrease in power (desynchronization) within the α3 and lower beta bands in central and posterior cortical regions, signifying enhanced cortical activation and the processing of emotionally salient information. This phenomenon reflects the brain’s allocation of additional resources to support emotional and cognitive functions, with the post-central (somatosensory) cortex playing a key integrative role (Schubring & Schupp, 2019; Kim et al., 2021; Gkintoni & Halkiopoulos, 2025).

During directed odor detection, there was a simultaneous increase in interhemispheric coherence within the θ1 and α2 bands (notably at the F4 electrode), as well as in the upper frequency cognitive-active bands (α3, β1, and β2). This pattern also reflected an overall rise in brain activation and excitability. Increased interhemispheric coherence in the α2 and β EEG bands during directed odor detection reflects enhanced integration and coordination between the brain's hemispheres, supporting efficient sensory and cognitive processing. In the α2 band, this coherence facilitates the collaborative processing of olfactory information, likely aiding in the integration of sensory input and the lateralization of olfactory functions, which is important for accurate odor detection and discrimination under cognitively demanding conditions (Zhang et al., 2019; Cavelius et al., 2021). In the β band, heightened coherence is

associated with the coordination of information transfer across distributed neurocognitive networks, underpinning sensory perception, reward processing, and the evaluation of odor valence. Beta oscillations are particularly important for integrating activity across cortical regions, enabling the brain to process motivational and affective aspects of olfactory stimuli efficiently (Kepler et al., 2022). Together, increased coherence in these bands signifies the brain's dynamic allocation of resources and synchronization of activity necessary for effective olfactory perception and higher-order cognitive functions during directed odor detection (Kepler et al., 2022).

During a prolonged period (3 minutes) of directed perception in the control condition of olfactory testing (olfactory placebo/smell placebo-controlled study), we observed a generalized decrease in β-activity, returning to baseline levels, along with a reduction in low-frequency EEG components to below their initial values (Fig. 2, A, B). In contrast, extended exposure to a real odor maintained elevated β-network activity - indicative of sustained attentional processes - while the activity of limbic θ-networks diminished and remained close to baseline (Fig. 2, C). We interpret these changes as evidence of adaptation to olfactory stimulation, with continued enhancement of cognitive functions such as working memory, emotional processing, focused attention, and selective sensory integration (Klemm et al., 1992; Kukleta et al., 2009; Engel & Fries, 2010).

Alterations in the brain’s information processing capacity mirrored the above-mentioned described changes in neural network activity. During extended odor perception, the spatial extent of coherence changes across the cortex became more restricted, except in the β2 and θ1 EEG bands, where increased long-range synchronization of potentials - particularly in the β2 subband - was evident. This pattern suggests ongoing engagement of cognitive processes, including mechanisms of working memory and semantic processing (θ1 and α3 subbands), external attention, and the formation of subjective attitudes toward the odor (α2 and β1 subbands) (Fig. 2, C). The observed state of active internal mental activity likely reflects the conscious awareness of the odor’s presence, its identification, associative processing, multimodal interference, and subjective evaluation.

Increased interhemispheric coherence in the θ1 (theta) and α2 (alpha) EEG bands is strongly associated with improved behavioral performance in odor detection tasks. Specifically higher theta (θ1) coherence, especially in frontal regions, correlates with greater accuracy and cognitive effort during odor discrimination. Early theta-band activity encodes low-level odor features, and the fidelity of this coding predicts both trait-level discrimination ability and trial-by-trial accuracy. Increases in frontal theta power after odor inhalation are statistically associated with higher accuracy in discrimination tasks (Kay, 2005; Morozova et al., 2023; Kato et al., 2025). Increased coherence in the α2 band, particularly in bilateral temporal and frontal regions, supports perceptual binding and integration of sensory information, facilitating efficient processing and higher accuracy in odor detection. Additionally, higher pre-stimulus alpha activity (including α2) is associated with faster reaction times in sensory discrimination tasks, indicating that increased α2 coherence may facilitate more efficient processing and quicker responses (Harada et al., 1998; Brickwedde et al., 2026). These coherence patterns are most pronounced during directed odor detection tasks that require focused attention and discrimination, and are less evident

during passive perception, which is associated with lower coherence and reduced behavioral performance (Kato et al., 2025; Morozova et al., 2023). In summary, enhanced interhemispheric coherence in θ1 and α2 bands facilitates the integration of sensory and cognitive processes necessary for accurate and efficient odor detection, serving as a robust neurophysiological marker of behavioral performance in these tasks.

Olfactory perception is a complex cognitive process (Savic, 2001; Seo & Hummel, 2017) and the main results from Experiment 1 on directed analytical odor detection not only confirm the crucial role of attentional mechanisms in olfactory perception, determining whether and how odors are consciously detected, discriminated, and processed in the brain (Plailly et al., 2008; Fallon et al, 2018; Singh et al, 2019), but also demonstrate that valuation and awareness of odors begin at the earliest stages of sensory stimulation.

Experiment 2

Experiment 2 investigated the most common form of olfactory perception in daily life: the passive and involuntary detection of environmental scents.

Experiment 2 investigated the most prevalent form of olfactory perception in daily life: the passive, automatic detection of ambient environmental odors.

Passive detection of irrelevant odors was characterized by the emergence of primary, involuntary attention to the odorant (orienting response) (Fig. 3). This response involved a reduction in normalized spectral power (NSP) in the α1 and α2 subbands, alongside distinct shifts in the interplay between activating limbic regions (θ-band activity in frontal areas, linked to working memory processes) (Klimesch, 1999; Gudi-Mindermann et al, 2020) and regulatory cortical centers (β1 system) (Engel & Fries, 2010). Furthermore, increases in NSP within the α3 and β2 subbands (Klimesch, 1999) reflected heightened activity in top-down cortical control systems and the activation of emotional-cognitive processes.

During periods of distant synchronization, the greatest alterations in average coherence are found within the temporo-parieto-occipital cortex. This region is closely associated with mechanisms underlying perception and the primary evaluation of sensory inputs (Farah, 1995). Notably, it plays a key role in the integration of visual and olfactory information, as demonstrated in previous studies (Österbauer et al., 2005; Gottfried, 2010; Zhou et al, 2019).

Several lines of evidence supported other statement that the temporo-parieto-occipital cortex is not responsible for the primary evaluation of sensory inputs, but instead serves as a higher-order multisensory association. Initial sensory processing occurs in the primary sensory cortices (such as the striate cortex for vision), and only after this stage does information reach the temporo-parieto-occipital cortex for further integration and association. Studies using transcranial magnetic stimulation and neuroimaging have shown that the temporo-parieto-occipital cortex is activated later in the sensory processing stream and is specifically involved in integrating information from multiple sensory

modalities, rather than in the initial detection or evaluation of sensory inputs (Patzwahl et al., 1996; Anand et al., 1998; Fattori et al., 2009; Quinn et al., 2014).

Alterations in distant EEG synchronization were marked by increased intra- and interhemispheric interactions within the θ, α1, α3, and β2 subbands, alongside decreased connectivity in the α2 subband (focused in posterior regions) and in the β1 subband (notably in anterior-central and right temporal connections). The most prominent enhancements in average coherence were observed in the α1 subband (left temporal and right occipital zones) and the β2 subband (right frontal region). These patterns are currently linked to the activation of neural networks involved in memory, analytical and semantic processing, as well as positive emotional arousal - particularly the synchronization increase in the α1 subband concurrent with a significant reduction in the α2 subband (Petsche et al., 1997; Klimesch et al., 2000; Aftanas & Golocheikine, 2001). Notably, the consistent involvement of the right frontal area in these integrative processes suggests an olfactory origin for the observed changes (Royet et al., 1999) (Fig. 3, C).

Increased intra- and interhemispheric coherence in theta, alpha, and beta bands, particularly in frontal and temporal regions, is positively associated with executive functions, attentional control, and cognitive integration. This reflects enhanced communication and integration of information across brain regions during cognitive processing (Basharpoor et al., 2019; Gorantla et al., 2020; Wang et al., 2020). Specific increases in coherence in the alpha 1 and beta 2 subbands in left temporal, right occipital, and right frontal regions have been linked to memory, analytical, semantic, and emotional processing, as well as positive emotional arousal (Aftanas & Golocheikine, 2001; Seleznov et al., 2019). Decreased coherence in the alpha 2 subband (posterior regions) and beta 1 subband (anterior-central and right temporal regions) is interpreted as reduced involvement or functional segregation of these areas during the observed cognitive or sensory state (Basharpoor et al., 2019; Gorantla et al., 2020). Overall, these changes point to a reorganization of brain activity, where certain networks become more engaged and others less so, depending on the cognitive or sensory demands at that moment.

Thus these results indicate that the exposure to an odor in the ambient air induces EEG changes that signify the swift engagement of memory, multisensory association, and emotional processing mechanisms. This activation of internal mental activity occurs in response to alterations in the olfactory environment, even when the individual is in a resting state.

Previous research (Zima et al., 2014) has shown that extended periods of rest during control tests are marked by the activation of neural networks that emerge specifically in the absence of external sensory input, supporting internal integrative and cognitive processes. Consistent with these findings, our data indicate that prolonged quiescent states (enforced inactivity) foster the development of internal mental activity. This phenomenon is described in the key studies of Greicius et al. (2003) and Mason et al. (2007) as the activation of resting state networks (RSN). RSNs are implicated in the representation and processing of both internal and external stimuli - including self-reflection, thought, episodic memory, internal speech, mental imagery, emotions, and future planning - characterizing the so-called "wandering

mind. Empirical studies confirm that the DMN/RSN is more active during rest and is considered the neural substrate for internally oriented mental activity (Jerbi et al., 2010; Gruberger et al., 2011; Heine et al, 2012; Sharaev et al., 2016; Poerio et al., 2017).

Analysis of normalized spectral power (NSP) in EEG rhythms revealed that, unlike control conditions, the resting state during odor stimulation - beginning immediately at odor delivery (Fig. 4, a) - was marked by a sustained increase in NSP within the α3 subband (generalized) and θ2 subband (anterior-central zones), alongside a decrease in NSP in the α1 subband (frontal zones and right temporal area). These spectral changes indicate a deepening of internal concentration and mental activity, occurring in the context of a positive mood (Scheeringa et al., 2008).

Alterations in EEG spectral power were generally paralleled by changes in average coherence. Notably, there was a pronounced increase in both interhemispheric and right-hemispheric functional connectivity within the α3 band - indicative of enhanced cognitive processing - as well as in interhemispheric connections of the central-posterior regions within the α1 subband, which are associated with positive mood (Everhart & Demaree, 2003) and states of relaxation (Travis, 2011) (Fig. 4, C). Contemporary research (Sauseng et al., 2005; Başar, & Güntekin, 2012; Moretti, 2015a; Moretti, 2015b; Lejko et al., 2020; Viviani, & Vallesi, 2021) indicates that the upper alpha/alpha 3 as a key neural correlate of higher-order cognitive processing, including working and long-term memory, intellectual behavior, perceptual and semantic processing, planning, and decision-making. Moretti (2015) demonstrated that upper alpha activity specifically reflects encoding and retrieval memory processes, as well as semantic and executive functions (Moretti, 2015a; Moretti, 2015b). Conversely, a marked reduction in α1 oscillatory intensity, along with decreased coherence in the α2 subband (frontal right hemisphere) and β1 subband (frontoparietal cortex), likely reflects diminished activity in the cortico-thalamic feedback loops that regulate external attention (Wróbel, 2000; Sauseng et al., 2005).

Simultaneous fMRI and EEG studies demonstrate that any internal focus of mental processes is accompanied by activation of neural networks - including the cingulate gyrus, insula, thalamus, and frontal neocortex - which significantly enhance perception and cognitive activity. According to Sadaghiani et al. (2010), this state is characterized by synchronized alpha oscillations (primarily in the high-frequency range) and, to a lesser extent, beta1-band activity. This pattern is associated with tonic alertness - a state of heightened readiness, mental clarity, and efficient processing of incoming information (Posner & Rothbart, 1998; Sadaghiani et al., 2010; Lomas, Ivtzan, & Fu, 2015). Our findings fully support that this state is induced by odor application (odor use variant), contributing to improved well-being.

Simultaneous fMRI and EEG studies have shown that any internal focus of mental processes is accompanied by the activation of a neural network - including the cingulate gyrus, insula, thalamus, and frontal neocortex - which significantly enhances subsequent perception and cognitive activity (Taylor et al, 2009; Metzger et al, 2010; Wang L., et al, 2020; Antonucci et al, 2021; Wang, 2024). According to Sadaghiani et al. (2010), this state is characterized by the synchronization of alpha oscillations (primarily

in the higher frequency range) and, to some extent, the β1 band. This neural state is associated with tonic alertness, reflecting a heightened readiness for action, mental clarity, and efficient processing of incoming information (Posner, & Rothbart, 1998; Sadaghiani et al., 2010; Lomas et al, 2015). Our findings fully support that this state is induced under conditions of odor exposure, contributing to an overall sense of well-being.

Based on our results, we conclude that during heightened internal mental activity and the organization of neural networks associated with readiness to respond (α3-subband), the resting state under odor stimulation was marked by overall calming and signs of relaxing comfort (α1-subband). This indicates a simultaneous presence of relaxation and inner vigilance - an attentive mind. Our findings align with tomographic studies (Savic & Berglund, 2004) and support the view that even the simplest form of olfactory perception, such as passive exposure, triggers semantic brain activity through the immediate formation of associations and judgments about the odor.

Experiment 3

In 3rd series of experiments, we examined how changes in breathing type (nose-mouth-nose) affect the electrical activity of the human brain. Odor discrimination is initiated both by olfactory stimuli and the physical impact of airflow on olfactory sensory neurons (Iwata et al, 2017); however, our experimental conditions excluded any mechanical effects from airflow. This approach was particularly valuable for studying olfactory dysfunction - which epidemiological studies estimate affects from 3–20% of the population (Brämerson et al., 2004; Boesveldt et al., 2017) to 13–24% of adults, and up to 30–40% of older adults, with anosmia (complete loss) in 3–14% of adults and up to 22% of those over 60 (Yang, & Pinto, 2016; Desiato et al, 2021; Oleszkiewicz et al., 2025). COVID-19 has caused surges in olfactory dysfunction, with prevalence in infected individuals ranging from 5% to over 50% (von Bartheld, & Wang, 2023; Ota et al, 2025; Tukaiev, & Alves Ferreira 2026).

While it is known that olfactory loss triggers neural reorganization in the brain (Boesveldt et al., 2017), the central mechanisms underlying this process remain largely unclear (Kollndorfer et al., 2014; Kollndorfer et al., 2015). Chronic anosmia is associated with altered global functional connectivity in the brain (Kollndorfer et al., 2014; Kollndorfer et al., 2015). Our findings show that short-term nasal breathing blockage (a form of temporary anosmia) elicited negative emotional responses, as reported by participants. The onset of orthonasal olfactory sensory blockage was marked by increased local synchronization of beta frequencies in caudal brain regions, enhanced theta-band coherence in parietal-occipital areas, and increased interfrontal and intrahemispheric interactions in the beta2 sub-band (F3-O1 on the left; F4-T4 and F4-P4 on the right) (see Fig. 5, I). We interpret these results as evidence that abrupt loss of olfactory input activates thalamo-cortical loops and top-down control systems (orientating response - initiating a search for olfactory signals), reflected in increased F4-T4-P4 connectivity and emotionally colored changes in caudal theta-band coherence (Davidson et al., 1999).

Extended nasal blockage, even when retronasal odor perception is stimulated with lemon essential oil, resulted in pronounced inhibition of distant interactions in the posterior brain regions within the theta

frequency band, as well as a significant reduction in right-brain long-range and parieto-occipital beta2-subband functional connectivity (Fig. 5, II). It means that when the nose is blocked, the brain's back regions (posterior areas) show less communication and coordination with each other, especially in the theta (4–8 Hz) and beta2 (20–30 Hz) frequency ranges. Specifically, there is a reduction in long-range connections within the right hemisphere and between parietal and occipital regions. This decrease in functional connectivity indicates that the brain's ability to integrate and process information is diminished (Ma et al, 2023 Kuang et al, 2025), which may correspond to the negative feelings or reduced mental sharpness (Zacharia et al, 2022) often experienced during a cold, even without direct effects from inflammation.

Restoring continuous nasal breathing - and thus olfactory perception - leads to robust activation of both long- and short-range interhemispheric information exchange in the theta1,2 and beta1 frequency bands (Fig. 5, III). This activation reflects heightened cognitive activity in the brain, including the development of memory processes, real-time sensory and cognitive-emotional regulation of behavior, focused attention, and evaluation of significant stimuli (Cómez et al., 1998; Wilson et al, 2006; Engel & Fries, 2010; Seleznov et al., 2019; Gorantla et al., 2020; Tan et al., 2024; Haddon et al., 2025). This outcome is both natural and logical, as the recovery of olfaction and odor perception following sensory (olfactory) deprivation is highly significant.

Discussion

The results of current studies indicate that activation of the olfactory system influences the functional state of the brain in humans, even though humans are considered a 'microsmatic' species. This effect occurs during both directed, analytical odor detection and passive odor perception. The distinction is as follows: passive odor perception engages internal motivational attention systems (θ, α1 subbands) and modulates neural networks associated with the resting state, such as those affected by phytotherapy in park-like recreational environments. In contrast, active odor perception is marked by cognitive changes during external analytic olfactory tasks, including activation of working memory mechanisms (frontal θ rhythm), subjective emotional evaluation of stimuli, and the polymodal internal associations triggered by odor memory, as well as external attention networks (α1,2, β1 rhythms). Notably, relevant odor assessment happens quite rapidly.

The findings can be explained by the developed neural network of the olfactory center (olfactory bulb–piriform cortex), which is extensively interconnected with both olfactory and non-olfactory higher-order brain regions, including the amygdala, parahippocampal gyrus, entorhinal cortex, anterior cingulate cortex, insula, locus coeruleus, centers of other sensory modalities, orbitofrontal cortex, and even the cerebellum (Fjældstad et al., 2017; Freiherr, 2017; Brandt, & Huppert, 2025; Ferdowsi et al, 2025; Stenwall et al, 2025; Yang et al, 2025). The rapid analytic and associative processing is due to direct olfactory inputs to the limbic system and neocortical areas, bypassing the thalamus. The connections between the piriform and orbitofrontal cortices and the thalamus (the medial dorsal nucleus of the thalamus) serve primarily to amplify, modulate, and support higher-order functions such as attention and

discrimination, rather than acting as primary sensory relays. This unique architecture underlies the speed, emotional salience, and associative power of olfactory perception in mammals (Plailly et al, 2008; Milardi et al, 2017). Notably, the olfactory neural network is characterized by branched feedback connections among its centers (Li, & Hertz, 2000; Gottfried, 2010; van Hartevelt, & Kringelbach, 2012; Freiherr, 2017), which provide high sensitivity in olfactory detection and enable effective learning, as well as the formation and retention of complex mental images in memory.

Our EEG results, together with tomographic research, indicate that olfactory perception in humans relies on synthetic integrative mechanisms involving higher-order brain structures beyond the primary olfactory centers. This hierarchical processing means that the influence of olfactory stimuli on behavior and neural activity is shaped by past experiences, environmental context, and internal state. Notably, many of these regions are also key components of the brain's default mode network (Sporns, 2011). This supports the view among psychologists and aromatherapists that aroma perception can modulate mental and emotional states even during rest, thereby enhancing the brain's reserve capacity, stress resilience, and work efficiency.

Declarations

Institutional Review Board Statement

This study was conducted in accordance with the Declaration of Helsinki and approved by an Ethics Committee for studies involving humans.

Informed Consent Statement

Informed consent was obtained from all subjects involved in the study.

Conflicts of Interest:

The authors declare no conflicts of interest.

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Author Contribution

All authors contributed equally to this work, read and approved the final manuscript.

Data Availability

Data are available upon request to the corresponding author.

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Figures

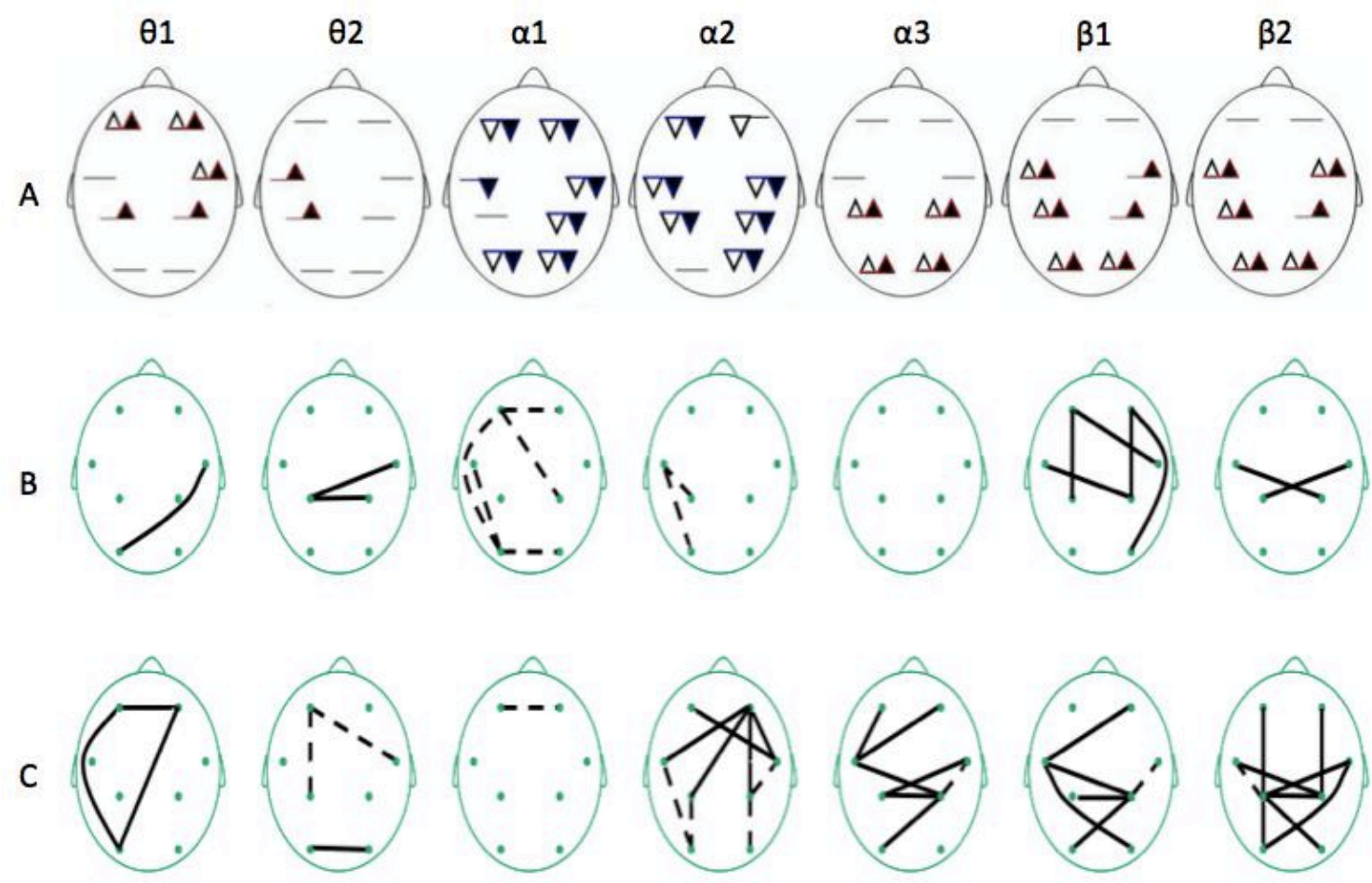

Figure 1

Changes in the normalized spectral power (NSP) (A), the meanconnectivity of EEG rhythms (B – control (the distilled water), C - "real" odor exposition) at the onset of the active odor perception (1st minute of odor exposition).

1. Δ – changes of NSP in control (distilled water); ▼ – changes of NSP in "real" odor exposition;

2.Δ/▼ -significant increase/decrease of NSP of the corresponding EEG rhythms (p<0,05);

3. ▬/----- significant increase/decrease of coherence of the corresponding EEG rhythms (p<0,05).

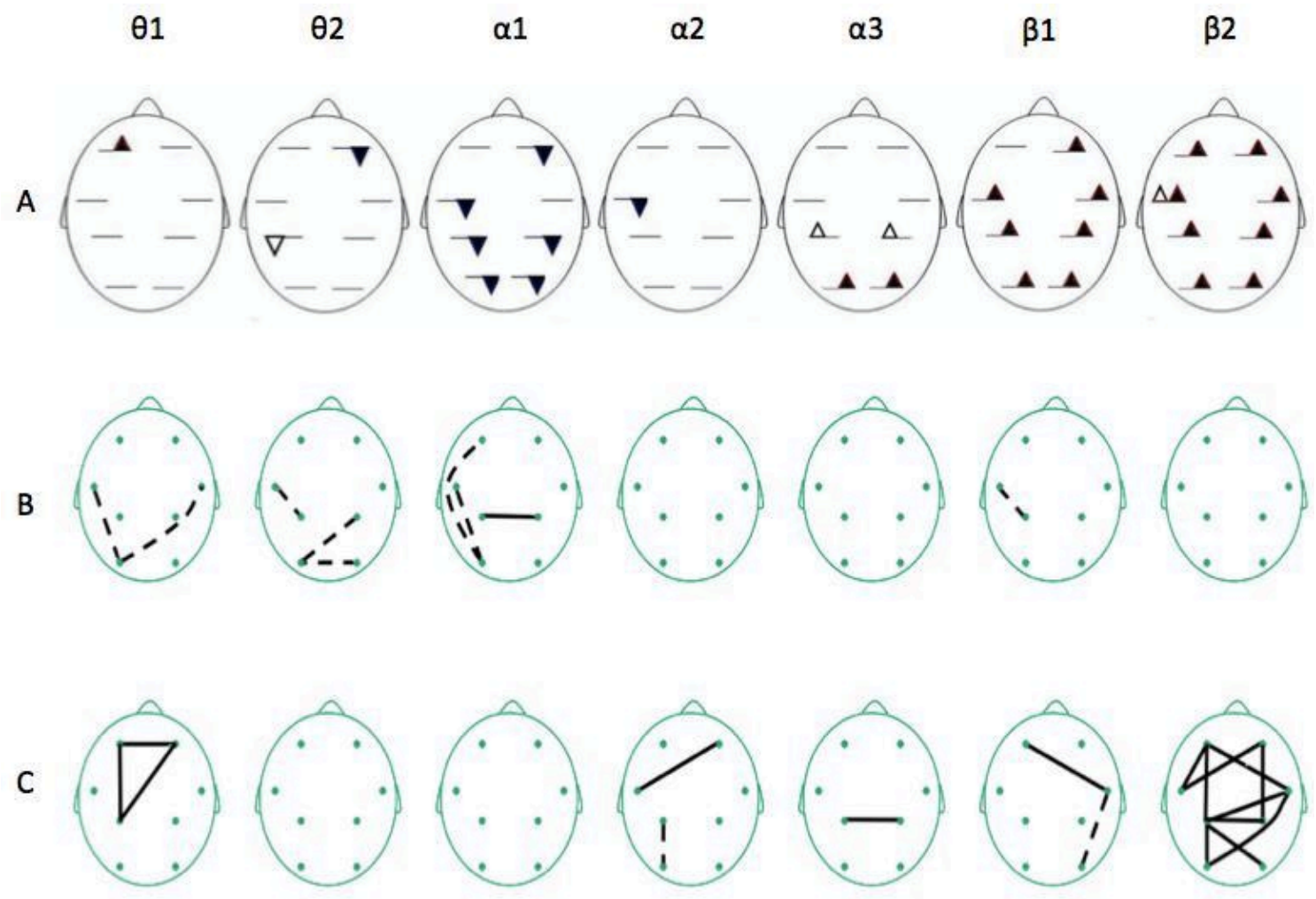

Figure 2

Changes in the normalized spectral power (NSP) (A), the meanconnectivity of EEG rhythms (B – control (the distilled water), C - "real" odor exposition) during development of the active odor perception (3rd minute of odor exposition).

1.Δ – changes of NSP in control (distilled water); ▼ – changes of NSP in "real" odor exposition;

2.Δ/▼ -significant increase/decrease of NSP of the corresponding EEG rhythms (p<0,05);

3. ▬/----- significant increase/decrease of coherence of the corresponding EEG rhythms (p<0,05).

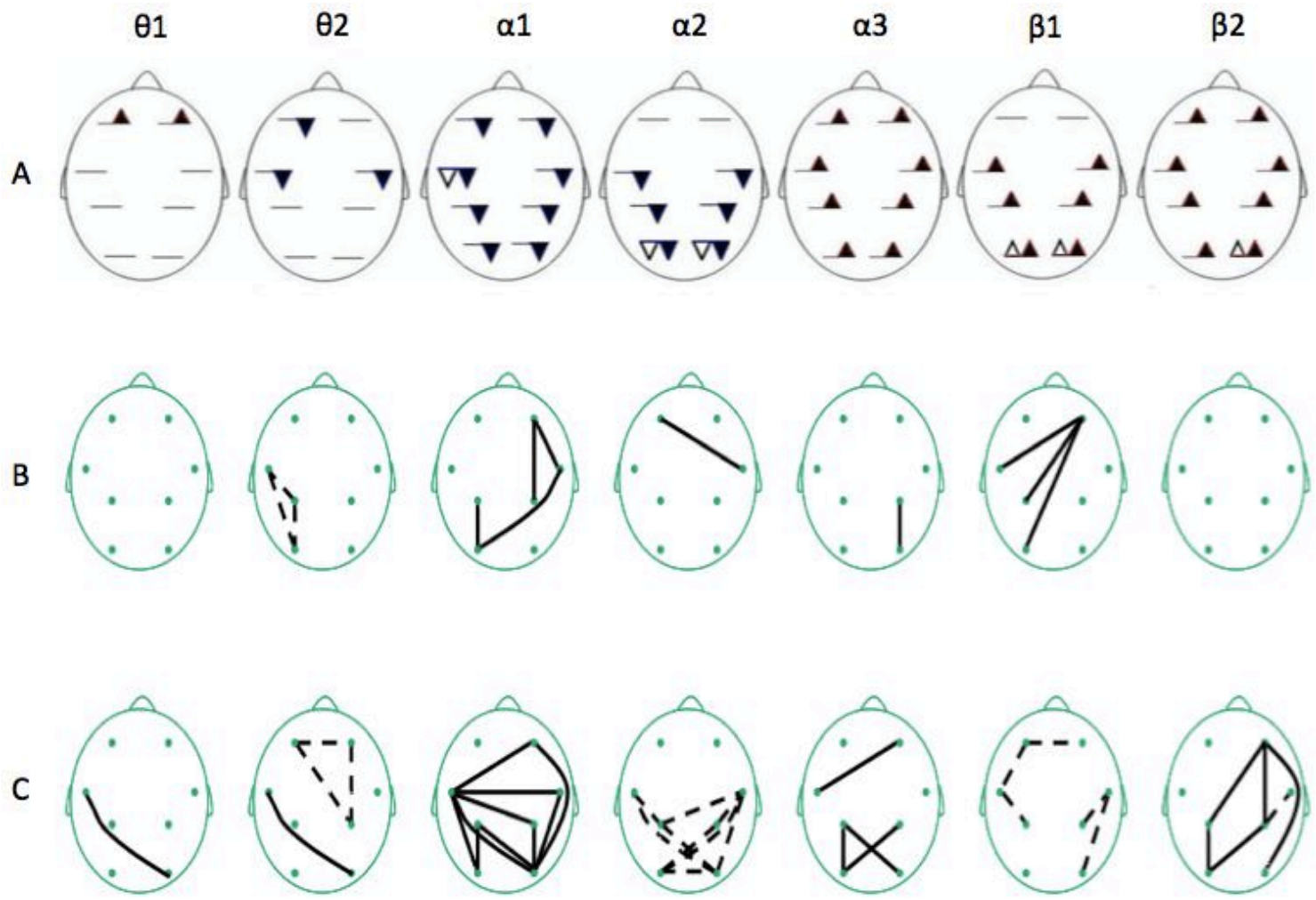

Figure 3

Changes in the normalized spectral power (NSP) (A), the meanconnectivity of EEG rhythms (B – control (the distilled water), C - "real" odor exposition) at the onset of the odor delivery or simulation (1st minute of “passive smelling”).

1.Δ – changes of NSP in control (distilled water); ▼ – changes of NSP in "real" odor exposition;

2.Δ/▼ -significant increase/decrease of NSP of the corresponding EEG rhythms (p<0,05);

3. ▬/----- significant increase/decrease of coherence of the corresponding EEG rhythms (p<0,05).

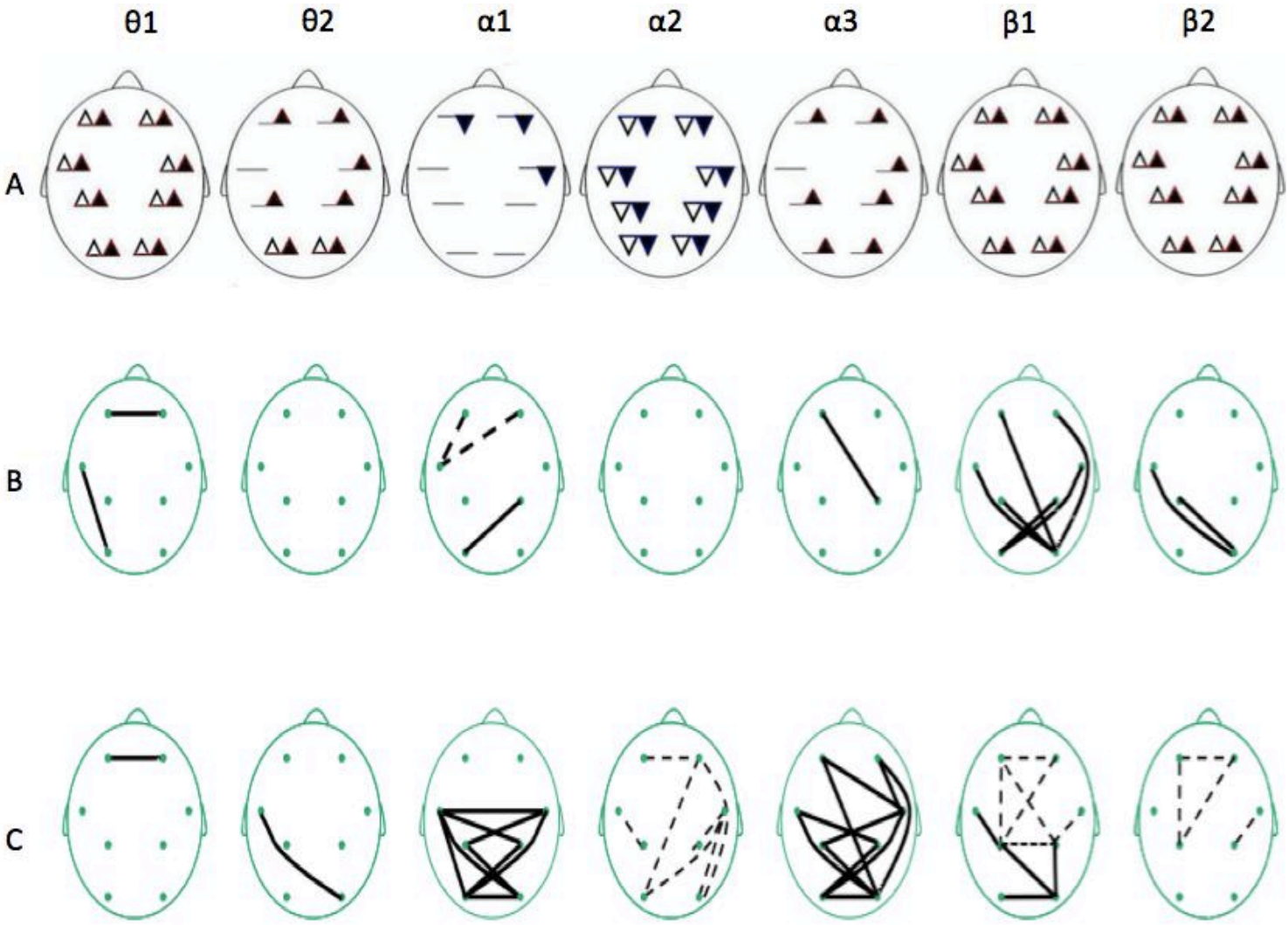

Figure 4

Changes in the normalized spectral power (NSP) (A), the meanconnectivity of EEG rhythms (B – control (the distilled water), C - "real" odor exposition) during the passive perception of the environment odor in the prolonged resting state. The data represent in comparison with the initial state.

1.Δ – changes of NSP in control (distilled water); ▼ – changes of NSP in "real" odor exposition;

2.Δ/▼ -significant increase/decrease of NSP of the corresponding EEG rhythms ($p<0,05$);

3. ▬/----- significant increase/decrease of coherence of the corresponding EEG rhythms ($p<0,05$).

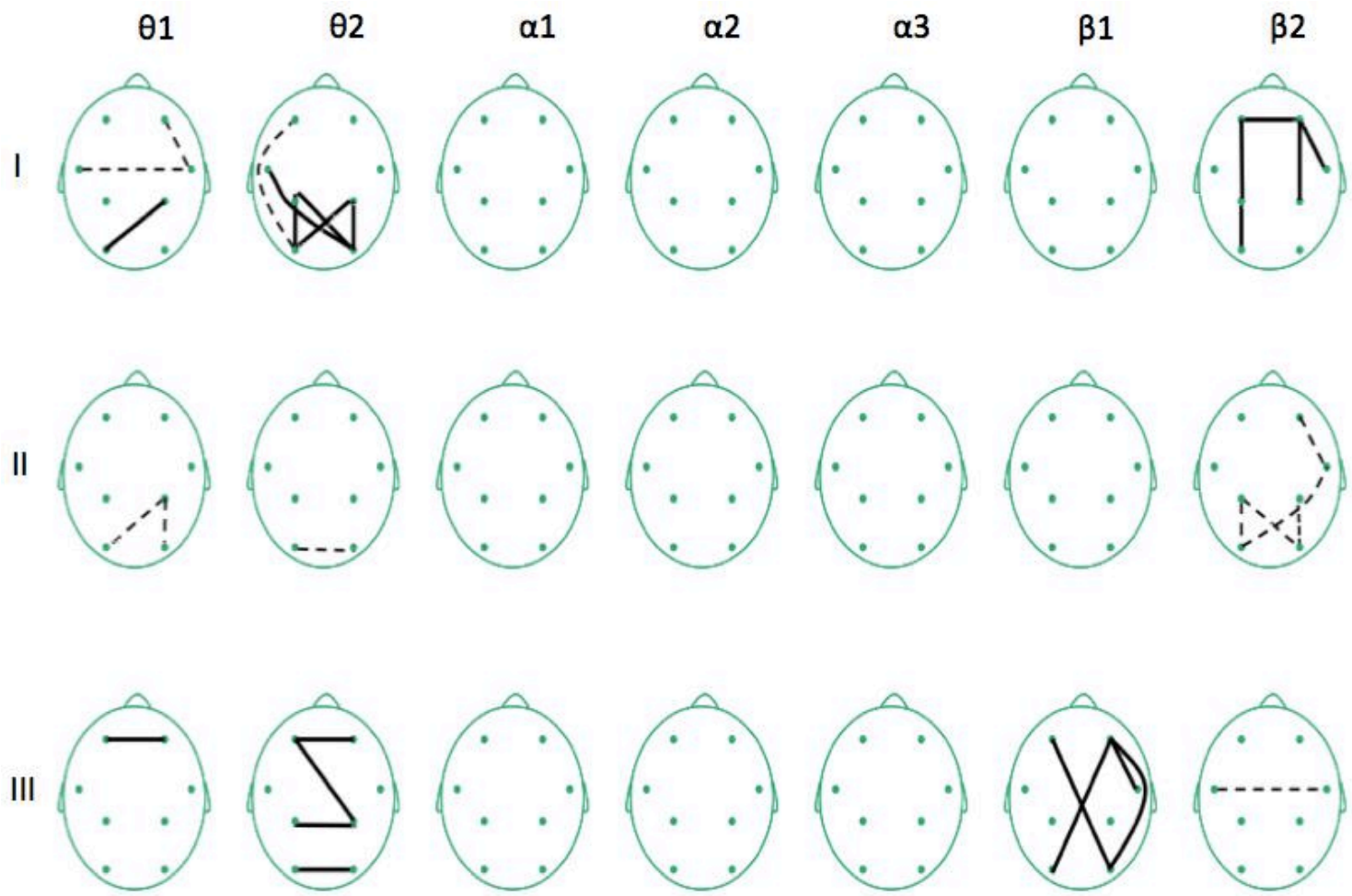

Figure 5

Connectivity fingerprint of theEEG rhythms under changing the types of breathing (nose-mouth-nose): I – the blockage of nasal breathing – the mouth breathing; II – the mouth breathing with odorizedair; III – the nasal breathing with odorizedair.

▬/----- significant increase/decrease of coherence of the corresponding EEG rhythms ($p<0,05$).