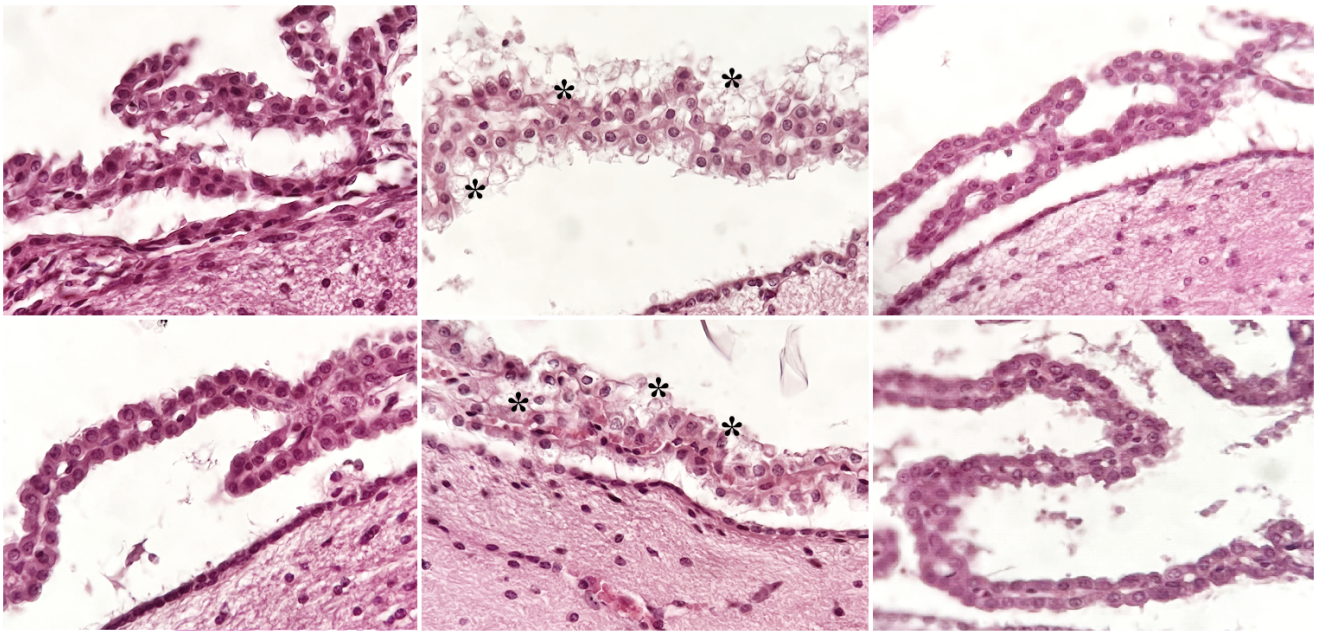


Figure 6. Representative micrographs of sagittal sections from mouse brain illustrating details of choroid plexuses in H&E staining. (**a**) sham group; (**b**) laboratory-device-emitted RF exposure group; (**c**) Wi-Fi router-emitted RF exposure group; * vacuolations.

3.3. Global DNA Methylation in the Brain

Global DNA methylation was assessed at the end of the experiment by quantifying the percent of 5-methylcytosine (5 mC). Mice exposed to RF radiation emitted by the Wi-Fi router had significantly lower levels of 5 mC compared to sham-exposed mice (two-sample *t*-test $p = 0.03$). The results are illustrated in Figure 7.

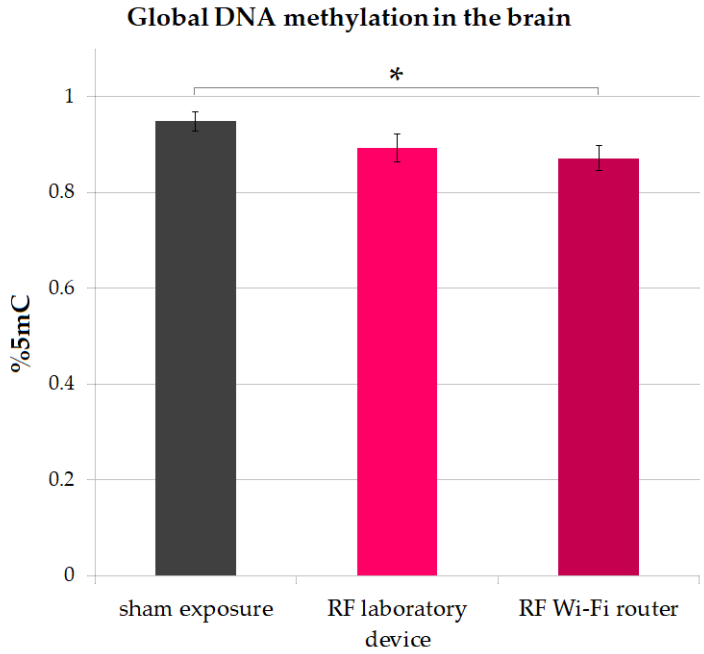


Figure 7. Global DNA methylation in the brains of mice, quantified as % of 5-methylcytosine (5 mC), after 16 weeks' exposure to RF radiation. Data are represented as means and standard error of the mean (SEM). * $p = 0.03$.

Additionally, DNA methylation of isocortex cells was quantified by immunofluorescent staining (Figure 8). There was significantly lower 5 mC in the cells of mice exposed to RF emitted by the Wi-Fi router compared to the other two experimental groups (one-way ANOVA $p < 0.001$).

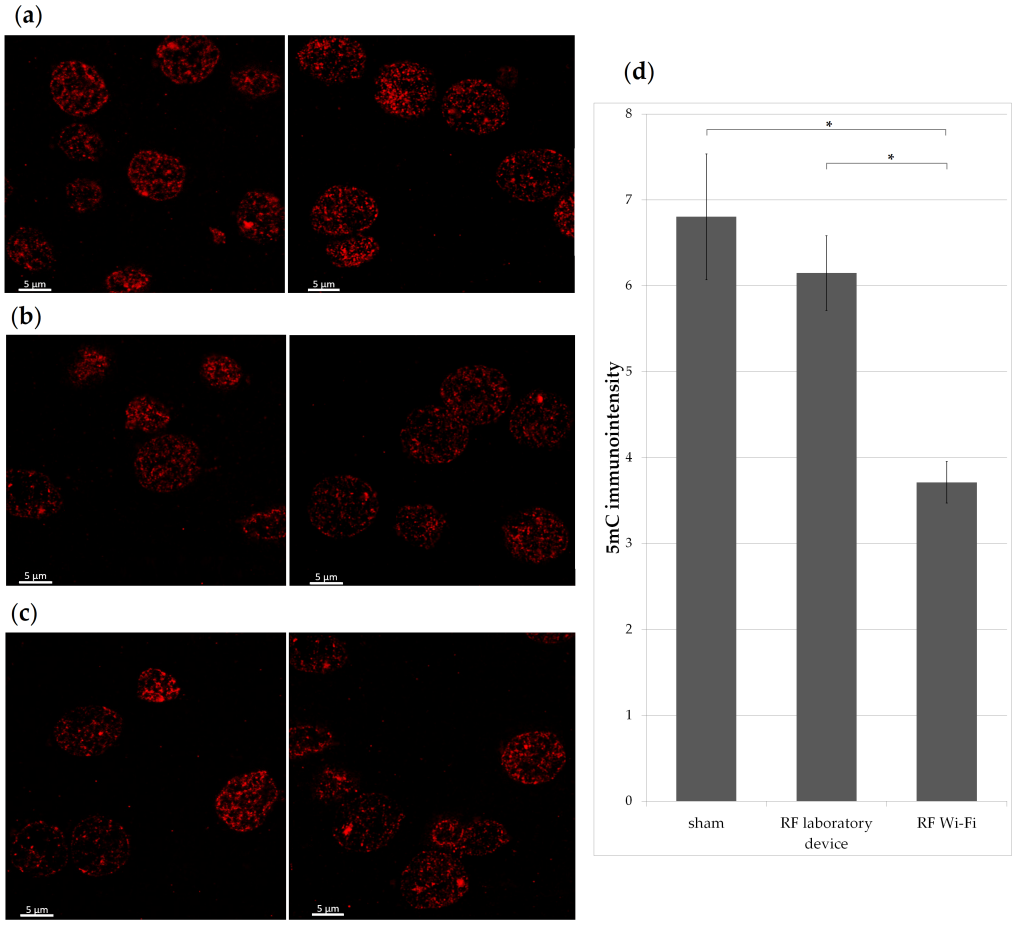


Figure 8. Levels of 5-methylcytosine (5 mC) in the brain of analyzed animals. Representative photomicrographs of 5 mC immunostaining in brain cross-section capturing the isocortex of mice: (**a**) sham group; (**b**) laboratory-device-emitted RF exposure group; (**c**) Wi-Fi router-emitted RF exposure group; scale bar = 5 µm; (**d**) immunointensity of 5 mC depicted by red fluorescence signals were measured and presented in a bar graph. * $p < 0.01$.

4. Discussion

There has been increasing public concern about the potential negative effects of RF radiation on health, particularly on the brain, due to the widespread use of communication devices in daily life. To this day, the most compelling evidence correlating RF exposure to biological effects with health consequences is the presence of oxidative stress in RF-exposed animals [14,15]. Oxidative stress was associated with neurodegenerative conditions such as Parkinson's disease, Alzheimer's disease [16], amyotrophic lateral sclerosis [17,18], and Huntington's disease [19]; thus, investigating further the effects of RF radiation the brain is crucial.

Concerns have also been raised about the potential behavioral effects that RF radiation exposure can have; there is evidence that exposure to GSM RF radiation can have a slight impact on attention and memory in human adults [20], yet its overall effects on behavior are debatable [21]. Additionally, in animal studies the findings are inconsistent; while some suggest RF exposure may not exert any effect on behavior [22] or have a beneficial effect by improving the behavioral impairment in animal studies [23–25]. As a result, the effects of RF radiation exposure on memory are still a matter of debate.

Exposure to environmental stressors and pollutants can lead to a range of structural and functional changes in the brain that are detrimental to normal functioning [26]. Electromagnetic fields have long been considered environmental pollutants [27]; thus, we hypothesized long-term exposure to RF radiation may have an impact on the behavior of exposed animals, namely mice in this study.

We exposed mice continuously for 16 weeks. This duration is considered a long-term exposure for mice considering their average lifespan and aging process [28] and covers a substantial part of a mouse's lifespan, making it suitable for observing the long-term effects of exposure to various factors. Nevertheless, it is not of sufficient length for the mice to reach the stage of senescence, which could interfere with the interpretation of data gathered during the exposure experiment.

Our findings suggest that RF radiation exposure increased the locomotor activity of mice, as indicated by the total distance traveled and average speed during the test. To date, there are conflicting results on whether RF impacts the locomotor activity in animal models. Some studies reported no significant changes in the locomotor activity of animals exposed to RF radiation in different frequencies range (e.g., rats exposed to 1.2 GHz [29], 905-MHz [30], and 900 MHz [31], and mice exposed to 1950 MHz [32]), while others report a decrease in the locomotor activity (in rats exposed to 2.5 GHz RF radiation [33] and 900 MHz radiation [34]. There are also data suggesting RF-exposed animals have higher locomotor activity [35,36]; our results linking RF exposure with increased locomotor activity support these latter findings.

The reduction in time spent in the center of the arena in the OFT is considered a behavioral indicator of elevated anxiety levels. We did not find any significant differences between the trajectory patterns of mice from the three groups in the OFT at the beginning and end of the experiment, nor between the different groups of mice at the two time points (Figure 4).

Although we did not find a direct link between RF exposure and anxiety-like behavior in our study, we observed that mice in all groups tended to avoid the center of the arena. This suggests that there may be other factors, such as handling [37], influencing the animals' behavior that should be taken into consideration when conducting studies and interpreting their results. There is also an ongoing debate about the extent to which the OFT accurately assesses emotionality [38]; early activity in the OFT can indicate anxiety, as it may evoke separation stress (due to the separation from cage-mates) and agoraphobia (as being exposed to a large arena that differs from the familiar holding cage) [39]. Thus, we cannot conclude whether or not exposure to RF in our experimental settings had any impact on the anxiety-like behavior of mice in our groups.

In terms of memory performance, exposure to 2450 MHz RF radiation has been found to cause spatial reference memory deficits in rats, as measured by water-maze performance [40]. Mice exposed to 800–1900 MHz cellphone signals in utero also showed impaired neurodevelopment and behavior [41]. Nevertheless, other research teams have found that exposure to 900–2450 MHz RF radiation did not cause spatial or non-spatial memory deficits in rats [42] or mice [43] when memory was evaluated through behavioral testing. Moreover, other studies reported exposure to pulse-modulated RF resulted in slower reaction times and improved accuracy in a working memory task in humans [44], while exposure to RF in adult rats has been shown to disrupt monoamine neurotransmitters, which may contribute to negative effects such as memory and learning impairments and stress [45]. Therefore, the impact of RF radiation exposure on memory remains controversial. Our findings did not reveal any significant differences in working memory in the mice at the beginning and end of the experiment, nor between the different groups of mice at the two time points.

As reviewed in recent study, locomotion in rodents is driven by complex brain-wide network; the initiation of locomotion in different higher-order states is driven by involving excitatory circuits in the cortex, midbrain, and medulla and is regulated by neuromodulatory circuits in the basal forebrain, hypothalamus, and medulla. The maintenance of locomotion involves motor, sensory, and associative cortical elements and circuits within

the superior colliculus, cerebellum, periaqueductal gray, mesencephalic locomotor region, and medullary reticular formation. The ability to cease locomotion during a defensive emotional state, such as anxiety, is controlled by specific areas in the brain including the hypothalamus, amygdala, periaqueductal gray, and medullary premotor centers [46]. The neurons in the motor cortex have "memory" properties, contributing to learning or storing motor skills and behavioral adaptation [47]. Additionally, it has been shown that motor cortex of rodents, is involved in sensory guided coordination of movement, generating an appropriate behavioral response to sensory perturbations [48]. Moreover, the functional interconnections of the hippocampus with the prefrontal cortex are critically related with the integration of emotional and cognitive aspects of behavior such as working memory [49].

Here, we focused on the structural and morphological changes in the cortex, hippocampus and cerebellum. Previous studies showed long-term exposure to cellphone RF radiation at 900 MHz resulted in vacuolation diffusely in the brain parenchyma [50]. Others showed prolonged exposure to RF 900 MHz microwaves (specific absorption rate = 6 W/kg) was linked to persistent astrocyte activation in the brains of rats, which is a potential indicator of gliosis. There was no significant evidence of morphological changes or astrocyte activation in animals from this study; nonetheless, vacuolation in the ependymal cells of the choroid plexuses was observed in the animals exposed to RF emitted by the laboratory device (Figure 6), supporting previous findings [50]. The potential physiopathological effect of these changes may be related to disruptions in cerebrospinal fluid drainage, yet further testing is needed to confirm this observation and to exclude possible confounding factors.

Although there are limited data associating exposure to RF with brain structural and morphological changes, there is a line of evidence showing that exposure to RF may more commonly lead to changes in the activity of the brain (e.g., changes in electrocorticography activity of the cortex and hippocampus cells in vivo [51] and changes in the excitability of primary hippocampal neurons in vitro [52]). We did not assess the functional changes in the brains of the tested animals and further research is necessary to determine any potential connections between morphological changes and functional changes in the brain.

DNA methylation, an important epigenetic change, plays a key role in the regulation of gene expression and is involved in the development of complex behaviors [53]. Exposure to stress can alter DNA methylation patterns, potentially influencing gene expression and contributing to disease development [5,54] and behavioral changes [55,56]. The brain is composed of various types of cells, including neurons and glial cells, each of which have distinct functions and are at different stages of development. In addition, the patterns of DNA methylation vary between different types of cells [57]. In the brain, DNA methylation in the hippocampus area, more precisely in the dentate gyrus, was shown to control behavior and stress-induced gene expression [58]. DNA methylation in the neurons could be leveraged through adaptive modifications in gene expression during memory formation, and this change would be sustained as the memory is consolidated [59]. Studies have shown that cells within the isocortex [60] experience a decrease in DNA methylation as they age. Additionally, there is evidence of a naturally occurring gradient of DNA hypomethylation, particularly in excitatory neurons of mice, as they are distributed in different layers of the cortex [61].

There is limited research on the potential for RF-radiation exposure to alter DNA methylation patterns. To date, it has been suggested that RF radiation can alter DNA methylation in the estrogen receptor of colon cells of rats [62]; a single study reported modified DNA methylation patterns in the brain of rats, more precisely in the hippocampus [63] as a result of RF exposure.

Our results show a lower level of global DNA methylation quantified as the percentage of 5 mC in the brains of mice exposed to RF radiation compared to sham-exposed counterparts (Figure 7). The global levels of 5 mC in mice from the Wi-Fi router exposure group was significantly lower compared to sham (two-sample t-test $p = 0.03$). We found similar results when analyzing only the cells from the isocortex of mice (Figure 8), where the levels of 5 mC were notably decreased in mice exposed to the radiofrequency radiation emitted by the Wi-Fi router when compared to both a sham and laboratory-device-exposed groups ($p < 0.001$).

Our results are in accordance with the previous findings reporting a hypomethylation in the hippocampus of rats exposed to RF radiation [63]; however, this change was not associated with working memory or spatial learning impairment in our groups.

One of the challenges in investigating the impact of RF radiation on behavior and the brain is that various studies have employed dissimilar devices and methods for RF radiation exposure, making it hard to match and compare the outcomes. Despite the difficulties associated with studying RF radiation, there is some evidence that it can influence the behavior of both animals and humans. To gain a more comprehensive understanding of the potential impacts of RF radiation and to increase the reliability and validity of the research, it is important for future studies to standardize as much as possible. This may include using similar devices and protocols for RF radiation exposure, as well as similar approaches when testing hypotheses.

5. Conclusions

Our findings showed long-term exposure to 2.45 GHz RF radiation lead to an increase in mice's locomotor activity. These findings were not supported by changes in the morphology of the mouse brains, as no significant structural or morphological changes were observed, with the exception of some ependymal cell abnormalities. Global DNA methylation was lower in mice exposed compared to sham counterparts, supporting the previous literature. Our results indicated there are no significant differences in the effects of RF radiation emitted by the Wi-Fi router and the laboratory device. However, further research is needed to fully understand the potential effects of RF radiation on brain function.

Author Contributions: Conceptualization, S.S.-D. and G.R.; methodology, S.S.-D., A.-M.C., O.C.V. and L.T.; validation, O.C.V. and A.-M.C.; formal analysis, O.C.V., A.A., S.R., C.H., D.M.P. and V.S.; investigation, A.-M.C., A.A., S.R., C.H., D.M.P. and V.S.; data curation, O.C. and L.T.; writing—original draft preparation, S.S.-D.; writing—review and editing, A.-M.C., O.C. and S.S.-D.; supervision, G.R. and O.B. All authors have read and agreed to the published version of the manuscript.

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Informed Consent Statement: Not applicable.

Data Availability Statement: The data presented in this study are available on request from the corresponding author. The data are not publicly available as they contain additional information not presented and discussed in the study.

Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

The exposure system was designed for investigating the effects of long-term, continuous exposure to ambient electromagnetic fields. The standard TEM-cell setup was not suitable for this purpose, so an antenna system was adapted to reduce the stress on the animals during the experiment. The antenna system consisted of a commercial off-the-shelf Wi-Fi whip antenna and cylindrical reflectors. The whip antenna was a standard rubber duck antenna mounted on the axis of the reflector at its focus point. The parabolic cylindrical reflector had a surface contour generated according to the equation $y = 0.083 \times x^2$ to enhance directivity (Figure A1). The experimentally determined beam width was $2\alpha = 25.5$ degrees at the 3 dB half-power point and $2\beta = 46.5$ degrees at 10 dB from the maximum value. The adapted antenna had a gain of G = 5.67 dBi, which is higher than the 2.5 dBi gain of a standard whip antenna.

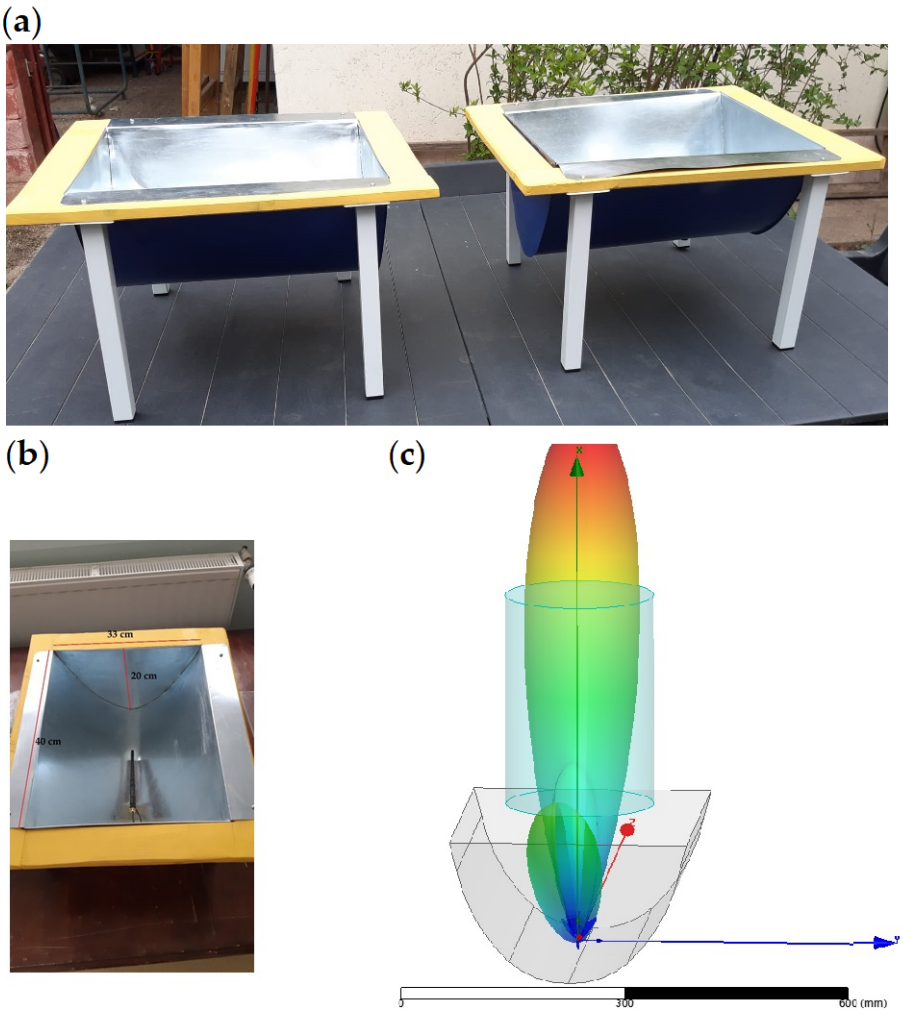


Figure A1. The adapted antenna system used for the experiment: (**a**) antenna systems—overall view; (**b**) dimensions of the cylindrical reflector; (**c**) simulation of the antenna system directivity with the cylindrical enclosure on top of the reflector.

Each antenna system used for the RF-exposure groups was connected to a generator: a standard Wi-Fi router (representing a "real-world" source) and a laboratory radiofrequency generator. The exposed animals from each group were placed in cylindrical enclosures (with 10 mice per enclosure) with a diameter of 24 cm, located about 5 cm from the reflector edge and 20 cm from the whip antenna. At this distance, the antenna beam width (2β = 46.5 degrees) was approximately 18 cm wide, covering almost the entire area explored by the mice, taking into account the thickness of the glass.

Taking into account that the spherical wave emitted by the whip antenna was reflected and transformed into a plane wave at the reflector edge, it was assumed that the far-field condition was obeyed and the Friis formula was used to calculate the power density (S) at a distance of 20 cm from the whip antenna (which was located at the center of the cylindrical enclosure), for the maximum rated power of the generator (71 mW)—the worst-case scenario. The calculated power density was S = 0.52 W/m^2, and the corresponding electric field strength was E = 14 V/m. To calculate the specific absorption rate (SAR) in the mouse body, a simplified layered biological model was considered and constructed in the Ansys HFSS environment, which employs the frequency and time domain finite element method. The mouse body was approximated with an ellipsoidal shape that consisted of several layers, representing the skin, adipose tissue, muscles, and internal organs, as shown in Figure A2a. For the purpose of simplification, the tissues were assumed to be homogeneous, linear, and isotropic media. The tissues' electric parameters, permittivity,

and conductivity were taken from the literature [64] and their frequency dependence is depicted in Figure A2b,c, respectively.

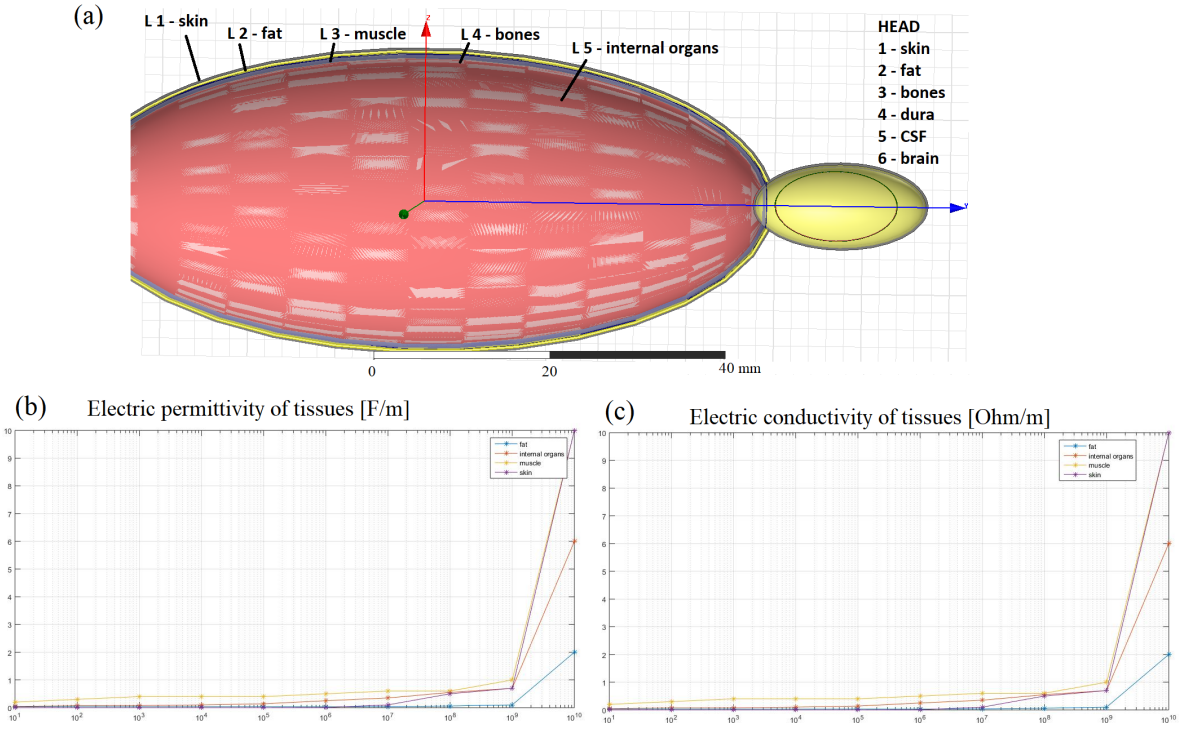


Figure A2. The mouse model used for SAR simulation: (**a**) the geometric model comprised of body with five layers and head with six layers; (**b**) electric permittivity of biological media depending on frequency; (**c**) electric conductivity of biological media depending on frequency.

The dosimetry analysis was focused on the worst-case scenario, using the maximum field emitted by the Wi-Fi generator. SAR was calculated for a plane wave excitation with linear polarization and electric field strength of 14 V/m, directed upwards from below the body, as in the experimental setup. The orientation of the mouse body relative to the field polarization, represented by angle alpha, varied from 0 degrees (longitudinal position, with the body parallel to the polarization) to 90 degrees (transverse position, with the body perpendicular to the polarization) as the mice were able to move freely inside the cylindrical enclosure.

Both local and average SAR was computed using different methods. The local SAR was computed for each mesh node using a simplified equation that takes into account the electric field E, the electrical conductivity σ, and the mass density ρ of the dielectric material. The average SAR was calculated using the IEEE STD P1528.4/D1.0 method. Figure A3 displays the local and average SAR in a sagittal plane for both longitudinal polarization (alpha = 0 degrees) and transverse polarization (alpha = 90 degrees). The same representation range of 0.62 mW/kg to 1.4 mW/kg was used in Figure A3 to show the higher values in the longitudinal case. To further support that longitudinal polarization represents the worst-case scenario, Figure A3e shows the maximum local SAR value in the sagittal plane as a function of the alpha angle, which varies from 0 to 90 degrees in increments of 10 degrees. The variation follows $\cos^2\alpha$ dependence, as described by Malus' law of optics.

Therefore, for a single mouse exposed to the maximum power generated by the Wi-Fi router, the simplified model indicates a maximum local SAR of 17.86 mW/kg for longitudinal polarization. The mice, as they roamed freely, were exposed to various field polarizations, yet the worst-case scenario in terms of thermal effects corresponded to the electric field polarization along the mouse's body. The maximum local SAR value obtained

in the worst-case scenario was determined using an electric field strength of E = 14 V/m, which corresponds to the strongest Wi-Fi transmission at a single spectral component. For modulated transmissions, the energy is distributed across the entire channel bandwidth, resulting in a maximum power level of each spectral component in the OFDM modulated transmission that is 10 dB lower than in the previous case. As a result, the corresponding E-field peak value is approximately three times lower and the SAR is ten times lower. The laboratory source (USRP generator) was set to achieve E-field and SAR values similar to those of the average Wi-Fi transmission.

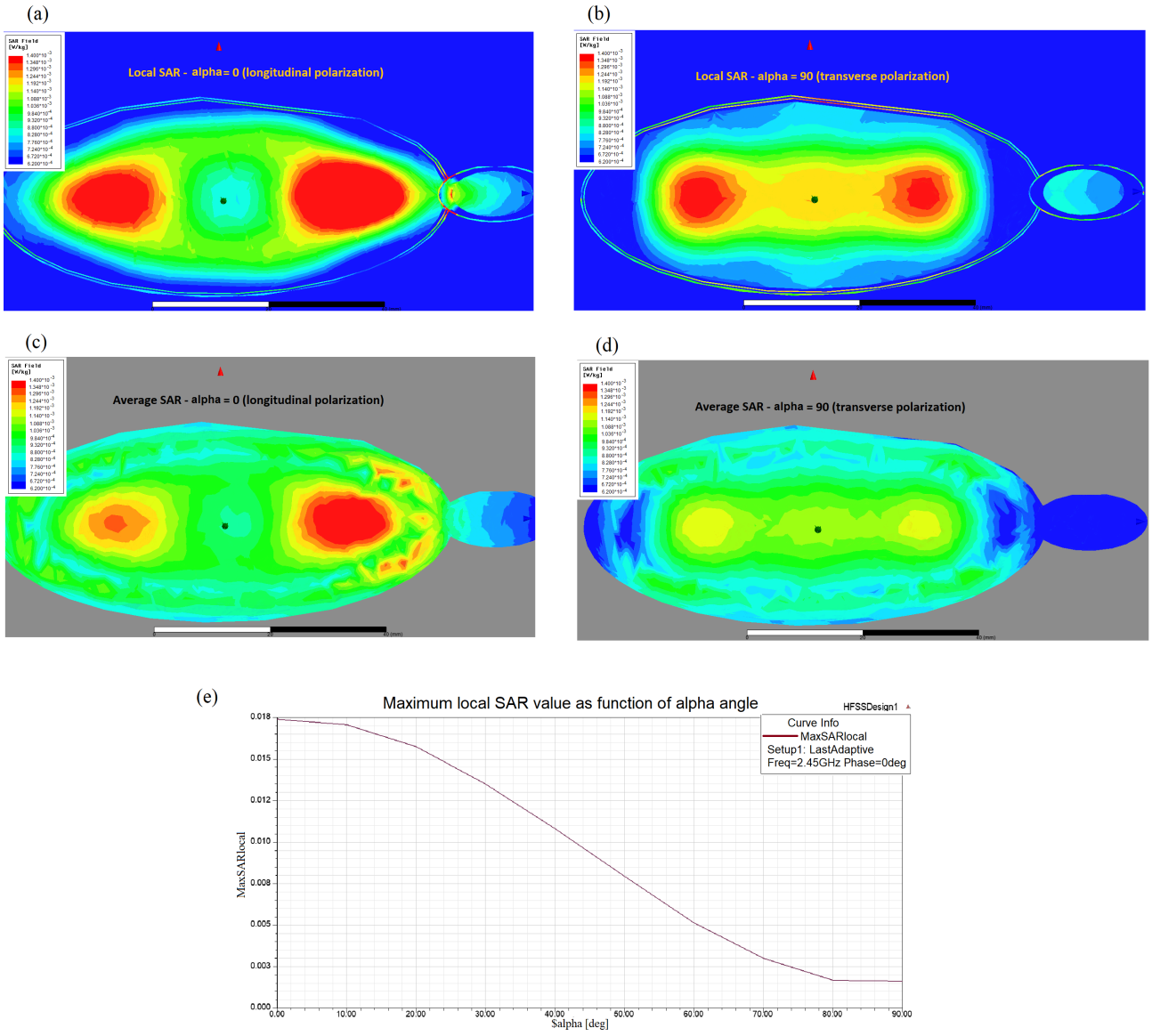


Figure A3. SAR distribution in the mouse's sagittal plane: (**a**) local SAR with longitudinal polarization; (**b**) local SAR with transverse polarization; (**c**) average SAR with longitudinal polarization; (**d**) average SAR with transverse polarization; (**e**) maximum local SAR value in the sagittal plane depending on alpha angle between the field polarization and the mouse body.

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