## Lateralized changes in the hippocampal theta activity of freely flying homing pigeons as revealed by combined EEG and GPS tracking

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Vyssotski AL<sup>1</sup>, Latanov AL<sup>13</sup>, Dell'Omo G<sup>1</sup>, Troester G<sup>2</sup>, Lipp HP<sup>1</sup>, Wolfer DP<sup>1</sup>

- 1. Inst. of Anatomy, Univ. Zurich, Switzerland
- 2. Inst. for Electronics, Swiss Federal Inst. of Technology, Zurich, Switzerland
- 3. Higher Nervous System Activity, Moscow State Univ., Russian Federation

Lesion studies have shown that the pigeon hippocampus is a critical structure for spatial orientation. There is also evidence for hemispheric specialization of pigeon homing mechanisms, and, possibly, for magneto-reception in caged birds. Since the occurrence of theta oscillations in the EEG has been associated with navigational behavior also in humans, we analyzed the EEG of freely flying homing pigeons in relation to their position as recorded by GPS.

12 Pigeons were implanted bilaterally with 4 electrodes per hippocampus. These were connected by fine wires to a backpack of 40 g consisting of a micro-GPS recorder storing flight positions with an accuracy of 6 m and an 8-channel EEGlogger storing the raw data (500 sps, 11-bit accuracy, +/-750 uV) in flash memory. From 81 releases, we collected 127 h of EEG containing 34.6 h of pigeon flight. Offline analysis performed on artifact-free subsets of data (66%) determined the proportion of theta oscillations in the EEG during bins of 2 sec of flight matched to GPS coordinates. The proportion of theta activity in the right hippocampus (33%  $\pm$  1) did not depend significantly on pigeon position whereas at the left side it was decreasing from 39% to 29% when pigeons flew towards the loft (p < 0.0001). In the left hippocampus the proportion of theta in sitting birds was also larger at the start place than in the loft, but in some birds the same tendency has been observed at the right side. Whereas the total EEG power having a maximum at 2.5 Hz reflects mainly the vigilance/sleep states of the bird, hippocampal theta power seems to be related to processing of visual cues during orientation. These findings corroborate functional lateralization of homing in the pigeon brain, and promise new approaches to analyze brain mechanisms underlying homing and navigation.

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