

# Reply to Rattenborg and Martinez-Gonzalez: Fundamental and divergent aspects of the neurobiology of episodic memory

To shed light on the evolution of episodic memory, we recently integrated the behavioral evidence across species with a comparative analysis of the underlying neurobiology and neural mechanisms (1). We conclude that fundamental features of episodic memory are present in mammals and birds and that a similar neural circuit could support this capacity across species (figure 2C in ref. 1). This circuit consists of homologous structures including the hippocampus (HC) and, to some extent, the mammalian parahippocampal region and avian area parahippocampalis (APH). The circuit also includes analogous structures, such as the mammalian prefrontal cortex (PFC) and avian nidopallium caudolaterale (NCL). In their Letter, Rattenborg and Martinez-Gonzalez (2) highlight anatomical differences between the bird and mammalian brain and argue that such divergences may make their episodic memories qualitatively different. We address their main points below.

First, we agree with Rattenborg and Martinez-Gonzalez (2) that there is no direct connection between the NCL and the APH or HC. In our article, we acknowledge an indirect connection with a disconnected line in the circuit diagram (figure 2B in ref. 1) and in the text, although this topic could have been expanded. However, we disagree that a key component of the system is, thus, missing in the bird brain. Based on function and connectivity, the NCL is a good candidate for an executive area and analog of the

mammalian PFC (3). The lack of a direct connection between the APH and NCL is not necessarily problematic because indirect routes are available through the hyperpallium (see below) and nucleus posterioris amygdalopalli (4). Second, Rattenborg and Martinez-Gonzalez (2) affirm that the hyperpallium is connected with the HC, APH, and motor regions and, thus, may serve as an interface area bridging the HC and the NCL. This information represents an important refinement to our model. Third, Rattenborg and Martinez-Gonzalez (2) state that the avian HC, unlike its mammalian counterpart, only receives olfactory and visual information. Although this is true of direct connections, Atoji and Wild (4) suggest that other modalities can reach the HC indirectly. More importantly, there is no explicit requirement that episodic memories must contain information from all modalities or be “modality-equivalent” across species. In fact, even within mammals, there are significant differences in the weights and routes of sensory inputs to the HC (5). Although these divergences undoubtedly lead to qualitative differences in the content of episodic memory, they do not preclude overarching similarities in events-in-context associations.

In conclusion, although the points raised by Rattenborg and Martinez-Gonzalez (2) are valid, they do not compromise the conceptual framework we proposed (1). Although our article emphasizes a fundamental circuit for episodic memory across species, we also

discuss evolutionary differences. We contend that species-specific behavioral attributes of episodic memory are associated with variations on the proposed circuit. Finally, because little is known about the neural mechanisms of episodic memory, more detailed comparative analyses will require significant advances in our understanding of the functional relationships among the different regions of the fundamental episodic memory circuit.

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- 1 Allen TA, Fortin NJ (2013) The evolution of episodic memory. *Proc Natl Acad Sci USA* 110(Suppl 2):10379–10386.
  - 2 Rattenborg NC, Martinez-Gonzalez D (2013) Episodic-like memory and divergent brain systems in mammals and birds. *Proc Natl Acad Sci USA* 110:E3741.
  - 3 Güntürkün O (2005) The avian ‘prefrontal cortex’ and cognition. *Curr Opin Neurobiol* 15(6):686–693.
  - 4 Atoji Y, Wild JM (2004) Fiber connections of the hippocampal formation and septum and subdivisions of the hippocampal formation in the pigeon as revealed by tract tracing and kainic acid lesions. *J Comp Neurol* 475(3):426–461.
  - 5 Furtak SC, Wei S-M, Agster KL, Burwell RD (2007) Functional neuroanatomy of the parahippocampal region in the rat: the perirhinal and postrhinal cortices. *Hippocampus* 17(9):709–722.

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The authors declare no conflict of interest.

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