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# Gamma oscillations in the midbrain spatial attention network: linking circuits to function

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Gamma-band (25–140 Hz) oscillations are ubiquitous in mammalian forebrain structures involved in sensory processing, attention, learning and memory. The optic tectum (OT) is the central structure in a midbrain network that participates critically in controlling spatial attention. In this review, we summarize recent advances in characterizing a neural circuit in this midbrain network that generates large amplitude, space-specific, gamma oscillations in the avian OT, both *in vivo* and *in vitro*. We describe key physiological and pharmacological mechanisms that produce and regulate the structure of these oscillations. The extensive similarities between midbrain gamma oscillations in birds and those in the neocortex and hippocampus of mammals, offer important insights into the functional significance of a midbrain gamma oscillatory code.

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## Introduction

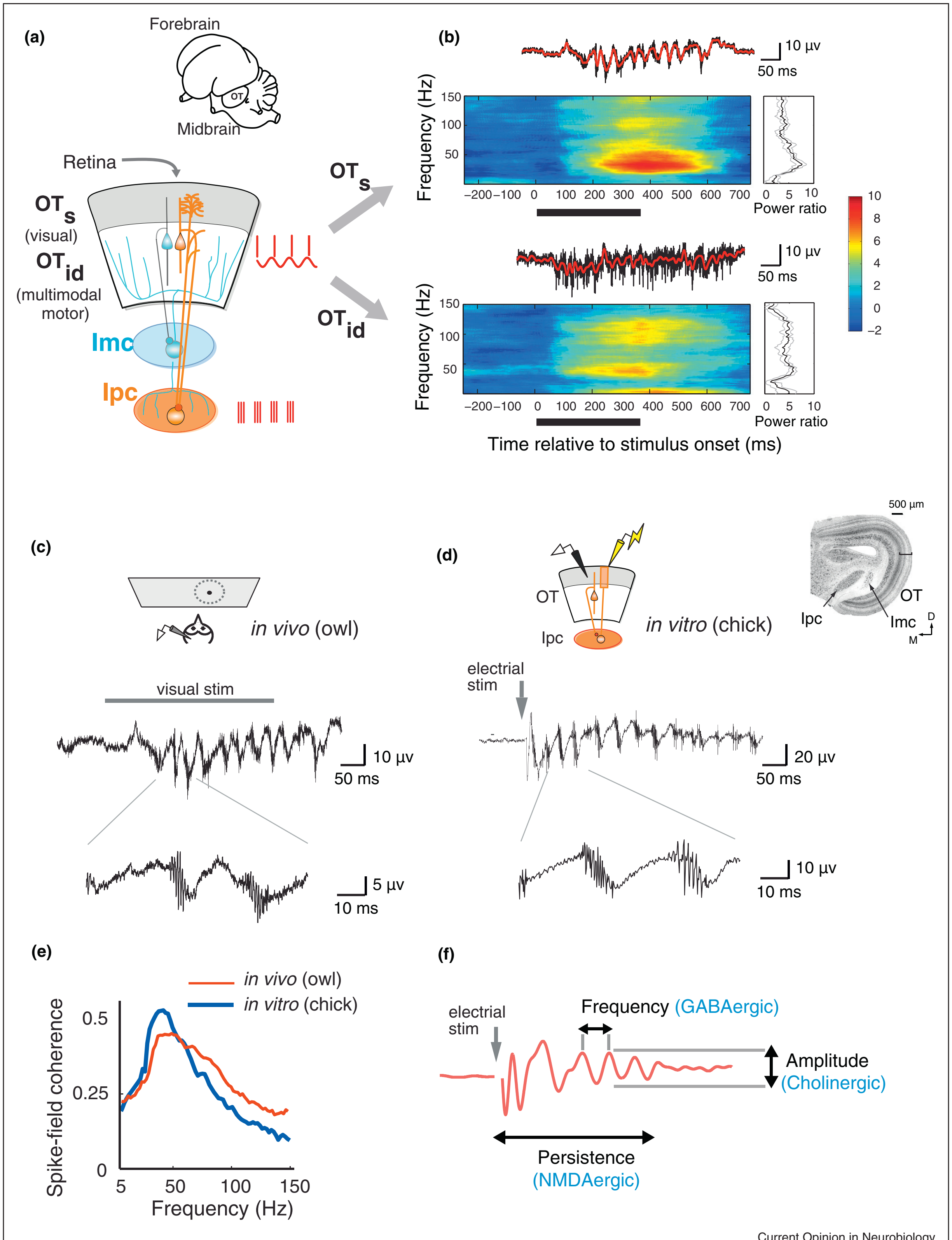
Gamma-band (25–140 Hz) oscillations of network activity, measured as rhythmic fluctuations in the extracellular local field potential (LFP), are observed in many regions of the forebrain [1]. Gamma power is modulated during mnemonic and cognitive processes. In the hippocampus, for example, LFP gamma power is modulated during the encoding of novel information [2], and the strength of gamma power predicts the precision of subsequent recall [3]. In the neocortex, gamma power is modulated by attention: directing attention to a particular stimulus typically increases the amplitude of gamma oscillations and increases the synchronization of spikes to these oscillations within neocortical regions that encode the stimulus [4]. Attention also increases the synchronization of spikes and LFPs in the gamma band across distant regions of the neocortex [5].

Despite these well-established empirical observations, it is unknown whether gamma-band synchronization actually plays a role in neural information processing or if gamma oscillations are simply epiphenomenal manifestations of neural processing [6–9,10•,11]. Here we describe the recent discovery of a neural circuit in a midbrain network in birds that generates and broadcasts large amplitude gamma oscillations. Results from experiments in birds and mammals demonstrate that the specific mechanisms for generating and shaping gamma oscillations are strikingly similar in widely different parts of the brain and across species separated by >300 million years of evolution, arguing for a conserved, functional role of gamma oscillations [12].

The midbrain spatial attention network consists of the optic tectum (OT; superior colliculus, SC, in mammals) and a number of interconnected tegmental nuclei. The OT and each of the component nuclei contain a multimodal, topographic map of space. The OT is a multilayered structure that combines sensory spatial information with descending spatial information from the forebrain, including the goals of impending orienting movements, and encodes the highest priority location for the animal's attention [13–16]. Each of the various tegmental nuclei receives focal, topographic input directly from the OT, and feeds back in an architecturally unique pattern to the OT (Figure 1a) [17,18]. The circuits formed by these tegmental nuclei play critical roles in generating the representation of the highest priority location in the OT space map.

The midbrain attention network is most differentiated in birds, in which the OT consists of 15 distinct layers and the tegmental network components are differentiated into several distinct nuclei (Figure 1a,d inset) [15]. Superficial layers of the OT (OTs, layers 1–9) receive direct retinal input as well as input from primary and secondary visual areas in the forebrain, and project to visual nuclei in the thalamus. The intermediate/deep OT layers (OTi/d, layers 10–13) receive multimodal sensory inputs as well as movement-related information, and project via thalamus to higher order forebrain areas

**Figure 1**




Properties and mechanisms of midbrain gamma oscillations. **(a)** Schematic of the midbrain network showing the pattern of connectivity between the optic tectum (OT) and adjacent tegmental nuclei: the GABAergic Imc (blue circuit) and the cholinergic Ipc (orange circuit). Superficial OT (OTs)