

This Week in The Journal

Inhibition of Striatal Output by Pedunculopontine Nucleus

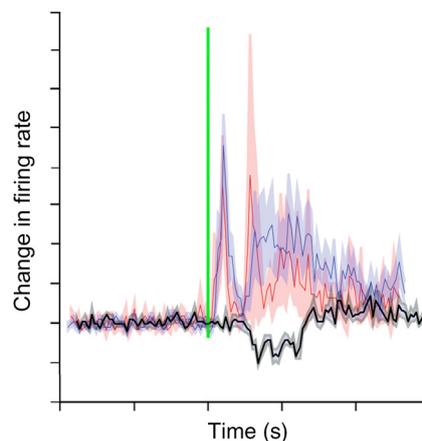
Maxime Assous, Daniel Dautan, James M. Tepper, and Juan Mena-Segovia

(see pages 4727–4737)

The pedunculopontine nucleus (PPN) is part of the mesencephalic locomotor region, which is involved in general arousal and cortical activation, as well as locomotion. These functions are mediated by widespread projections of cholinergic, glutamatergic, and GABAergic PPN neurons. The functions of specific projections are not fully understood, but connections between the PPN and basal ganglia are likely to be particularly important in motor learning, action selection, and goal-directed locomotion. Indeed, an article last week in this journal showed that inhibitory projections to the PPN from a primary output nucleus of the basal ganglia inhibit escape from threat-predicting cues (Hormigo et al. 2019 *J Neurosci* 39:4576). Assous, Dautan, et al. now report that glutamatergic PPN neurons provide feedforward inhibition to spiny projection neurons (SPNs), the principal neurons of the striatum, the main input nucleus of the basal ganglia.

The authors' previous work had shown that cholinergic PPN neurons increase the activity of striatal cholinergic interneurons, leading to inhibition of SPNs. That work showed that many non-cholinergic PPN neurons project to the striatum as well. The new study shows that many of these non-cholinergic projections innervate broad regions of dorsal and ventral striatum and are glutamatergic. Activation of channelrhodopsin-expressing glutamatergic PPN axons in midbrain slices evoked large, short-latency EPSPs in all types of GABAergic and cholinergic interneurons in the striatum. In contrast, only 1 of 46 recorded SPNs was excited by activation of PPN projections. Instead, activation of PPN glutamatergic fibers elicited longer-latency GABAergic IPSCs in SPNs. Consistent with this, activation of PPN glutamatergic neurons increased the firing rate of putative cholinergic and fast-spiking interneurons, reduced firing rate in putative SPNs, and produced head rotations toward the stimulated side *in vivo*.

These results indicate that PPN glutamatergic projections to the striatum predominantly innervate interneurons, and thus produce feedforward inhibition of SPNs. This is notable because all other known excitatory inputs to the striatum, including cortical and thalamic inputs, innervate SPNs as well as interneurons, thus producing biphasic excitation and inhibition in SPNs. Future work should record and manipulate the activity of striatum-projecting glutamatergic PPN neurons during ongoing behaviors to elucidate their function in locomotion and other behaviors.



Activation of PPN glutamatergic projections in the striatum (at time indicated by green bar) increased the firing rate of putative cholinergic (red) and fast-spiking (blue) interneurons and, after a delay, reduced firing of putative SPNs (black). See Assous, Dautan, et al. for details.

Anger in Dreams Related to Frontal Alpha Asymmetry

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(see pages 4775–4784)

EEG recordings often show interhemispheric differences in cortical activation across individuals and behavioral states. For example, the power of alpha-frequency oscillations (8–13 Hz), which typically correspond to cortical inactivation, can differ between left and right frontal cortex in people at rest. This so-called frontal alpha asymmetry has been proposed to reflect various cognitive or emotional states, including emotional valence (with greater activation

on the left associated with positive emotions), approach motivation (with greater left-hemisphere activation associated with approach rather than avoidance), and emotional control (with greater activation on the right associated with inhibition of emotions).

Emotional states vary not only while we are awake, but also during dreams. To examine relationships between frontal alpha asymmetry and affective states in dreams, Sikka et al. recorded brain activity as volunteers slept. They woke the participants after each bout of rapid eye movement (REM) sleep to get reports of dream content and emotional state, then assessed the relationship between frontal alpha asymmetry and the two most commonly reported emotion categories: Interest/Curiosity and Anger/Annoyance/Frustration. Notably, both of these emotional states are thought to motivate approach, but they have opposite valence and are differently prone to inhibition.

Individuals' frontal alpha asymmetry scores were similar in the evening before sleep and during REM sleep. Regression analyses indicated that greater alpha power in right than in left frontal cortex was associated with higher anger scores. In contrast, frontal alpha asymmetry was unrelated to curiosity or any other emotional state in dreams except Hatred/Suspicion. Furthermore, alpha asymmetry in other cortical areas and asymmetry in oscillations at other frequencies were unrelated to anger in dreams.

These results suggest that frontal alpha asymmetry before sleep can predict asymmetry and emotional experiences during subsequent REM sleep and dreams. Specifically, when alpha power is greater (suggesting activation is lower) in right frontal cortex than left, people are more likely to experience emotions related to anger during dreams. Along with the lack of a relationship between frontal alpha asymmetry and the experience of curiosity in dreams, this supports the hypothesis that inactivation of right frontal cortex is related to reduced control over emotions. Future work should determine whether manipulating frontal alpha oscillations influences the emotional content of dreams.