

The Primate Thalamus Is a Key Target for Brain Dopamine

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The thalamus relays information to the cerebral cortex from subcortical centers or other cortices; in addition, it projects to the striatum and amygdala. The thalamic relay function is subject to modulation, so the flow of information to the target regions may change depending on behavioral demands. Modulation of thalamic relay by dopamine is not currently acknowledged, perhaps because dopamine innervation is reportedly scant in the rodent thalamus. We show that dopaminergic axons profusely target the human and macaque monkey thalamus using immunolabeling with three markers of the dopaminergic phenotype (tyrosine hydroxylase, dopamine, and the dopamine transporter). The dopamine innervation is especially prominent in specific association, limbic, and motor thalamic nuclei, where the densities of dopaminergic axons are as high as or higher than in the cortical area with the densest dopamine innervation. We also identified the dopaminergic neurons projecting to the macaque thalamus using retrograde tract-tracing combined with immunohistochemistry. The origin of thalamic dopamine is multiple, and thus more complex, than in any other dopaminergic system defined to date: dopaminergic neurons of the hypothalamus, periaqueductal gray matter, ventral mesencephalon, and the lateral parabrachial nucleus project bilaterally to the monkey thalamus. We propose a novel dopaminergic system that targets the primate thalamus and is independent from the previously defined nigrostriatal, mesocortical, and mesolimbic dopaminergic systems. Investigating this "thalamic dopaminergic system" should further our understanding of higher brain functions and conditions such as Parkinson's disease, schizophrenia, and drug addiction.

Key words: dopamine; dopamine transporter; dopaminergic systems; thalamus; human; monkey

Introduction

The thalamus transfers sensory information from the periphery to the cortex through first-order relay nuclei. In addition, it is a nodal point in cortico-cortical communication through higher-order relay or association nuclei (Sherman and Guillery, 1996). These functions are subject to extensive modulation, and thus the transfer of information through the thalamus depends on the state of wakefulness of the subject and on attentional or behavioral demands (McCaig, 1992; Sherman and Guillery, 1996; Steriade et al., 1997; Guillery and Sherman, 2002). In fact, the vast majority of synapses in the thalamus are from modulatory afferents. The other main targets of thalamic efferents are the striatum, the nucleus accumbens, and the amygdala (Steriade et al., 1997).

Dopamine is an important transmitter molecule in the brain. By modulating neuronal excitability and synaptic plasticity

(Nicola et al., 2000; Bissiere et al., 2003), dopamine is essential for motor control (Agid, 1991), working memory (Brozoski et al., 1979), sensorimotor learning (Aosaki et al., 1994), and reward-related learning and motivation (Schultz, 2002). These functions depend on the dopamine innervation of the striatum, cerebral cortex, nucleus accumbens, and amygdala. This innervation originates in dopaminergic neurons of the ventral mesencephalon and makes up the nigrostriatal, mesocortical, and mesolimbic dopaminergic systems (Lewis and Sesack, 1997).

The presence of dopamine in the thalamus of primates was reported a long time ago using biochemical tools (Brown et al., 1979; Goldman-Rakic and Brown, 1981). More recently, axons that were immunoreactive (ir) for the dopamine transporter (DAT) have been reported in the monkey mediodorsal thalamic nucleus (MD) (Melchitzky and Lewis, 2001). Despite these reports, the notion of a significant and widespread dopamine innervation of the primate thalamus is not currently recognized (Sherman and Guillery, 1996, 2004; Steriade et al., 1997), probably because the dopamine innervation of the rodent thalamus is reportedly scant (Groenewegen, 1988; Papadopoulos and Parnavelas, 1990). However, thalamic abnormalities related to dopamine and its receptors have been found in the thalamus of schizophrenic patients (Oke and Adams, 1987; Talvik et al., 2003; Yasuno et al., 2004), and thalamic alterations exist in Parkinson's disease (Ruf et al., 2002), a disorder in which dopamine plays a major role.

The present study examines the presence of dopamine in the thalamus of adult human and macaque monkey brains using antibodies against tyrosine hydroxylase (TH; one of the enzymes in the dopamine synthesis pathway), dopamine, and DAT. In

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