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Minireview

Anatomical and Functional Comparison of the Caudate Tail in Primates and the Tail of the Striatum in Rodents: Implications for Sensory Information Processing and Habitual Behavior

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https://doi.org/10.14348/molcells.2023.0051
www.molcells.org

The tail of the striatum (TS) is located at the caudal end in the striatum. Recent studies have advanced our knowledge of the anatomy and function of the TS but also raised questions about the differences between rodent and primate TS. In this review, we compare the anatomy and function of the TS in rodent and primate brains. The primate TS is expanded more caudally during brain development in comparison with the rodent TS. Additionally, five sensory inputs from the cortex and thalamus converge in the rodent TS, but this convergence is not observed in the primate TS. The primate TS, including the caudate tail and putamen tail, primarily receives inputs from the visual areas, implying a specialized function in processing visual inputs for action generation. This anatomical difference leads to further discussion of cellular circuit models to comprehend how the primate brain processes a wider range of complex visual stimuli to produce habitual behavior as compared with the rodent brain. Examining these differences and considering possible neural models may provide better understanding of the anatomy and function of the primate TS.

Keywords: habit, modality-converged system, modality-selective system, primate caudate tail, rodent tail of striatum

INTRODUCTION

The striatum is a crucial brain region involved in goal-directed behavior, habit, learning, and value process and is associated with various brain disorders, including Parkinson's disease, Huntington's disease, and schizophrenia (Cools et al., 2001; Delong and Wichmann, 2007; Ferrante et al., 1985; Howes and Kapur, 2009; Schmack et al., 2021; Simpson et al., 2010; Vonsattel et al., 1985). To better understand human cognitive behavior and develop effective treatments for brain disorders, it is essential to identify the similarities and differences between rodent and primate brains and assess the applicability of data from the rodent striatum to humans.

Among the striatum regions, the caudate head (CDh) in primates and the dorsomedial striatum (DMS) in rodents, both located in the anterior-dorsal-medial part of the striatum, play important roles in motor control, action selection, decision-making, cognitive flexibility, and reinforcement learning (Brovelli et al., 2011; Grahn et al., 2008; Kim and Hikosaka, 2013; Knowlton and Patterson, 2018; Richfield et al., 1987; Yin, 2005a; 2005b; Yin and Knowlton, 2006). Recent studies have suggested that these regions may be functionally homologous, particularly in their involvement in goal-directed behaviors (Broschard et al., 2023; Kim and Im, 2019; Mestres-Missé et al., 2012). However, controversy remains re-

Received March 31, 2023; revised May 13, 2023; accepted May 26, 2023; published online July 17, 2023

eISSN: 0219-1032

garding the homology of the primate caudate tail (CDt) and the rodent tail of the striatum (TS), located in the caudal part of the striatum, due to their different anatomical inputs that may reflect distinct functions (Griggs et al., 2017; Jiang and Kim, 2018; Kim et al., 2014; 2015; Menegas et al., 2018; Seger, 2013; Valjent and Gangarossa, 2021; Yamamoto et al., 2013). Therefore, in this review, we examined and compared the functions and anatomical connections between the TS in rodents and the CDt in primates to help clarify their similarities and differences.

THE EXPANSION OF THE PRIMATE BRAIN ALONG THE ROSTRAL-CAUDAL AXIS RESULTS IN DIFFERENCES FROM THE RODENT BRAIN

One easily recognizable difference between rodent and primate brains is the complexity of the cortical areas. Primate brains have wider cortical areas and more gyri and sulci compared with rodent brains. This difference arises from the developmental process along the rostral-caudal axis of the brain (Fig. 1). After formation of the neural tube, cells proliferate inside the neural tube, and the shape of the tube expands differently across the rostral-caudal axis in rodent and primate brains (Copp et al., 2003; Stiles and Jernigan, 2010). The neural tube of the primate brain stretches more caudally compared with that of the rodent brain, resulting in more prominent structures, such as the temporal cortex and the cingulate cortex (Fig. 1).

In addition to the difference in the surface of the brain, there are also differences in the subcortical structures along the rostral-caudal axis. For example, the location of the hippocampus is different in rodent and primate brains: the hippocampus is in the dorsal part of the rodent brain, while in primates it is in the ventral part of the brain (Figs. 1 and 2) (Clark and Squirea, 2013; Strange et al., 2014). Even more striking than the differences in location are the differences in the shape of the structure arising from expansion along the rostral-caudal axis. The shape of the rodent striatum, which may include the caudate and putamen in primates, differs from that of the caudate in primates (Figs. 1 and 2). Notably, the caudal part of the caudate nucleus extends along the rostral-caudal axis of the primate brain to generate the CDt, which appears different from the rodent TS in the lateral view (Fig. 1) (Griggs et al., 2017; Jiang and Kim, 2018; Kim et al., 2014).

Overall, the expansion of the primate brain along the rostral-caudal axis leads to differences in the location and shape of brain structures compared with those in the rodent brain. Considering the differences in the anatomical circuits of rodent and primate brains along the rostral-caudal axis is important, as these differences may lead to differences in information processing and final output behavior.

THE TAIL OF THE CAUDOPUTAMEN IN RODENTS AND THE TAIL OF THE CAUDATE IN PRIMATES

The striatum is a nucleus in the subcortical basal ganglia that receives inputs from various cortical and subcortical areas and

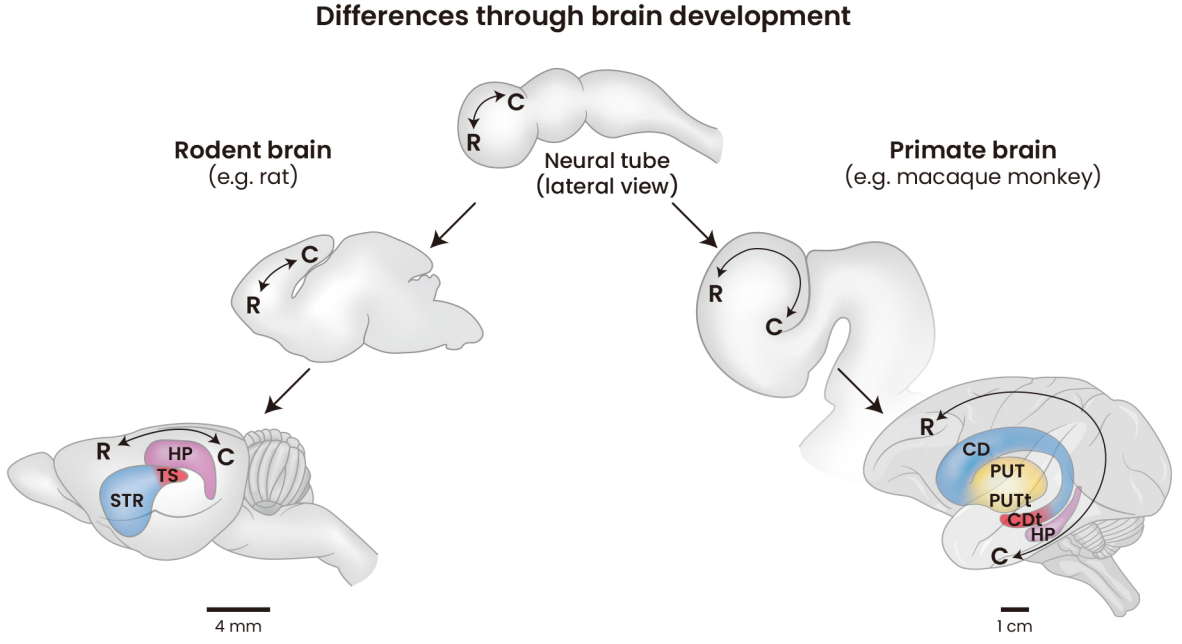

Fig. 1. Differences in structures between rodent and primate brains through brain development. Differences in brain development. Different expansions of the neural tubes along the rostral-caudal axis produce different locations and shapes of the structures between rodent and primate brains. R, rostral; C, caudal; STR, striatum; TS, tail of the striatum; HP, hippocampus; CD, caudate nucleus; CDt, caudate tail; PUT, putamen; PUTt, putamen tail.

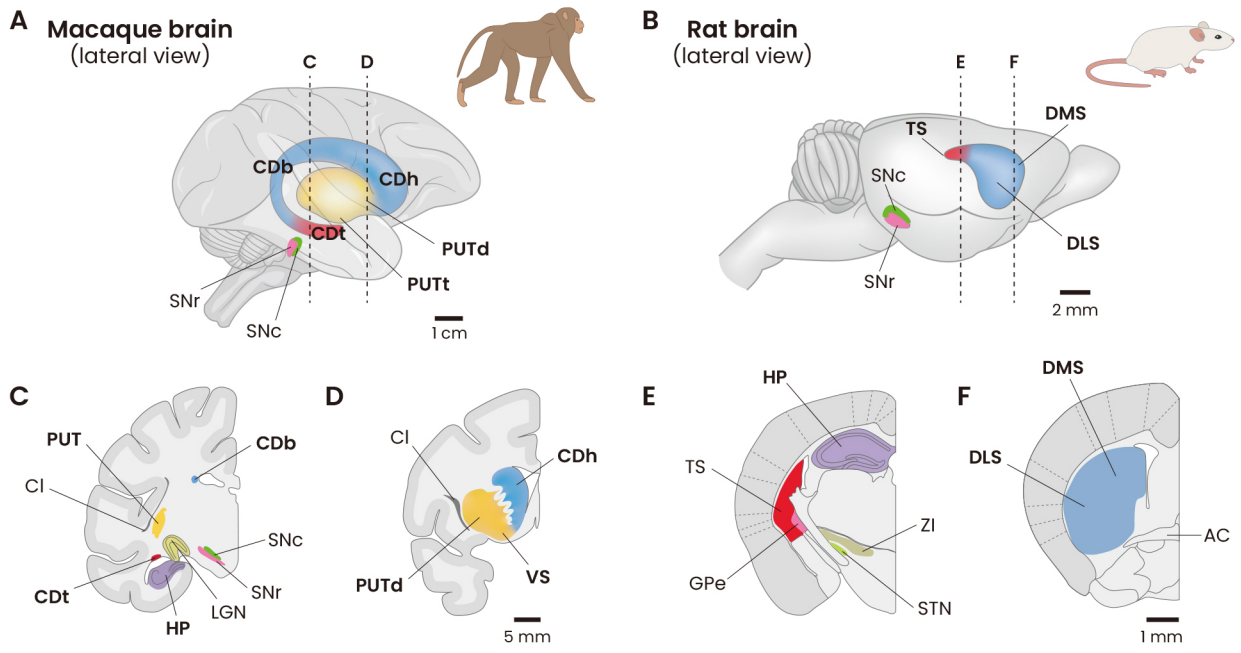

Fig. 2. Macaque and rat brains in the lateral view and coronal section. (A and B) Location of the macaque and rat striatum in the lateral view. Dashed line indicates the coronal planes in (C-F). (C and D) Macaque striatum and neighboring subcortical structures in the coronal section. Blue and yellow regions indicate the rostral striatum (CDh, CDb, VS, and PUTd). The red region indicates the CDt. (E and F) Rat striatum and neighboring subcortical structures in the coronal section. Blue regions indicate the rostral caudoputamen regions (DLS and DMS). The red region indicates the TS. CDb, caudate body; CDh, caudate head; CDt, caudate tail; SNr, substantia nigra pars reticulata; SNc, substantia nigra pars compacta; PUTd, dorsal part of the putamen; PUTt, putamen tail; TS, tail of the striatum; DMS, dorsomedial striatum; DLS, dorsolateral striatum; PUT, putamen; CI, claustrum; HP, hippocampus; LGN, lateral geniculate nucleus; VS, ventral striatum; GPe, globus pallidus externa; STN, subthalamic nucleus; ZI, zona incerta; AC, anterior commissure.

plays a crucial role in functions such as motivation, goal-directed behavior, and habit (Balleine and O'Doherty, 2010; Liljeholm and O'Doherty, 2012; Tricomi et al., 2009). Although the rodent and primate striatum have been regarded as analogous structures, there are differences in their shape, location, and anatomical connections (Balleine and O'Doherty, 2010; Heilbronner et al., 2016; Woolley et al., 2013). The primate striatum is divided into three regions: the caudate nucleus, putamen, and ventral striatum (Figs. 2A and 2D). In contrast, the rodent striatum, known as the caudoputamen, consists of a single structure in which the caudate nucleus and putamen are not separated (Figs. 2B and 2F). In both rodents and primates, the rostral part of the striatum is the largest, and it tapers as it progresses towards the caudal end, forming a tip referred to as CDt in primates (Figs. 2A and 2C) and TS in rodents (Figs. 2B and 2E). However, the primate CDt is a distinct anatomical region that arises from the caudate nucleus, whereas in rodents, the TS is a structure that may merge with the caudate and putamen. Due to this difference in the striatal organization, whether the tail of the rodent caudoputamen (TS) is homologous to the CDt remains unclear. The differences in the anatomy of the striatum between primates and rodents raise questions about whether these regions have homologous anatomical connections and functions.

ANATOMICAL SIMILARITIES IN THE CONNECTIONS OF THE RODENT TS AND THE PRIMATE CDt FOR VALUE-BASED BEHAVIORAL CONTROL

Previous studies have shown the cortical and subcortical connections with the TS and CDt (Griggs et al., 2017; Jiang and Kim, 2018). Jiang and Kim (2018) investigated the rostral-caudal distributions of retrogradely labeled TS-projecting neurons in the whole rodent brain and found that the TS primarily received inputs from the caudal regions of the cortex and subcortex, while the DMS received inputs mainly from the rostral regions. Similarly, in primates, CDh-projecting neurons were predominantly located in the rostral regions of the cortex (A17 to A32), whereas CDt-projecting neurons were primarily located in relatively posterior regions (A3 to A11) (Griggs et al., 2017; Haber et al., 2006; Middleton and Strick, 1996; Seger, 2013). Moreover, as retrograde tracer injections progressed more posteriorly into the caudate, the labeled cortical regions topographically shifted posteriorly (Saint-Cyr et al., 1990). This suggests that the distribution of striatum-projecting neurons is driven by the rostral-caudal axis rather than being heterogeneously distributed.

The subcortical inputs into the TS and CDt have been identified. Griggs et al. (2017) demonstrated that neurons in the caudal claustrum, thalamus, lateral substantia nigra pars compacta (SNc), and medial dorsal raphe nucleus (DRN) in-

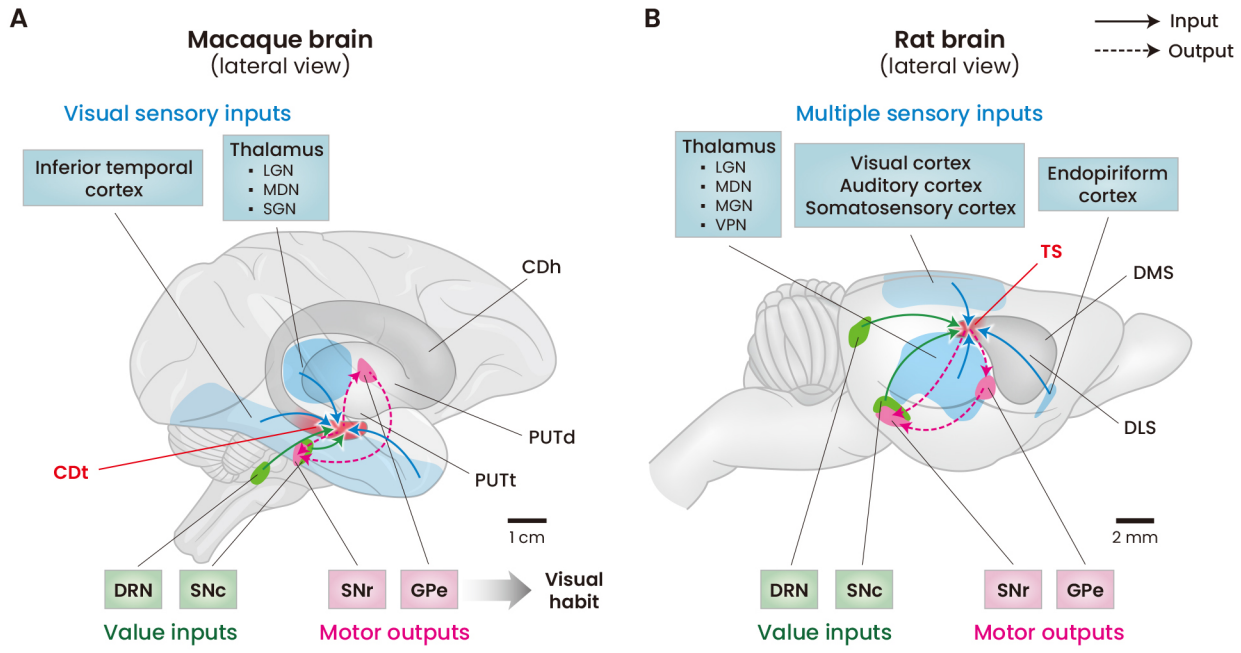

Fig. 3. Corticostriatal and subcorticostriatal connections of primate and rodent brains in the lateral view. (A and B) Inputs and outputs of macaque CDt and rat TS. Blue regions and arrows indicate the sensory inputs to TS and CDt. Green regions and arrows indicate the value inputs to TS and CDt. Magenta regions and dashed arrows indicate the motor outputs from TS and CDt. CDt and TS are indicated by the red regions. LGN, lateral geniculate nucleus; MDN, medial dorsal nucleus; SGN, suprageniculate nucleus; CDh, caudate head; CDt, caudate tail; PUTd, dorsal part of the putamen; PUTt, putamen tail; DRN, dorsal raphe nucleus; SNc, substantia nigra pars compacta; SNr, substantia nigra pars reticulata; GPe, globus pallidus externa; MGN, medial geniculate nucleus; VPN, ventral posterior nucleus; TS, tail of the striatum; DMS, dorsomedial striatum; DLS, dorsolateral striatum.

nervated the CDt in the macaque monkey (Fig. 3A) (Griggs et al., 2017; Kim et al., 2014). Similarly, in rats, the TS receives inputs from the claustrum, thalamus, lateral part of the SNc and the DRN (Fig. 3B) (Jiang and Kim, 2018).

Outputs of the primate CDt were identified by anterograde tracer injections. Labeled axon terminals of medium spiny neurons located in the globus pallidus (GP) and substantia nigra pars reticulata (SNr), which are the motor output structures in the basal ganglia (Fig. 3A) (Hikosaka and Wurtz, 1983; Parent et al., 2000; Saint-Cyr et al., 1990; Zhou and Lee, 2011). The terminals of the rodent TS are also distributed to the GP and the lateral edge of the SNr (Fig. 3B) (Haber et al., 2000; Ogata et al., 2022; Tulloch et al., 1978). This suggests that the TS and CDt receive value inputs from dopamine neurons in the SNc and serotonin neurons in the DRN and send motor outputs through the SNr. This anatomical evidence suggests that the rodent TS and primate CDt may have similar functions in reward value-guided motor control. Therefore, the TS and CDt can be considered homologous structures based on their anatomical positions and subcorticostriatal connections (Fig. 3).

ANATOMICAL DIFFERENCES IN INPUTS BETWEEN THE RODENT TS AND THE PRIMATE CDt

There are differences in the anatomical connections between the rodent TS and the primate CDt when considering the inputs from the sensory cortex and thalamus. In the primate brain, the CDt is innervated by neurons in the ventral inferior temporal cortex, which mainly processes visual information (Fig. 3A) (Baizer et al., 1993; Griggs et al., 2017; Saint-Cyr et al., 1990). CDt-projecting neurons were found in the medial dorsal nucleus (MDN), suprageniculate nucleus (SGN), and lateral geniculate nucleus (LGN) of the thalamus, which are responsible for monitoring saccadic eye movements, processing visual value, and relaying visual information, respectively (Fig. 3A) (Griggs et al., 2017; Hu and Jayaraman, 1986; Kim et al., 2020; Sommer and Wurtz, 2008; Takada et al., 1985). Thus, the primate CDt appears to receive inputs from cortical and thalamic regions specialized in visual processing.

In contrast to the primate CDt, the rodent TS receives inputs from various sensory modalities, including the visual, auditory, somatosensory, temporal, and endopiriform cortices, suggesting its involvement in processing multiple sensory modalities (Fig. 3B) (Jiang and Kim, 2018). Moreover, the TS receives inputs from sensory regions in the thalamus, including the lateral geniculate nucleus, medial geniculate nucleus, and ventral posterior nucleus, which process visual, auditory, and somatosensory information, respectively (Fig. 3B) (Guillery and Sherman, 2002; Jiang and Kim, 2018; Landisman and Connors, 2007; Ogata et al., 2022; Oliveira-Maia et al., 2011). These findings suggest that the primate CDt is specialized for processing visual information, while the rodent TS is involved in multisensory processing.

ROLES OF THE TS IN RODENT AND PRIMATE BRAINS

The CDt is involved in multiple aspects of visual processing such as object recognition, visual salience, and object value-based habitual behavior (Brown et al., 1995; Caan et al., 1984; Fernandez-Ruiz et al., 2001; Kim and Hikosaka, 2013). Neurons in the CDt process both feature and location information of visual objects to guide saccadic eye movements (Yamamoto et al., 2012). Moreover, several studies have demonstrated that the CDt and its connected structures are involved in visual habit, where primates automatically make saccades towards valuable objects (Hwang et al., 2022; Kang et al., 2021; Kim, 2021; Kim and Hikosaka, 2013; Mishkin et al., 1984; Yamamoto et al., 2013). Neurons in the CDt selectively encoded long-term value memory of visual objects, and inactivation of CDt neurons impaired habitual saccade to previously learned high-valued objects (Kim and Hikosaka, 2013). Taken together, these electrophysiology and behavior studies with the primate brain indicate that the CDt contributes to encoding long-term value memory of visual objects and guiding automatic saccades toward valuable objects (Kim and Hikosaka, 2013; Yamamoto et al., 2013).

Recent studies have shown that in rodents, the TS processes sensory signals from multiple sources beyond visual stimuli. For instance, optogenetic activation of TS neurons in rats resulted in a bias against ipsilateral choices in auditory decisions, while inactivation of these neurons weakened auditory discrimination performance (Guo et al., 2018). Additionally, dopamine axon terminals in the TS responded to stimuli across different modalities, including visual, auditory, olfacto-

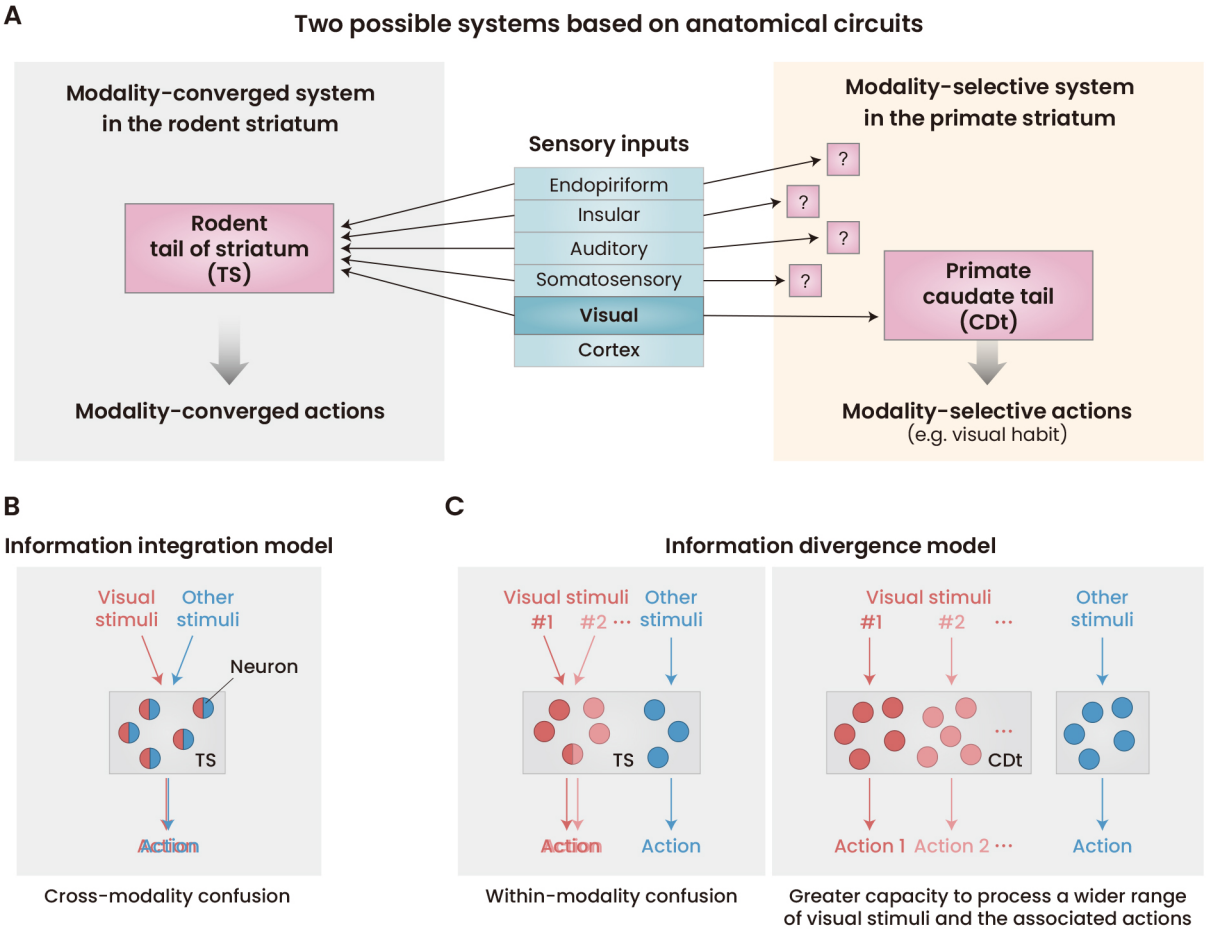

Fig. 4. Two possible systems in rodent and primate brains for processing each sensory modality-generated action. (A) Sensory modality-converged system and sensory modality-selective system. Anatomical inputs from all five sensory modalities converge in the tail of the rat striatum, potentially generating modality-converged actions. In contrast, an input from visual system selectively projects to the tail of the primate caudate, potentially producing modality-selective actions. (B) Information integration model in the tail of the rat striatum. Individual neurons that receive multi-sensory information may cause confusion between different modalities in action generation. (C) Information divergence model in the tail of the rodent and primate striatum. The primate CDt has a larger number of neurons compared to the rodent TS, providing the capacity to process a wider range of visual stimuli and their associated actions. A circle indicates a single neuron. Each color represents modality information.

ry, and somatosensory, with a higher response to novel and intense stimuli, implying the role of the TS in the processing of the novelty and intensity of stimuli (Akiti et al., 2022; Menegas et al., 2018).

IS THERE A TAIL OF THE PUTAMEN SEPARATE FROM THE CDt?

The caudoventral portion of the putamen is located adjacent to the CDt and can be anatomically regarded as the tail of the putamen (PUTt) (Fig. 3A). PUTt and CDt share anatomical inputs and outputs, and both regions receive inputs from extrastriate and temporal visual cortical areas that are responsible for object recognition in the ventral visual pathway (Kravitz et al., 2013; Yeterian and Pandya, 1995; 1998). The GP and SNr are the output structures of the PUTt and CDt, which are connected to the superior colliculus and motor cortex. Like the CDt, the PUTt is also innervated by dopamine neurons in the SNc.

From previous data that the PUTt shares similar anatomical connections with the CDt, it can be assumed that the PUTt may also play a role in habit formation and expression (Saint-Cyr et al., 1990). Indeed, previous research has shown that the PUTt is involved in habitual behaviors. Buerger et al. (1974) found that lesions in the caudoventral putamen including the PUTt impaired retention of visual discrimination but did not affect their ability to perform auditory discrimination tasks. Fernandez-Ruiz et al. (2001) also demonstrated that neurotoxic lesions in the area including the PUTt impaired learning of 24-h intervals between learning trials for a given stimulus pair but did not affect performance in a delayed non-matching to sample tasks. Finally, a recent electrophysiology study identified neurons in the PUTt that encode the long-term value memory of visual objects and possibly control habitual behavior (Kunimatsu et al., 2019). Previous studies, along with the anatomical similarities between the PUTt and CDt, suggest the involvement of the PUTt in visual habit. However, whether the two brain regions contribute differently to habitual behavior and how they work together or separately to achieve the same goal remain unclear. Further research is needed to address these questions.

HOW DO ANATOMICAL DIFFERENCES BETWEEN THE TS IN RODENT AND PRIMATE BRAINS CONTRIBUTE TO DIFFERENCES IN THEIR RESPECTIVE FUNCTIONS?

Previous studies have shown differences in the anatomical inputs to the rodent TS and the primate CDt. Notably, brain regions processing all five sensory modalities project to the rat TS, while visual areas selectively project to the macaque CDt (Fig. 4A) (Griggs et al., 2017; Jiang and Kim, 2018; Kim et al., 2014). This anatomical difference suggests a possible difference in the way sensory information is processed: a modality-converged process in the rodent striatum versus a modality-selective process in the primate striatum (Fig. 4A). Anatomy and electrophysiology results indicate that the caudal striatum is mainly involved in the generation of automatic behaviors based on long-term memory (Brown et al., 1995; Choi et al., 2020; Guo et al., 2018; Jiang and Kim, 2018; Kim, 2021; Kim et al., 2014; Kim and Hikosaka, 2013). Along with the previous results, we can expect differences in the sensory-to-action outcome process through the caudal striatum between rodent and primate brains.

First, it is possible that neural pathways from five sensory inputs in the rodent brain are integrated into single neurons within the TS (information integration model) (Fig. 4B). In this case, inputs from different sensory modalities may not be fully discriminated, resulting in a non-selective motor response that is not associated with a particular sensory modality. For example, a visual stimulus associated with a reward produces automatic nose-poking behavior, but an auditory stimulus (or any other salient sensory stimuli) may also produce the same nose-poking behavior (cross-modality confusion) (Fig. 4B).

Another possibility is that separate groups of neurons within the TS selectively receive each of the five sensory inputs (information divergence model) (Fig. 4C, left panel). In this case, however, the TS may have fewer modality-selective neurons compared with the CDt, which has neurons that selectively respond to visual stimuli in the primate brain (Fig. 4C, right panel). Having a greater number of neurons dedicated to visual processing may increase the ability to process a wider range of visual stimuli and generate the associated motor outcomes. There may not be enough neurons in the rodent TS to process a large number of visual stimuli compared with those in the primate CDt, resulting in a limit on the capacity for visual stimuli–action associations (within-modality confusion) (Fig. 4C, left panel).

Thus, the possibility of the modality-selective system in the primate striatum (Fig. 4A) may lead to a greater capacity to encode a wider range of sensory stimuli–action associations and better discriminate between sensory stimuli to generate automatic responses more accurately according to various conditions compared with the modality-converged system in the rodent striatum (Fig. 4C, right panel).

It is worth noting that a single region in the rodent striatum receives input from all five sensory modalities, making it easier to find significant results in a single structure study using any type of sensory modality (Akiti et al., 2022; Guo et al., 2018). However, to apply knowledge obtained from rodent studies to primates, it is necessary to identify the regions in the primate brain that process each sensory modality and decode their neural codes.

Previous studies on the anatomy of the primate brain have shown that different regions of the striatum receive inputs from different cortical areas that selectively process each sensory modality. For example, the insular cortex, auditory cortex, and somatosensory cortex project to subregions of the putamen, but not to the CDt (Flaherty and Graybiel, 1991; Fudge et al., 2005; Griggs et al., 2017). These findings suggest that each subregion of the primate caudate and putamen may process the value information associated with each modality. However, how value information of each modality is processed to generate each sensory modality-induced automatic action in the primate brain remains unclear. Addressing this question will be crucial for understanding how primates segregate and combine values associated with diverse sensory modalities.

CONCLUSION

In this review, we highlight the importance of considering the similarities and differences in the anatomy and function of the striatum between rodent and primate brains. Understanding the similarities and differences can provide insights into how the human brain processes and integrates different types of sensory information and how this varies across different animal species. This knowledge can further our understanding of the neural basis of primate perception, cognition, and behavior and may have implications for the study and treatment of brain disorders.

ACKNOWLEDGMENTS

This work was supported by the Neurological Disorder Research Program (NRF-2020M3E5D9079908), the Korea Research Institute of Bioscience and Biotechnology (KRIBB) Research Initiative Program (KGM4562121) and the Basic Science Research Program (NRF-2019R1A2C2005213) of the National Research Foundation (NRF) by the Korean government (MSIT). Creative-Pioneering Researchers Program through Seoul National University supported this work.

AUTHOR CONTRIBUTIONS

K.L., S.A., J.P., S.L., and H.F.K. wrote the original draft. K.L. and H.F.K. reviewed and finalized the manuscript.

CONFLICT OF INTEREST

The authors have no potential conflicts of interest to disclose.

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