Regional specialization within the human striatum for diverse psychological functions

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Decades of animal and human neuroimaging research have identified distinct, but overlapping, striatal zones, which are interconnected with separable corticostriatal circuits, and are crucial for the organization of functional systems. Despite continuous efforts to subdivide the human striatum based on anatomical and resting-state functional connectivity, characterizing the different psychological processes related to each zone remains a work in progress. Using an unbiased, data-driven approach, we analyzed large-scale coactivation data from 5,809 human imaging studies. We (*i*) identified five distinct striatal zones that exhibited discrete patterns of coactivation with cortical brain regions across distinct psychological processes and (*ii*) identified the different psychological processes associated with each zone. We found that the reported pattern of cortical activation reliably predicted which striatal zone was most strongly activated. Critically, activation in each functional zone could be associated with distinct psychological processes directly, rather than inferred indirectly from psychological functions attributed to associated cortices. Consistent with well-established findings, we found an association of the ventral striatum (VS) with reward processing. Confirming less well-established findings, the VS and adjacent anterior caudate were associated with evaluating the value of rewards and actions, respectively. Furthermore, our results confirmed a sometimes overlooked specialization of the posterior caudate nucleus for executive functions, often considered the exclusive domain of frontoparietal cortical circuits. Our findings provide a precise functional map of regional specialization within the human striatum, both in terms of the differential cortical regions and psychological functions associated with each striatal zone.

human striatum | parcellation | corticostriatal circuits | coactivation analysis | NeuroSynth

In addition to its central role in selecting, planning, and executing motor behavior (1, 2), the human striatum has been reported to be involved in diverse psychological functions, including emotion generation and regulation (3, 4), reward-related processes and decision making (5, 6), and executive functions (7, 8). These discrete functions are thought to map onto distinct functional striatal zones, which participate in separable basal ganglia-thalamocortical circuits (9–12) and are critical for the organization of behavior.

Following this logic, recent attempts to parcellate the human striatum using diffusion tensor imaging (DTI) (13, 14) and resting-state functional connectivity (RSFC) (15–17) have relied on patterns of corticostriatal connectivity to identify striatal zones. Although very useful, these studies have been limited to inferring striatal function indirectly via psychological functions of connected cortical regions. In addition, it remains unclear how anatomical connections and RSFC map onto different psychological processes (18). Finally, RSFC is sometimes epiphenomenal (19), and fiber tract reconstruction with DTI is inaccurate for complex axonal projections underlying frontal corticostriatal connectivity (17).

A separate body of work has attempted to differentiate striatal contributions directly to behavior empirically. However, these empirical investigations have focused on a restricted set of paradigms that may fail to capture the full range of striatal function, especially in humans. For example, converging evidence suggests a division of labor between the ventral striatum (VS) and dorsal striatum for Pavlovian and instrumental conditioning, respectively (20, 21). Within the dorsal striatum, medial regions support behavioral flexibility and lateral regions support well-learned behavior (22, 23). This work has greatly advanced our understanding of the similarities of striatal function in human and nonhuman animals. However, because of this strong reliance on classic learning paradigms, the integration of ideas about how the striatum is involved in uniquely human psychological functions, such as working memory, planning, and language, remains a work in progress.

To generate a comprehensive and precise functional map of the human striatum, in terms of associations with both cortical brain regions and psychological tasks, we simultaneously analyzed corticostriatal coactivation patterns and the frequency of psychological terms in the full text of 5,809 neuroimaging studies (24). In contrast to studies of RSFC, we defined corticostriatal associations based on coactivation in task-related responses across studies. A cortical voxel and a striatal voxel were coactivated if a study reported activation in both voxels. This metric groups voxels that are associated with similar psychological processes. Similar to RSFC, this metric does not imply direct functional coupling of coactivated voxels. In contrast to existing work, we attempted to associate psychological functions with striatal areas directly, rather than inferring them indirectly based on the psychological functions of connected cortical areas. Sampling across a broad spectrum of neuroimaging studies, without regard for the psychological process under investigation, allowed a large-scale comparison of associations of striatal subregions with diverse psychological processes. This data-driven approach allowed us to (*i*) localize five striatal zones based on their coactivation with cortical brain areas and (*ii*) simultaneously characterize the association of each zone with psychological states in a relatively unbiased manner, including potential associations overlooked in both individual hypothesis-driven studies and studies of RSFC.

Significance

The subcortical striatum is critical for the planning and execution of motor behavior, and its dysfunction is associated with disorders such as Parkinson's disease. More recently, the human striatum has also been reported to be involved in heterogeneous nonmotor psychological functions. However, detailed functional mappings of human psychological processes to striatal regions have been bound by theoretical and methodological limitations, including a strong focus on experimental paradigms derived from animal research, and the tendency to infer function from anatomical connectivity, rather than task-related activation. To overcome these limitations, we used a large-scale, unbiased, data-driven approach, and generated a precise, comprehensive functional map, directly associating striatal zones with the broadest range of psychological processes to date.

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Results

We identified functional zones in the striatum based on the similarity among striatal voxels in their coactivation with distal, cortical brain areas (details are provided in *Materials and Methods*). A comparison of the cluster quality of different subdivisions of the striatum into two to 20 zones, assessed in terms of within- vs. between-cluster coherence, revealed that all cluster solutions were clearly better than chance (*SI Appendix*, Fig. S1), but none emerged as a clear winner, as is typical with cluster analyses of data with complex dimensional distributions (25). This pattern is also consistent with previous results suggesting a continuum-based organization of the striatum, compared with a discrete categorical parcellation (26). Nevertheless, it is still useful to draw discrete boundaries for the purposes of identifying the central tendencies of different zones within this continuum. Therefore, we focus the following analyses on the five-cluster solution (Fig. 1*A*) because (*i*) in this solution, each functional zone was large enough to be robustly detectable in human imaging (a probabilistic map is shown in *SI Appendix*, Fig. S2); (*ii*) activation in each zone was correlated strongly across the two hemispheres, but not with other zones (*SI Appendix*, Fig. S3); (*iii*) there were clear distinctions among the five regions in associated cortical and functional circuits; and (*iv*) this solution demonstrated a high degree of overlap with the regions commonly distinguished in nonhuman primates (9–12). However, because parcellations with more zones may be useful for some purposes, we also show seven- and 17-cluster solutions in *SI Appendix*, Fig. S4. All of these parcellations were highly symmetrical across hemispheres, demonstrating strong bilateral symmetry in striatal function overall.

Distinct Cortical Regions Are Associated with Each Striatal Zone. Because it was possible to identify striatal regions based on their coactivation patterns with cortical voxels, it should be possible to train a naive Bayes classifier to use the pattern of cortical activation reported in a study to predict which, if any, functional zones of the striatum should be the most active. Doing so would demonstrate predictive utility of corticostriatal associations at the individual study level, and establish significant differences across striatal zones in their cortical activation profiles. To evaluate the performance of the classifiers, we examined the confusion matrix of correct and incorrect predictions for each striatal zone (Fig. 1*B*), determined its sensitivity and precision (i.e., positive predictive value) (Fig. 1*C*), and found that the classifier clearly exceeded chance performance established through a permutation test. Across striatal zones, the mean sensitivity was 0.47 [SD = 0.12; chance level: 0.16 (SD = 0.05)] and the mean precision (positive predictive value) was 0.46 [SD = 0.15; chance level: 0.16 (SD = 0.07)].

Next, we investigated which cortical areas are distinctly associated with only one of the striatal zones. Specifically, we calculated for each cortical voxel the maximum a posteriori estimate that this voxel is more strongly associated with one striatal zone than any of the other striatal zones. This approach contrasts with previous studies (17, 24, 27), which were restricted to reporting only the maximal association. Unlike previous work, our approach provides confidence intervals for whether a cortical voxel is more strongly associated with a particular striatal zone than with any other striatal zone. Despite the classifier's naivety (which treats each voxel's "vote" independent from the votes of its surrounding voxels), a clear topography of cortical-striatal coactivation emerged (Fig. 1*D*), with a clear anterior-posterior gradient on the medial cortical surface. As with the striatal parcellation, cortical voxels were very reliably associated with one zone more than others, usually with strong bilateral symmetry. *SI Appendix*, Fig. S5 shows, for each striatal zone, how reliably each cortical voxel predicted activation in this zone. Most voxels significant in the overall analysis in Fig. 1*D* were associated with one striatal zone more strongly than any other with >95% confidence.

Consistent with previous findings, we found that the anterior putamen (Pa) was associated with lateral sensorimotor cortex and supplementary/presupplementary motor area (11, 28), and with the intraparietal sulcus. The VS was strongly associated with ventromedial prefrontal cortex (vmPFC), posterior cingulate, superior frontal gyrus (rostral dorsomedial PFC), and lateral orbitofrontal cortex (OFC). Both the anterior caudate (Ca) and posterior caudate (Cp) were associated with distinct portions of lateral PFC, inferior parietal cortex, and dorsomedial PFC. The posterior putamen (Pp) had a very different connectivity profile, with medial sensorimotor cortex, posterior and midinsula and the overlying operculum, and medial temporal lobes.

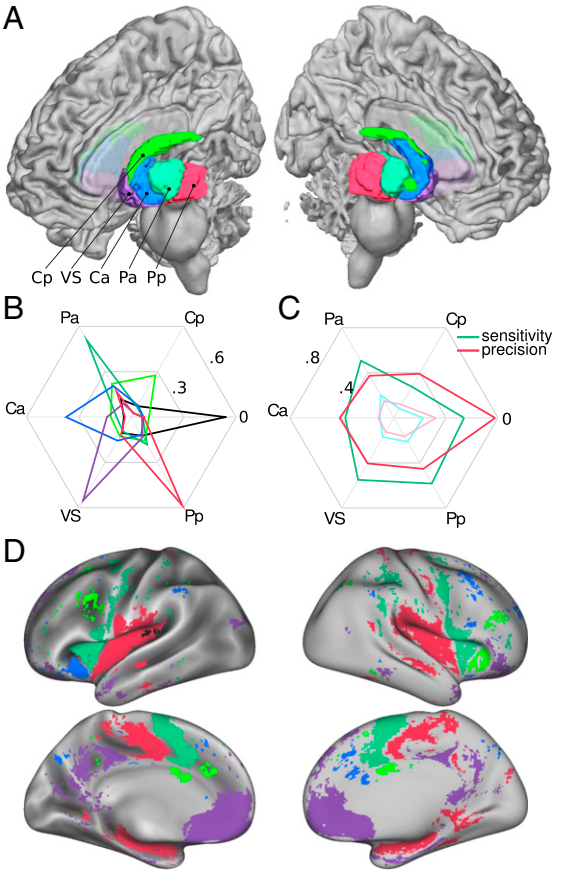

Fig. 1. (*A*) Cluster analysis (*k*-means, $k = 5$) of corticostriatal coactivation patterns across imaging studies identified distinct striatal zones. The five zones showed strong bilateral symmetry. Symmetry analysis is shown in *SI Appendix*, Fig. S3, and results with different values of *k* are shown in *SI Appendix*, Fig. S4. (*B*) Based on the pattern of reported cortical activation, a naive Bayes classifier predicted which striatal zone was the most active one. The confusion matrix, shown as a polar plot, indicates the probability that the classifier predicted activation in the correct zone and the probability that it incorrectly predicted activation in one of the other zones. Category "0" represents studies with no striatal activation (i.e., no active zone). (*C*) Sensitivity (dark green) and precision (i.e., positive predictive value, dark red) of the classifier for each functional zone. Attenuated colors (light green and red) indicate chance performance levels in the permutation test. Actual performance exceeded chance levels substantially for each category. (*D*) Maximum a posteriori estimates from the naive Bayes classifier indicate which striatal zone is most strongly coactivated with each cortical voxel ($q < 0.05$, false discovery rate-corrected).

In addition to confirming and extending established topography, this analysis yielded several findings related to lateralization. The bilateral Ca was more strongly correlated with the right than left PFC. In addition, the Ca was associated with left anterior insula, whereas the Cp was associated with right anterior insula. This lateralization will be discussed below in the context of the psychological functions of the two zones within the caudate nucleus.

Comparison with Recent Striatal Parcellations. We next compared our parcellation with findings from a recent RSFC analysis that identified seven striatal regions (17). As discussed above, we chose to focus on our five-cluster solution so as to relate it to a highly cited previous paper on corticostriatal circuits in nonhuman

primates (11). Although it seems nonintuitive to compare our five-cluster solution with Choi et al.'s seven-cluster solution (17), two of their clusters were substantially smaller than the others, whereas all our clusters were of similar size. Thus, our five-cluster solution is closer to Choi et al.'s parcellation (17) than our seven-cluster solution. The comparison of our five-, six-, and seven-cluster solution with Choi et al.'s solution (17) revealed similar Dice's coefficients of 0.51, 0.54, and 0.47, respectively. A side-by-side comparison of the two solutions revealed that the corresponding zones of the two solutions only partially overlapped (Fig. 2*A* and *B*; a comparison of our seven-cluster solution with the existing solution is shown in *SI Appendix*, Fig. S6). Thus, our parcellation provides a complementary and nonredundant picture of striatal organization.

Our findings also converge with the findings of another recent study, which used anterograde tracer injections into PFC to reveal corticostriatal projection patterns in nonhuman primates (26). Consistent with previous studies (9, 10, 29, 30), this study found that the VS receives dense projections from ventromedial PFC and OFC, the central striatum from the dorsal anterior cingulate cortex (dACC), and the dorsal striatum from dorsolateral PFC, but the study also identified a significant degree of overlap among projections (Fig. 2*C*). We found a similar differentiation in coactivation among striatal and frontal cortical Brodmann regions (Fig. 2*D*), including each of the three associations between cortical and striatal zones mentioned above. As in the findings of Haber and Knutson (26), we also observed significant overlap among the regions (*SI Appendix*, Fig. S7), particularly when using broad, anatomically defined regions of interest. For example, the dACC appeared to be strongly associated with all striatal zones, consistent with its purported involvement in a wide range of psychological tasks (31). Although there is overlap in striatal voxels coactivated with the dACC as a whole, our analyses (Fig. 1*D* and *SI Appendix*, Fig. S5) reveal clear topography within the dACC in coactivation with specific striatal zones.

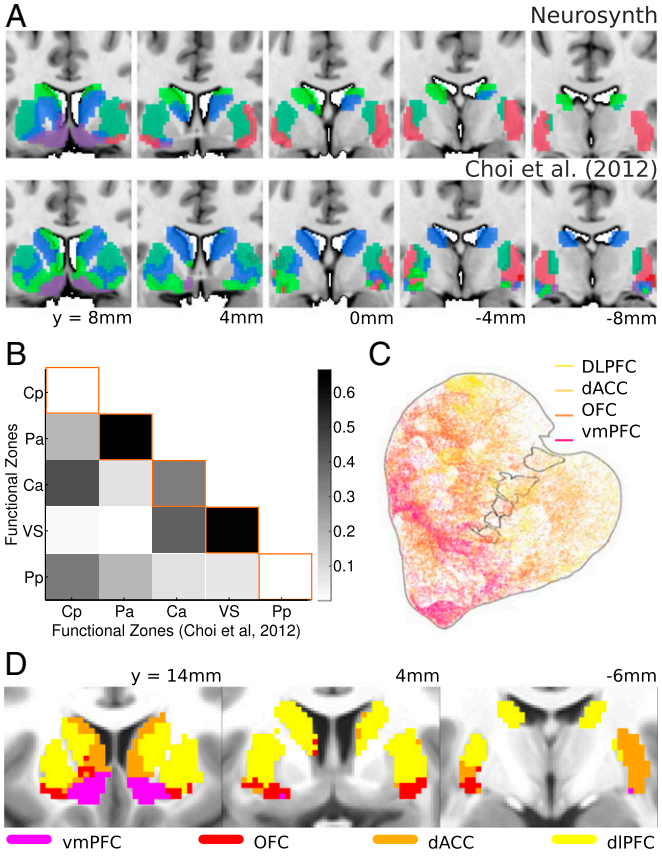

Fig. 2. (*A*) Side-by-side comparison of our parcellation with an existing $k = 7$ striatal parcellation (17), based on RSFC, indicates that the two approaches only lead to moderately overlapping results. (*B*) Dice's coefficients of a zone-by-zone comparison of our results with the existing solution. (*C*) Recent anterograde tracer study in nonhuman primates found strong evidence for a gradient of frontal cortical-striatal axon projections (26). dlPFC, dorsolateral PFC. (*D*) Analysis of coactivation of each striatal voxel with the different regions of interest in *C*, defined here based on the AAL atlas (61), show a similar pattern in humans. Reprinted from ref. 26.

Metaanalytic Decoding of Striatal Function. Most hypothesis-driven neuroimaging studies depend on forward inference, which answers questions such as, "Which brain areas become active when participants perform a foraging task?" Although forward inference has been a powerful tool, the approach does not allow for reverse inferences about task states, given brain patterns (24, 32). Reverse inference addresses critical, conceptually distinct questions about functional specialization; for example, "What does knowing that this brain area was activated imply about which task states were engaged?"

To identify associations between striatal activation and psychological functions with an unbiased, data-driven approach, we calculated, for every psychological term included in the NeuroSynth database, the likelihood ratio of hits to false alarm rates (i.e., the ratio between the number of studies reporting activation in a striatal zone when this term was vs. was not used in the article). Fig. 3*A* shows, for each striatal zone, the six psychological terms with the highest likelihood ratio for that zone, as well as the likelihood ratios of these terms for the other striatal zones [a similar analysis for Choi et al.'s solution (17) is shown in *SI Appendix*, Fig. S8]. These results show that each striatal zone was associated with distinct psychological terms. It takes into account both the mean word frequency of each term across studies (*SI Appendix*, Fig. S9) and the base rate of activation in each striatal zone. Although these results show that distinct psychological terms can be associated with each striatal zone, *SI Appendix*, Fig. S10 shows that the majority of studies investigating these psychological functions report activity preferentially in cortical areas, except for studies investigating reward-related and motor functions.

In addition to the detailed view represented by Fig. 3*A*, the description below provides an informal summary of the distinct associations of striatal zones with latent psychological functions (Fig. 3*B*). Because our metaanalytic approach was based on reported activations and word frequencies of psychological terms in the full text of studies, rather than on a detailed analysis of psychological tasks and statistical contrasts, representative studies from the NeuroSynth database were used to guide the labeling of the striatal zones (*SI Appendix*, Table S1). These studies were identified in a data-driven manner, based on selective activation of different functional striatal zones (Fig. 3*C*) and the word frequency of associated psychological terms in the full text of the study. An alternative data-driven approach to assigning latent psychological functions to the five striatal zones, using an author-topic model (33), is shown in *SI Appendix*, Fig. S11.

VS: Stimulus Value. We found that the VS zone was associated with psychological terms such as "reward," "losses," and "craving." The most representative study reported that monetary and social rewards activate overlapping regions within the VS (34). Together with the above finding of a reliable coactivation with OFC and ventromedial PFC, this finding suggests a broad involvement of this area in representing stimulus value and related stimulus-driven motivational states.

Ca Nucleus: Incentive Behavior. The adjacent Ca was associated with terms such as "grasping," "reaching," and "reinforcement." The most representative study reported a stronger blood-oxygen level-dependent (BOLD) response in this region during trials in which participants had a chance of winning or losing money in a card guessing game, in comparison to trials where participants merely received feedback about the accuracy of their guess (35). This result suggests a role in evaluating the value of different

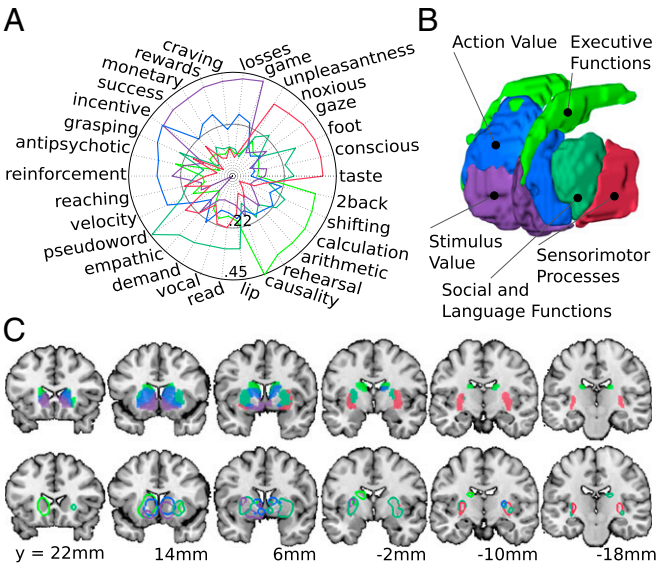

Fig. 3. To identify the psychological functions associated with each striatal zone, we calculated for each psychological term included in the NeuroSynth database its likelihood ratio of appearing in a study, given that activation was reported anywhere within a zone. (*A*) Distribution of likelihood ratios across functional zones indicates a clear functional dissociation. (*B*) Subjective summary of the main psychological function of each functional zone in a working model. (*C*) Based on the reported striatal activation and the occurrence of psychological terms in each study, it was possible to identify the most representative studies for each functional zone. The striatal zones identified in our coactivation analysis (*Top*) and a reconstructed outline of the activation reported in the representative studies (*Bottom*) are shown.

actions, contrasting with the above role of the VS in evaluating the value of stimuli (35, 36).

Pp: Sensorimotor Processes. The Pp was associated with psychological terms such as "foot," "noxious," and "taste." The most representative study reported activation of this region in response to painful stimulation at the back of the left hand and foot of participants (37). Anatomically, the most reliable and specific coactivation is with sensorimotor cortices, and the posterior and midinsula and operculum (secondary somatosensory cortex SII) in particular, some parts of which are specifically associated with pain (38). Together, these findings suggest a broad involvement of this area in sensorimotor functions, including aspects of their affective qualities.

Pa: Social- and Language-Related Functions. The adjacent Pa was associated with psychological terms such as "read," "vocal," and "empathic," and it is coactivated with frontal areas anterior to the ones coactivated with the Pp, demonstrating topography in frontostriatal associations. These anterior regions have been implicated in language processes (39, 40). The most representative study (41) partially supports a role of this area in social- and language-related functions; it reported a stronger activation of the Pa in experienced singers, but not when novices were singing.

Cp Nucleus: Executive Functions. This area was originally considered a part of the oculomotor circuit (11). In line with recent observations (42), we found that the Cp is associated with psychological terms such as "causality," "rehearsal," and "arithmetic." The representative study (43) reported this region to be part of a network that included dorsolateral PFC and ACC, which supported inhibitory control and task set-shifting. These results suggest a broad, and previously underappreciated, role for the Cp in cognitive control.

Discussion

We analyzed task-dependent changes in corticostriatal coactivation patterns across 5,809 studies to identify different functional zones within the striatum, and to decode the psychological function of these striatal zones simultaneously. Although we found evidence for a continuum-based organization of the striatum, we nevertheless were able to identify distinctive properties associated with five different striatal zones, with each making different contributions to human cognition and behavior. Our results expand on the results of previous studies, which delineated striatal regions based on anatomical criteria in animals (11) and on RSFC (17) and DTI (13–15) in humans. In relation to this previous work, we found that it was possible to (*i*) define striatal subregions based on a large sample of task-related neuroimaging data, (*ii*) predict striatal activation accurately based on patterns of cortical activation, and (*iii*) identify unique associations between regional striatal activation and both cortical networks and task types.

Some of the identified associations are now well established, such as the association between VS activation and reward. However, because we followed an unbiased, data-driven approach, we also identified associations between striatal activation and other psychological functions that have often been considered to be primarily cortical. In particular, cognitive functions, such as working memory and arithmetic, were associated with activation in the Cp, and social functions, such as language and empathy, were associated with activation of the Pa. Different aspects of affective function were associated with distinct zones, including stimulus-driven value associated with reinforcers such as money (VS), action-outcome value (Ca), social value (Pa), and somatosensory pain and pleasure (Pp).

Among the five striatal zones, we identified a VS cluster that contained the nucleus accumbens and ventral aspects of the Pa and Ca nucleus. This region was characterized by a strong coactivation with OFC and ventromedial PFC. This VS-OFC network was previously difficult to identify in humans through DTI, because of the diffuse nature of axonal projections between the two areas (17). The results of our decoding procedure for this functional zone are consistent with its well-established role in processing primary rewards, such as food, but also abstract rewards, such as money, as demonstrated by several recent human decision-making studies (34, 44).

Consistent with previous findings (28), we found that the Pa and Pp were topographically connected with different sensorimotor cortical areas. The two zones also differed functionally. Our term-based analysis suggests that the Pa is involved in language and other social functions, such as empathy. At the same time, the cortical coactivation maps suggest a strong association with Broca's area, which enables language production. In contrast to the Pa, we found that the Pp was associated with sensorimotor processes. Interestingly, we found that the most representative study for this region (37), according to our analysis, used painful stimulation of hands and feet. Previous studies of pain have identified a network of pain-associated somatosensory and perilimbic regions (e.g., medial thalamus, anterior insula, dACC) (45), but have seldom discussed the Pp as part of this circuit. Nonetheless, consistent with our findings here, this region was also identified to be preferentially activated during aversive conditions, compared with more anterior VS activation for appetitive conditions (46).

The results of our decoding procedure extend and refine a growing body of evidence for dissociation between the Ca and Cp (7, 8, 42, 43). This evidence suggests that the Ca is involved in a diverse set of functions supporting action evaluation and incentive behavior, whereas the Cp supports executive functions. These results contrast with taxonomies based on nonhuman primate data (11), which locate the body of the caudate within an oculomotor circuit. They also diverge from the conclusions of a recent human metaanalysis (47), which associated the caudate head with cognition and emotion and the caudate body with perception and action. We also found further evidence for a previously underdiscussed dissociation between VS and Ca, such that the VS may be involved in representing available rewards and the Ca in representing the expected outcome of different actions (5, 6).

Existing neural network models of corticostriatal interactions offer a mechanistic account of how the Cp may support executive functions (48). They postulate that the striatum modulates the destabilization of persistent patterns of activation in cortical areas, thus controlling

working memory updating, manipulation of items in working memory, and how cortical working memory circuits influence downstream areas. Future analyses may reveal further regional specialization within the caudate nucleus for different aspects of executive functions, given recent findings suggesting that common executive function tasks are overlearned and activate posterior parts of the PFC most closely associated with proximal action selection (49, 50), rather than anterior PFC circuits associated with goal formation and selection (51, 52).

Despite the fact that psychological functions of different striatal zones in the present study were identified solely based on striatal activation, rather than on cortical activation, the results may indirectly inform our understanding of the psychological functions of associated cortical areas. For example, the Ca showed a stronger coactivation with the right PFC and an involvement in incentive behavior, whereas the Cp showed a stronger coactivation with the left PFC and an involvement in executive functions. At the same time, we found that the left and right hemispheres of the Cp were only weakly correlated. This difference between the Ca and Cp nucleus represents an exception to the previously reported tendency of striatal areas to be interconnected to ipsilateral cortical areas (29). Furthermore, whereas the role of left dorsolateral PFC in executive function is well established, the role of right PFC is slightly less clear. Our analysis of striatal function suggests that this region may be involved in nonverbal executive functions in the support of incentive behavior (53–56).

To understand why our metaanalytic results only partially overlap with existing RSFC parcellations of the striatum, one has to appreciate the difference between the two approaches. In the present study, coactivation of two voxels indicates that a study reported significant task-related BOLD responses in both voxels in the same set of studies; that is, both voxels were correlated with experimental variables investigated in a study, but were not necessarily correlated with each other within an experimental session. Furthermore, although much has been made of similarities between task and resting-state data (57), resting-state data only represent a subset of tasks related to rest, with large contributions from (*i*) ongoing maintenance-related activation that is apparent even under anesthesia and (*ii*) spontaneous cognition, including mind-wandering and episodic retrieval/projection (18). Functional striatal zones can only then be dissociated if the tasks and psychological states included in the dataset differ in how they simultaneously modulate activation in striatal and cortical voxels. Thus, the divergence of our parcellation from RSFC parcellations may be explained by the fact that the NeuroSynth database includes studies using a wide array of different psychological tasks (58), and because it is based on coactivation rather than RSFC. Nevertheless, this divergence also suggests that even though the results of our cluster analysis were highly robust, different striatal zones may have emerged had we performed it on a measure other than coactivation. Interestingly (59), found that patterns of striatal dopamine release did not converge with structural subdivisions, but with corticostriatal activation patterns, which were also the basis of our parcellation (*SI Appendix*, Fig. S12 shows results based on the NeuroSynth database).

In summary, following a relatively unbiased, data-driven metaanalytic approach analyzing coactivation of striatal and cortical areas in 5,809 studies, we were able create a link between existing data on the anatomical and physiological characteristics of striatal regions and psychological functions. Because we did not limit our metaanalysis to studies that specifically targeted striatal function, our results extend previous knowledge of the involvement of the striatum in reward-related decision-making tasks, and provide a detailed functional map of regional specialization for diverse psychological functions, some of which are sometimes thought of as being the exclusive domain of the PFC.

Materials and Methods

Metaanalytic Coactivation Analysis. We relied on the NeuroSynth database to gain a comprehensive and unbiased window into coactivation of the striatum with other regions. The NeuroSynth database contains activation coordinates for 5,809 functional MRI (fMRI) studies that were not selected for specific criteria, or with regard to the psychological processes under investigation, but only for the presence of reported brain activations; hence, it is highly representative of the broader neuroimaging field (26). In this database, 10-mm boxcar smoothing was applied to activation coordinates to increase the robustness against differences in smoothing kernels across studies. We used *k*-means clustering to identify functional striatal zones, based on whether they showed similar corticostriatal coactivation patterns across studies. Details are provided in *SI Appendix*.

Naive Bayes Classifier. The classifier estimated for each functional striatal zone the posterior probability of it being the most active one in a study, given the pattern of cortical activation reported in a study. We used a bootstrapping approach to establish confidence intervals for whether a cortical voxel is more strongly associated with a particular striatal zone than with any other striatal zone. Details are provided in *SI Appendix*.

Comparison with the Results of Haber and Knutson. To compare our parcellation with the results of Haber and Knutson (26), we evaluated, for each striatal voxel, with which frontal cortical region of interest (ROI) of this previous work it exerted the strongest correlation across studies. For this purpose, we calculated for each study the proportion of active voxels within each ROI. In contrast to the analyses above, which depended on complex global patterns of cortical activation, we only considered positive correlations in this comparison, because Haber and Knutson (26) investigated direct corticostriatal projections with local injections of anterograde tracers in cortex. Convergent input from a cortical region is often thought to have an excitatory effect on striatal neurons (60). Correlations of each frontal ROI were Z-scored across striatal zones, because of all frontal ROIs, the dACC demonstrated the strongest correlation with a large majority of striatal voxels (*SI Appendix*, Fig. S7). ROIs were defined according to the automated anatomical labeling (AAL) atlas (61).

Term-Based Analysis. To identify the psychological functions associated with each striatal zone, we calculated the likelihood ratio *LR* that a psychological term occurred in the full text of a study (*T*+), given that activation was reported anywhere within the striatal zone (BG_k+): $LR = Pr(T+|BG_k+)/Pr(T-|BG_k+)$. For each functional zone, we report the six terms with the highest likelihood ratio and the likelihood ratio for this term for the other zones, yielding a total of 30 psychological terms. By reporting the likelihood ratio as defined above, the results are intentionally biased toward also identifying terms that only appeared in very few of the studies included in the database. This analysis was performed over a core set of 525 psychologically relevant terms included in the NeuroSynth dataset. These terms were not specifically chosen for the present metaanalysis, but were determined in a previously published study (24). The terms were not associated with any specific fMRI activity, but only with the article as a whole.

Representative Studies. We defined the representativeness of a study for striatal zone *k* as the product of how selectively the study reported activation in this zone, and the sum of the frequencies at which the psychological terms associated with the functional zone occurred in a study. Specifically, we divided the sum of activated voxels within each functional zone by the sum of total activated striatal voxels: $A_k = \sum_n a_n \delta_{nk} / \sum_n a_n$, where $\delta_{nk} = 1$ if voxel *n* is in zone *k* and $\delta_{nk} = 0$ otherwise. The sum T_k of the word frequencies of the psychological terms associated with a functional zone was calculated as $T_k = \sum_m t_{mk}$, where t_{mk} is the frequency of term *m*, associated with zone *k*. The study with the highest product $A_k T_k$ was selected as the most representative one for zone *k*.

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