The Potential Role of the Striatum in Antisocial Behavior and Psychopathy

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In this review, we examine the functions of the striatum and the evidence that this brain region may be compromised in antisocial individuals. The striatum is involved in the processing of reward-related information and is thus important in reward-based learning. We review evidence from a growing number of brain imaging studies that have identified differences in the structure or functioning of the striatum either in antisocial groups or in relation to personality traits that are associated with antisocial behavior such as impulsivity and novelty seeking. Evidence from structural imaging studies suggests that the volume of the striatum is increased in antisocial populations, although evidence of localization to specific subregions is inconsistent. Functional imaging studies, which similarly tend to find increased functioning in the striatum, suggest that the striatum is not necessarily hypersensitive to the receipt of reward in antisocial individuals but instead may not be appropriately processing the absence of a reward, resulting in continuous responding to a stimulus that is no longer rewarding. This may impair the ability of individuals to flexibly respond to the environment, thus contributing to impulsivity and antisocial behavior. We conclude by discussing genetic and environmental factors that may affect the development of the striatum.

Key Words: Antisocial, brain imaging, impulsivity, psychopathy, reward, striatum

Across many subtypes of antisocial individuals, several features appear to be consistent: impulsivity, novelty seeking, reward seeking, and poor decision making. Many studies examining the neural correlates of antisocial behavior have focused on the prefrontal cortex because of its demonstrated importance for inhibition, behavioral control, and decision making. However, the striatum may be equally important in vulnerability to these symptoms because of its involvement in reward processing, learning, and altering behavior.

In this review, we discuss studies examining the striatum in antisocial groups or in relation to individual differences in personality traits observed in antisocial individuals, such as increased approach-related behavior, reward sensitivity, or impulsivity (1). Antisocial is a heterogeneous category that includes violent offenders, incarcerated and nonincarcerated adults with antisocial personality disorder, youth with conduct disorder, and youth and adults with psychopathic traits. Psychopathy is a more specific classification of antisocial individuals, describing those who exhibit interpersonal and affective features such as manipulativeness, superficial charm, deceitfulness, emotional shallowness, and a lack of guilt, remorse and empathy (2) in addition to traits that may be more common to antisocial individuals in general, such as impulsivity, sensation seeking, and disinhibition. A central question is whether deficits in the striatum are related to the former and/or latter features of psychopathy.

The striatum is a region that is affected by substance abuse and dependence (3), which is common in antisocial individuals. Although several studies we review control for substance abuse/dependence, it is important to keep in mind that many do not. Future studies, particularly in youth populations, may be able to elucidate whether striatum abnormalities are a risk factor for, versus a result of, substance abuse and antisocial behavior.

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Functional Neuroanatomy of the Striatum

The striatum has two major parts, the caudate nucleus and the putamen, which are separated by a white matter tract. Adjacent to the putamen is the globus pallidus; the putamen and globus pallidus combined are referred to as the lenticular nucleus. Collectively the caudate, putamen, and globus pallidus are referred to as the corpus striatum (Figure 1). The most significant functional differentiation is the distinction between the dorsal and ventral striatum. The ventral striatum (VS) consists primarily of the nucleus accumbens, located ventral to the caudate and putamen, and the olfactory tubercle. The putamen and the head of the caudate are referred to as the dorsal striatum.

Numerous cognitive, emotional, and motor functions rely on the integrity of the striatum. The dorsal striatum is hypothesized to be associated with two general categories of functions (4). The first is stimulus-response habit formation, based on reinforcement contingencies in a given situation. The dorsal striatum is thus involved in procedural learning, reference memory, egocentric orientation, and rule-based learning. The second category of functions involve selecting different behavioral responses in the presence of changing task requirements, which may include motor planning and control, error correction in responding, strategy selection, and set switching (4), which requires monitoring of cues in the environment and altering behavioral responding when contingencies change (5). The dorsal striatum, as well as the VS, is also thought to facilitate appetitive or reward-dependent behaviors (6). Both regions are critically involved in reinforcement learning (7) and are active during the anticipation of reward (8). Activity in the VS increases in response to the receipt of rewarding stimuli and is thought to play a role in signaling errors in the prediction of reward (9). In addition, it has also been found to be activated more broadly by salient aversive, novel, and intense stimuli (10,11).

Functional Imaging Findings in Antisocial Populations

Three early studies used single photon emission computed tomography to examine brain activity in antisocial individuals. Tiihonen *et al.* (12) found that violent, but not nonviolent, patients with alcoholism had increased dopamine transporter densities in the striatum relative to control subjects. Amen *et al.* (13) found that psychiatric patients who demonstrated aggression had increased perfusion in the basal ganglia compared with nonaggressive patients. However, Soderstrom *et al.* (14) found reduced perfusion in the head of the caudate in violent offenders scoring higher on

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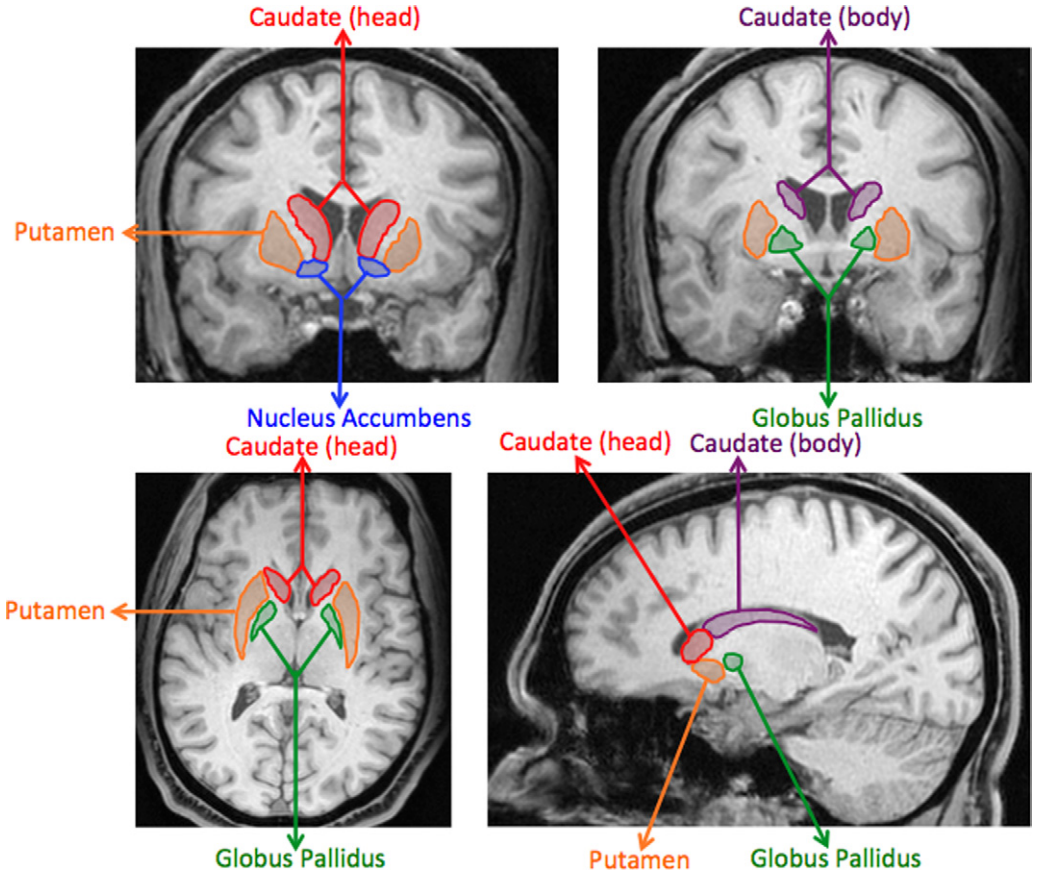

Figure 1. Coronal (top), axial (bottom left), and sagittal (bottom right) slices of the striatum illustrating the caudate (head and body), putamen, nucleus accumbens, and globus pallidus.

interpersonal and affective features of psychopathy but not with those scoring higher on impulsive and antisocial features.

Later studies, using functional magnetic resonance imaging (fMRI), have examined the functioning of the striatum using a number of different tasks and populations. These studies have identified altered functioning primarily in two subregions of the striatum: the caudate, which is part of the dorsal striatum, and the ventral striatum/nucleus accumbens.

Caudate

The caudate is a region that is important in being able to flexibly respond to the environment. It is activated in response to reward but not nonreward. This differential signaling by the caudate may be necessary for individuals to shift their behavioral response pattern. Based on the studies reviewed below, we suggest that in antisocial individuals, the caudate may not exhibit this differential response to reward and nonreward.

Vollm *et al.* (15) examined brain activity in individuals with either antisocial personality disorder or borderline personality disorder compared with control subjects. Reward processing was examined by implementing a task in which participants' correct behavioral responses were rewarded during some portions of the task but not others. Compared with control subjects, individuals with personality disorders (PD) had less activity in the caudate during rewarded trials compared with nonrewarded trials. Interestingly, this finding could be interpreted in two different ways. One possibility is that the participants with PD demonstrate less activity in the caudate during rewarded trials than control subjects. However, an alternative possibility is that PD participants demonstrate activity in the caudate during both the rewarded and the nonrewarded portions of the trial. This would result in PD participants showing less of a difference between rewarded and nonrewarded trials. In other words, control participants may show a greater difference in caudate activity between reward and nonrewarded trials.

We raise this as an alternative explanation because of findings from two subsequent studies. Gatzke-Kopp *et al.* (16) examined activity in the striatum during a similar task involving rewarded and nonrewarded blocks in youth with externalizing disorders compared to control subjects. Control subjects exhibited appropriate differential activity in the caudate; during rewarding trials, the caudate was activated, but during nonrewarding trials it was not. In contrast, youth with externalizing disorders exhibited activity in the caudate during both rewarding and nonrewarding trials (Figure 2). This suggests that individuals with externalizing psychopathology may not be oversensitive to reward but instead may have deficits in processing the omission of reward, which may make it difficult to shift their behavior when environmental contingencies change.

This idea is further supported in a study by Finger *et al.* (17), which examined brain activity in youth with psychopathic traits during a probabilistic reversal task. In this task, participants selected one of two stimuli and received either positive or negative feedback. Half-way through the session (i.e., after associations are formed), the reinforcement contingency was reversed (i.e., the good stimulus becomes bad and the bad stimulus becomes good). The authors compared the trials in which participants failed to appropriately reverse a response following the change in con-

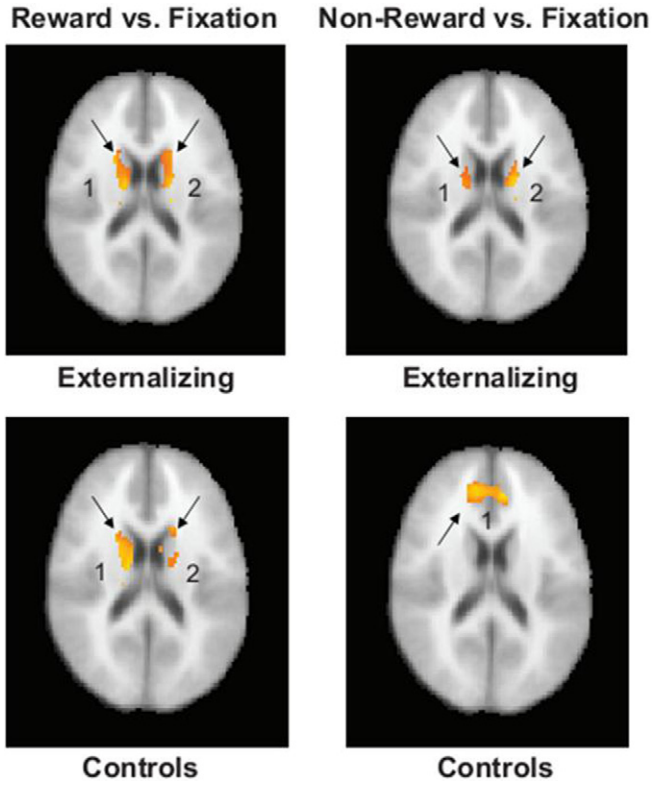

Figure 2. Results from study by Gatzke-Kopp *et al.* (16). Control subjects showed differential responding in the caudate during rewarding and nonrewarding trials. In contrast, youth with externalizing disorders demonstrated activity in the caudate during both rewarded and nonrewarding trials. (Reprinted with permission from Gatzke-Kopp *et al.* [16].)

tingency versus the rewarded correct responses. Children with psychopathic traits had increased activity in the caudate during the punished errors, whereas healthy children showed decreased activity. This could suggest that children with psychopathic traits continue to find previously rewarded responses to be rewarding, even after the feedback has changed from reinforcement to punishment (17).

Finally, one study found similar effects in individuals with an increased tendency for approach-related behavior (18), a trait that is observed in antisocial individuals (1). These individuals demonstrated increased activity in the caudate during a set-switching task in which participants were instructed to attend to either the color or the shape of figures on a screen. During the trials in which participants were required to make the cognitive shift from color to shape, or vice versa, participants scoring higher on approach-related behavior had more activity in the caudate. This may similarly suggest that the caudate continues to respond despite cues indicating that a particular response is no longer correct.

This failure to distinguish between reward and nonreward, or other indicators of changes in contingencies, may mean that the caudate is unable to send signals indicating that contingencies have changed. This may contribute to the deficits observed in antisocial individuals, such as perseveration in responding, even after the response is no longer rewarded (19). In a real-world context, this may have several implications for antisocial behavior. Youth may persist in the use of aggression or manipulation despite the fact that these behaviors are no longer rewarded. Continued activity in the caudate during nonrewarded events may also contribute to impulsive, risk-taking behaviors and increase risk for substance abuse and gambling. Additional research examining striatum activity during tasks in which reward contingencies change will be helpful in clarifying whether altered caudate functioning is in fact a risk factor for antisocial behavior and related tendencies for risk taking and substance abuse.

It should be noted that not all studies have observed this pattern of increased activity in the caudate during nonrewarded events. Finger *et al.* (20) examined brain activity in youth with psychopathic traits during a passive avoidance task. In this task, participants had to learn to respond to stimuli that were followed by reward while refraining from responding to stimuli followed by punishment. Particularly during the early learning phase (block 1), youth with psychopathic traits demonstrated reduced activity in the caudate. No differences were observed in later learning phases. Thus, findings regarding the caudate are somewhat mixed, with three studies reporting increased activity in antisocial groups (16,17) or in relation to approach-related tendencies (18), one study reporting reduced activity (20), and one study requiring further evaluation (15).

Ventral Striatum

Only a few studies of antisocial individuals have identified the VS as a region that functions differently. However, activity in the VS has been repeatedly associated with individual differences in traits such as reward sensitivity and impulsivity, which are common in antisocial groups. For example, studies have examined the relationship between the striatum and the tendency for approach-related behavior. Gray (21) defined a behavioral activation system (BAS) that underlies individual differences in positive incentive motivation and impulsivity. BAS is described as a system in the brain that is triggered by signals of reward or the relief of punishment and that facilitates approach-related behavior. BAS has been equated with trait reward sensitivity and is sometimes referred to as Gray's impulsivity (22).

Antisocial behavior and psychopathic traits have been associated with BAS functioning, as measured by two personality questionnaires: the BIS (behavioral inhibition system)/BAS Scales (23) and the Sensitivity to Reward scale of the Sensitivity to Punishment and Sensitivity to Reward Questionnaire (24). Scores on these measures are positively correlated with the interpersonal and affective features of psychopathy and strongly correlated with the impulsive and antisocial features of psychopathy in an offender population (1).

Higher scores on these same measures of BAS have been associated with increased activity in the VS while viewing pictures of appetizing foods (25), anticipating (26,27; but see [28]) and receiving (28) monetary rewards, and receiving positive feedback (29). Although some caveats exist (e.g., in the study by Hahn *et al.* [27], the relationship between BAS and VS activity was present only in those with a specific polymorphism of the dopamine transporter gene), these findings suggest that higher BAS scores are associated with increased activity in the VS during reward processing. One study also examined the randomness of neural dynamics, measured by examining the fluctuations of the time series in fMRI data, during the resting state (i.e., when participants are not engaged in a task). They found that the randomness in the time-series data in the VS was increased in individuals with high BAS scores (22). This randomness may reflect the degree of organization and coordination of neurons (30), indicating that individuals with higher BAS scores show less coordinated neural firing (22), although this interpretation is speculative (for an introduction to randomness in fMRI resting-state data, see reference 30).

Together, evidence suggests that alterations in the VS may contribute to the individual differences in BAS that are observed in

antisocial individuals. Similar to antisocial individuals, those with a more active BAS have been found to have better appetitive learning but impaired processing of aversive cues when responding to reward (5,31). A more active BAS may predispose to perseverating in dominant, appetitive responses and to ignoring secondary cues. This may contribute to the impaired learning, self-regulation, and decision making observed in antisocial individuals.

Two studies have found associations between VS activity and psychopathic traits. Using positron emission tomography, Buckholtz *et al.* (32) found that the impulsive-antisocial traits of psychopathy were associated with dopamine release in the nucleus accumbens (the primary subregion of the VS) in response to the administration of amphetamine. In a follow-up using fMRI, impulsive-antisocial traits were also associated with increased activity in the VS during the anticipation of a monetary reward but not during the receipt of the monetary reward (32).

Kiehl *et al.* (33) found reduced functioning in the VS in psychopathic offenders during an affective memory task. Notably, this task involved negatively valenced stimuli, in contrast to the reward-related stimuli used in the previously discussed studies. One hypothesis that could be tested in future studies is whether abnormalities in the striatum in antisocial groups may be different, depending on the context (e.g., positive vs. negative stimuli).

Finally, Decety *et al.* (34) found that youth with conduct disorder showed increased activity in the VS when viewing images of others in pain (caused accidentally) compared with images of no pain. Although it may be tempting to speculate that increased VS activity indicates that youth with conduct disorder find the pain of others to be rewarding, the striatum is also activated by salient aversive, novel, and intense stimuli (10,11), so increased functioning does not necessarily signify that the stimuli were rewarding.

In summary, although five studies have observed an association between increased VS activity and BAS (25–29), only two studies have observed these increases in individuals with antisocial traits (32,34), and one study found reduced activity (33). Additional studies are needed to clarify how the VS may contribute to individual differences in reward processing and also whether the direction of VS deficits in antisocial individuals may depend on the particular type of stimuli being processed.

Structural Imaging Findings in Antisocial Populations

An advantage of structural imaging studies is that it is not always clear from fMRI studies whether altered functioning in a particular brain region is due to abnormalities within the region or due to altered input from other regions. By examining the structure, we can gain more information about whether a particular region is altered. However, structural findings may also be more difficult to interpret. Although the assumption is that increased volume reflects superior functioning (e.g., greater hippocampal volumes are observed in taxi drivers [35]), this may not always be the case.

Four structural imaging studies have found increased volumes in the striatum in antisocial groups, although increases were observed in different subregions. Barkataki *et al.* (36) reported increased volume in the putamen of individuals with antisocial personality disorder compared with controls. Schiffer *et al.* (37) found that violent offenders had larger volumes in the nucleus accumbens and the caudate head than nonoffenders. In youth, Ducharme *et al.* (38) found that bilateral caudate and putamen volumes were positively correlated with scores on the aggression subscale of the Child Behavior Checklist in healthy youth aged 6–18 years. This subscale is thought to measure impulsive forms of aggression.

Two studies have examined the volume of the striatum in relation to psychopathic traits specifically. Schiffer *et al.* (37) found that volumes of the nucleus accumbens and caudate were positively correlated with total psychopathy scores on the Psychopathy Checklist–Screening Version (39). The authors also examined the volume of these regions in relation to the four facets of psychopathy and found that the volume of the caudate head was correlated with affective and antisocial features. The volume of the nucleus accumbens was correlated with all features except the lifestyle features. The relationships with interpersonal and affective features remained significant, even after controlling for individual differences in impulsivity.

Glenn *et al.* (40) found a 9.6% increase in the volume of the total striatum (caudate, putamen, globus pallidus) in psychopathic individuals compared with a control group matched for age, sex, ethnicity, and substance dependence. Unlike the study by Schiffer *et al.* (37), analyses of the facets of psychopathy revealed that the caudate head was associated with lifestyle features but not related to the other facets. In addition, the caudate body was primarily associated with the interpersonal and affective features, and the lenticular nucleus (putamen and globus pallidus) was associated with all features except the interpersonal features. The nucleus accumbens was not delineated in this study.

Taken together, analyses of the four facets of psychopathy do not produce consistent results but do suggest that increased volumes in the striatum are not exclusively related to the impulsive and antisocial features but may also be associated with the interpersonal and affective features that are more unique to individuals with psychopathic traits.

Findings from healthy individuals also support the link between striatal structure and individual differences in antisocial-related traits. However, one structural imaging study found that undergraduate males with higher BAS scores demonstrated reduced, rather than increased, gray matter volumes in the caudate, putamen, and globus pallidus (41). Another study examined individual differences in novelty seeking and reward dependency in relation to the strength of white matter tracts connecting the striatum to cortical and subcortical regions. Novelty seeking, which describes the trait of looking for and feeling rewarded by new experiences, was associated with stronger white matter fiber tracts connecting the VS to both the hippocampus and amygdala (42). Reward dependency, or the tendency to rely on social approval and to continue previously rewarded behaviors, was associated with stronger fiber tracts connecting the striatum to several areas of the prefrontal cortex.

Overall, structural imaging studies parallel findings from functional studies, reporting increased volume of the striatum in antisocial groups. Future studies may benefit from assessing both volume and functioning within the same study to better understand how structure and functioning are related. In addition, longitudinal studies examining differences in the trajectory of striatal growth across developmental periods will be important for understanding how relationships between the striatum and antisocial behavior may change.

Development of Striatum Abnormalities

An important question is how differences in the striatum may develop. In this section we discuss genetic and environmental factors that may affect the structure and the functioning of the striatum.

Genetic Factors

The neurotransmitter dopamine plays a central role in the functioning of the striatum, so variants in genes associated with dopamine have been examined as potential contributors to individual

differences in striatal activity. One gene is the *DAT*1 gene (*SLC6A3*), which codes for the dopamine transporter, which is involved in regulating synaptic dopamine. Two variants of interest are a 9-repeat allele, which is associated with decreased synaptic dopamine in the striatum, and a 10-repeat allele, which is associated with increased synaptic dopamine. Dreher *et al.* (43) found that carriers of the 9-repeat allele had more activity in the VS and caudate during reward anticipation than individuals with the 10-repeat allele. Similarly, Forbes *et al.* (29) found that carriers of the 9-repeat allele had increased reward-related activity in the VS and higher scores on the Barratt Impulsiveness Scale. Greater reward-related VS activity was also observed in carriers of two alleles of dopamine receptor genes, *DRD2* (141C Del allele) and *DRD4* (7-repeat allele) (29).

The gene coding for catechol-*O*-methyltransferase (COMT), which catabolizes dopamine, has also been examined. Two variants, valine (val) and methionine (met), affect COMT enzyme activity. Individuals homozygous for the met allele (met/met) have 25–75% reduction in COMT enzyme activity compared with individuals homozygous for the val allele (val/val) and therefore have more baseline synaptic dopamine. Dreher *et al.* (43) found that met/met carriers had more activity in the VS than those with the val allele during reward anticipation (but also see [29]).

Environmental Factors

Evidence suggests that environmental factors from the prenatal period to adolescence may affect the development of the striatum. Qiu *et al.* (44) examined the shape and volume of the striatum in a sample of healthy 6-year-old boys born at term and within the normal range for birth weight. Boys with lower birth weight and shorter gestation had smaller volumes and altered shape of the caudate, suggesting that subtle variations in fetal development may alter the development of the striatum.

Environmental enrichment and stress early in life also may affect the development of the striatum. One study examined the effects of tactile stimulation as a form of environmental enrichment in rats. Tactile stimulation early in life (postnatal to weaning) resulted in enlargement of the striatum in adulthood (45). Despite this enlargement in the striatum, tactile stimulation was also associated with decreased novelty-seeking behavior. This pattern of findings (enlarged striatal volumes associated with reduced approach behavior) parallels the findings by Barros-Loscertales *et al.* (41) reviewed above, which demonstrate that individuals with lower BAS scores have larger volumes in the striatum.

It was suggested that the reduced novelty seeking observed in rats receiving tactile stimulation could serve as a protective factor against drug abuse propensity (45). In support of this hypothesis, rats that received tactile stimulation were less behaviorally sensitive to amphetamine exposure in adulthood. They also did not show the same postamphetamine enlargements in the striatum as rats without tactile stimulation. This suggests that environmental enrichment may alter the striatum in a way that allows it to be buffered against drug-induced structural changes. In other words, early environment may affect the development of the striatum in a way that alters future susceptibility to drug addiction and possibly impulsive, antisocial behavior.

In contrast, early life stress may sensitize the striatum. Animal studies have found that rats isolated from their mother for 1 hour per day during the first week of life showed much greater dopamine release in the VS after an amphetamine challenge than those who were not isolated (46). Chronic lead exposure after weaning in rats has also been found to affect dopamine-binding sites and dopamine release in the VS (47). Behaviorally, lead exposure resulted in increases in fixed interval schedule–controlled behavior response rates, which is associated with impulsivity in human infants and children (48).

During adolescence, exposure to social, but not nonsocial (foot shock), stress has been found to cause changes in the striatum. In a rat model, rats exposed to repeated social defeat during adolescence demonstrated altered dopamine functioning in the VS in response to amphetamine exposure in adulthood. Behaviorally, the rats exposed to the social stress also exhibited increased conditioned place preference for amphetamine in adulthood. This suggests that it is specifically social stress during adolescence that may predispose to drug-related behaviors later in life (49).

Together these studies suggest that a number of environmental factors may contribute to abnormalities in the striatum. These stressors may sensitize the striatum, altering reward processing and making later exposure to drugs that target this system more rewarding. Intervention studies providing early environmental enrichment may be able to test the hypothesis that enrichment alters striatal activity in a way that buffers against antisocial behavior and substance abuse.

Summary

Evidence reviewed here suggests that the volume of the striatum is increased in antisocial and psychopathic individuals and that functioning is also increased in specific contexts. Impairments in the caudate may result in a failure to signal when behaviors are no longer rewarding and thus may contribute to the perseveration of maladaptive behaviors such as aggression. Deficits in the VS may contribute to impulsivity, sensation seeking, and heightened sensitivity to reward. The striatum has been linked to both interpersonal/affective and impulsive/antisocial features of psychopathy, and alterations have been observed in both youth and adult populations. Discrepancies remain regarding the specific subregions of the striatum that may be compromised and the specific contexts in which functioning may be altered. Future research clarifying these issues will improve our understanding of how this brain region may contribute to antisocial behavior, psychopathy, and related personality traits.

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