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Subcortical Intelligence: Caudate Volume Predicts IQ in Healthy Adults

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Abstract: This study examined the association between size of the caudate nuclei and intelligence. Based on the central role of the caudate in learning, as well as neuroimaging studies linking greater caudate volume to better attentional function, verbal ability, and dopamine receptor availability, we hypothesized the existence of a positive association between intelligence and caudate volume in three large independent samples of healthy adults (total $N = 517$). Regression of IQ onto bilateral caudate volume controlling for age, sex, and total brain volume indicated a significant positive correlation between caudate volume and intelligence, with a comparable magnitude of effect across each of the three samples. No other subcortical structures were independently associated with IQ, suggesting a specific biological link between caudate morphology and intelligence. *Hum Brain Mapp 36:1407–1416, 2015.* © **2014 Wiley Periodicals, Inc.**

Key words: intelligence; IQ; caudate; dorsal striatum; magnetic resonance imaging

INTRODUCTION

Measures of intelligence predict a number of important life outcomes, are stable over many years, and are strongly genetically influenced [Deary et al., 2009]. Scientific evidence suggests that intelligence involves ability for planning, reasoning, comprehension, abstraction, and learning and that intelligence tests measure this general capability well [Gottfredson, 1997]. Intelligence, so defined, is integral to many aspects of psychological function, and understanding the biological systems that contribute to individual differences in intelligence is an important goal for differential psychological science [Deary et al., 2010].

Neuroimaging research has shown that variation in many different brain regions and neural parameters, both structural and functional, is associated with intelligence [Chiang et al., 2009; Choi et al., 2008; DeYoung et al., 2009; Gläscher et al., 2010; Jung and Haier, 2007; Shaw et al., 2006]. The Parieto-Frontal Integration Theory of intelligence [P-FIT; Jung and Haier, 2007] is the most comprehensive description to date of how individual differences in intelligence are reflected in the brain. The P-FIT synthesized existing research on the neurobiology of intelligence and concluded that individual differences in intelligence are due primarily to a network of brain regions across the parietal, frontal, and cingulate cortices, including both

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gray and white matter [Jung and Haier, 2007]. Most studies of brain structure support the idea that "bigger is better" for intelligence, the most classic example being the positive association of total brain size with intelligence [McDaniel, 2005]. This positive association appears to be reasonably consistent throughout the network of regions that make up the P-FIT [Jung and Haier, 2007].

One set of brain regions notably absent from the P-FIT model are subcortical structures, such as the basal ganglia. Jung and Haier [2007] noted that, in addition to frontal and parietal regions, a number of subcortical structures are likely to be involved in intelligent behavior. However, they speculated that the role of such regions is so fundamental to brain function in general that evolution is likely to have minimized variation in their structure and function, leading to an absence of individual differences meaningfully related to intelligence. The present research suggests that meaningful subcortical variation may exist after all, by examining evidence that one particular subcortical structure—the caudate nucleus—contributes to variation in intelligence.

The caudate nucleus is a bilateral structure that makes up the most dorsal and anterior portion of the striatum. Once considered to be primarily a center of motor control, the caudate is now recognized as crucial for learning, particularly when reinforcing or punishing feedback is received contingent on the individual's choices and actions [Packard and Knowlton, 2002; Tricomi et al., 2006]. The ability to learn effectively is central to most definitions of intelligence. Further, intelligence quotient (IQ) scores are associated with level of education, and reinforcement learning is likely to be crucial for the acquisition of knowledge and cognitive skills in the educational context [Deary et al., 2007]**.** The caudate is, therefore, a likely candidate as a subcortical structure implicated in the biology of intelligence.

Variation in volume of the caudate nucleus, compared to neighboring subcortical structures, appears to be under stronger genetic control [heritability = 80%; Giedd et al., 2007]; thus, substantial systematic variation in its volume does exist across individuals, and this variation may be related to intelligence. Moreover, a recent genome wide association study of over 120,000 individuals identified and replicated an association between three single nucleotide polymorphisms and educational attainment [a construct highly correlated with intelligence; Deary et al., 2007], and bioinformatics analyses indicated that the genomic regions tagged by these three loci include genes preferentially expressed in the anterior caudate nuclei [Rietveld et al., 2013]. The caudate was the only brain region specifically implicated by the bioinformatics analyses.

Other considerations that suggest the caudate's importance for intelligence include its relation to the neurotransmitter dopamine and its pattern of connections to brain regions identified in the P-FIT. The caudate is highly innervated with dopamine neurons from the substantia nigra, and dopamine function in the caudate appears to be centrally implicated in learning from feedback; specifically dopamine release in the caudate serves as a prediction-error signal coding the value of unexpected events [Bromberg-Martin et al., 2010; Reynolds et al., 2001]. Functional neuroimaging studies indicate that the caudate critically moderates the degree to which feedback influences learning [Tricomi et al., 2006]. A recent functional magnetic resonance imaging (fMRI) study of a simple decision-making task showed that intelligence predicted neural responses in the caudate known to correspond to the dopaminergic prediction-error learning signal [Hawes et al., 2014]. Intelligence also predicted decision-making behavior in the task. In combination, the neural and behavioral correlates indicated that intelligence was associated with speed of learning the task contingencies, a process critically involving the caudate.

Additionally, the caudate has both afferent and efferent connections to the prefrontal and anterior cingulate cortices [Voorn et al., 2004]. Dopaminergic tone in prefrontal and cingulate cortex is crucial for working memory, which is one of the most important cognitive processes contributing to intelligence [Arnsten and Robbins, 2002; Braver and Cohen, 2000; Conway et al., 2003; DeYoung et al., 2009]. Declines in cognitive function with aging have been linked to declining dopaminergic function [Erixon-Lindroth et al., 2005; Volkow et al., 1998]. Alteration of dopamine levels in the caudate modulates cortical dopaminergic function, and artificial manipulation of striatal dopamine levels has broad effects on working memory [Collins et al., 2000; Frank et al., 2001]. Taken together, the evidence suggests that intelligence is linked to the function of the caudate.

Functional differences are often reflected in structural differences [Zatorre et al., 2012], and several neuroimaging studies in clinically relevant samples have linked caudate volume to individual differences in intelligence or the conceptually related trait of cognitive flexibility. Caudate volume was correlated with IQ in 105 preadolescent children born preterm [Abernethy et al., 2004]. Another study found that caudate volume was correlated with verbal IQ (but not performance IQ) in 76 adolescents born preterm [Isaacs et al., 2008]. This sample additionally included an experimental comparison in which one group had been randomly assigned to receive a high-nutrient postnatal diet and the other had received a standard diet. Both caudate volume and verbal IQ were significantly higher in the high-nutrient group. These two studies suggest that caudate volume may be particularly sensitive to early developmental challenges and is a potential mediator of the effects of early nutrition on IQ. A third study, investigating the link between respiratory fitness and cognitive decline, found that caudate volume mediated the association between cardiopulmonary fitness and cognitive flexibility in 179 older adults [Verstynen et al., 2012]. Finally, a recent study revealed an association between intelligence and the geometric shape of right hemisphere striatial structures in a sample of 93 healthy adults, including the caudate, putamen, nucleus accumbens, and thalamus

[volumetric associations were not reported; Burgaleta et al., 2013].

Based on the importance of learning for intelligence, the link between intelligence and caudate function in a simple fMRI task [Hawes et al., 2012], previous research implicating caudate volume in intelligence in preterm children and in cognitive flexibility in an elderly population, the association of dopamine receptor availability in the striatum with both intelligence and caudate size, and the association of right striatal geometric shape with intelligence, we hypothesized that the volume of the bilateral caudate nuclei would be positively correlated with IQ in healthy adults, independently of total brain volume. Because previous research examining intelligence in the brain suggests partially distinct biological sources of verbal and performance IQ [VIQ and PIQ; e.g., Choi et al., 2008], and because one study of preterm children reported caudate volume to be significantly associated with VIQ only [Isaacs et al., 2008], we also conducted secondary analyses examining associations of caudate volume with these measures separately. To ensure the robustness of our results, we conducted analyses in three independent MRI samples of healthy adults.

Finally, although our only hypothesis concerned the caudate, we conducted secondary exploratory analyses of other subcortical structures—amygdala, putamen, globus pallidus, nucleus accumbens, thalamus, hippocampus—many of which are involved in various forms of learning that could plausibly be related to intelligence. We did not form any hypotheses about these structures, as less prior research links them to intelligence, but some studies do suggest that some of them might also be related to intelligence [e.g., Amat et al., 2008; Schumann et al., 2007]. Our primary purpose in examining these structures was simply to test whether our findings were specific to the caudate.

METHODS

Participants

Sample 1 consisted of 285 healthy volunteers (141 female) between the ages of 20 and 40 ($M = 26.2$; Standard Deviation (SD) = 5.0), recruited via www.craigslist.org in Hennepin County, Minnesota. Participants identified as 80% White, 9% Black, 6% American Indian, 6% Hispanic/Latino, 6% Asian; 7% of Sample 1 reported mixed heritage. All subjects were screened and excluded for presence of neuropsychiatric and psychological disorders as well as psychotropic drug use prior to inclusion in the study. The data collection protocol was approved by the University of Minnesota Institutional Review Board, and participants provided informed consent for all neuroimaging and behavioral data collection. Structural scans were visually inspected to evaluate the presence of movement or other scan artifacts, indicated by blurring or ghosting of the images, but this inspection did not result in the decision to exclude any participants.

Sample 2 consisted of 125 healthy volunteers (57 female) between the ages of 18 and 29 ($M = 21.7$; SD = 2.9). Subjects were recruited from postings on and around campus at the University of New Mexico in Albuquerque, NM. The study was approved by the Institutional Review Board of the University of New Mexico. No ethnicity questionnaires were administered in this sample. All subjects were screened for neuropsychiatric or psychological disorder, and provided written informed consent for the collection of all data and subsequent analyses. Based on visual inspections for movement and artifacts, six subjects were excluded from an initial sample size of 131.

Sample 3 consisted of 107 healthy, white, male volunteers between the ages of 18 and 38 ($M = 23.5$, SD = 5.1), recruited from the community around New Haven, Connecticut, primarily through Internet sites. (Restrictions by race and gender were for the purposes of genetic research not germane to the present study.) Students from Yale University and other nearby institutions constituted 54% of the sample. Participants were screened and excluded for histories of neurological or psychiatric disorder. The experimental protocol was approved by the Yale University Human Investigation Committee. Participants were included in the present analysis on the basis of high quality anatomical MRI scans (four additional subjects were excluded based on the presence of movement and artifacts).

Structural Image Acquisition

Sample 1

Structural imaging data was collected on a Siemens 3T Trio Scanner at the Center for Magnetic Resonance Research at the University of Minnesota in Minneapolis, MN. Three-dimensional brain images were obtained with a coronal T1-weighted Magnetization Prepared Rapid Gradient Echo (MPRAGE) sequence (time repetition [TR] = 2,530 ms, time echo [TE] = 3.65 ms, inversion time [TI] = 1,100 ms, 240 slices, voxel size = 1.0 mm × 1.0 mm × 1.0 mm, flip angle = 7°, field of view [FOV] = 256 mm).

Sample 2

Structural imaging data was collected using a 3T Trio Siemens MRI scanner using a 12-channel head coil. All scans were collected at the Mind Research Network in Albuquerque, NM. Three-dimensional brain images were obtained with a coronal T1-weighted multiecho MPRAGE sequence (TR = 2,530 ms, TE = 1.64/3.5/5.36/7.22/9.08 ms, TI = 1,200 ms, 240 slices, voxel size = 1.0 mm × 1.0 mm × 1.0 mm, flip angle = 7°, FOV = 256 mm).

Sample 3

Imaging data were collected using a 3T Siemens Trio scanner at the Yale Magnetic Resonance Research Center.

TABLE I. Sample characteristics

	Sample 1 ($N = 285$)		Sample 2 ($N = 125$)		Sample 3 ($N = 107$)			
	Mean	SD	Mean	SD	Mean	SD	F_0	P
Caudate volume (mm^3)	8454	1083.60	7877	940.66	8223	924.41	9.70	.002
IQ	114.18	15.62	119.49	13.13	122.85	11.45	32.72	<.001
VIQ	115.13	17.08	120.70	13.19	123.86	12.05	29.50	<.001
PIQ	108.32	13.18	110.46	13.76	117.82	12.76	6.54	.011
Total brain volume (mm^3)	1282320	141331.5	1280464	109427.4	1249231	93987.57	5.67	.018
Age	26.26	4.96	21.73	2.96	22.94	4.80	57.90	<.001

For each participant, a high-resolution T1-weighted anatomical image was acquired. (MPRAGE, TR = 2,500 ms; TE = 3.34 ms; TI = 1,100 ms; flip angle = 7; slices = 256, voxel size = 1 × 1 × 1 mm).

Behavioral Measures

Intelligence was assessed in Sample 1 using four subtests of the Wechsler Adult Intelligence Scale, fourth edition (WAIS-IV): Block Design, Matrix Reasoning, Vocabulary, and Similarities. In Sample 2, intelligence was assessed using the Wechsler Abbreviated Scale of Intelligence (WASI), which consists of the same four subtests used in Sample 1. In Sample 3, intelligence was assessed using the WAIS-III, again based on the same four subtests. In all three samples, Block Design and Matrix Reasoning scores were used to calculate Performance IQ (PIQ), Vocabulary, and Similarities scores were used to calculate Verbal IQ (VIQ), and all four subtests were used to estimate full scale IQ scores, as recommended by the WASI manual [Wechsler, 1999].

Subcortical Extraction

Subcortical measurement and extraction were carried out using FreeSurfer 4.5 software in all three samples [Fischl and Dale, 2000]. FreeSurfer has high reliability and accuracy with respect to measurement of the caudate [Morey et al., 2009, 2010]. Segmented structures included bilateral cortical white matter, gray matter, hippocampus, amygdala, caudate, putamen, globus pallidus, nucleus accumbens, and thalamus. Total brain volume estimates were calculated by summing the total of all segmented brain structures. All segmentation results were visually inspected for quality prior to inclusion in the present analyses. Numerical values of all brain measures are in cubic millimeters (mm^3), with the exception of total cortical volume, for which mm^3 was divided by 1,000 to avoid regression weights near zero.

RESULTS

Sample characteristics are presented in Table I. Because the three samples differed systematically in sex, age, IQ, and caudate volume and had significantly different variances for IQ (Levene's $test_{(2,\ 514)} = 6.01$, $P = 0.003$), we tested our hypothesis in two steps. First, we examined the prediction of intelligence by caudate volume in the three samples independently, including sex (in Samples 1 and 2), age, and total brain volume as covariates. Second, we fit the regression models for all three samples simultaneously [using group analysis in the program Amos 20.0 with maximum likelihood parameter estimation; Arbuckle, 2003] and constrained the effect of caudate volume on IQ to be equal across all three samples while leaving all other model parameters free to vary by sample. The initial regressions revealed a significant association between IQ and caudate volume in Samples 1 ($\beta = 0.21$, $P < 0.01$) and 2 ($\beta = 0.27$, $P < 0.01$) and a marginally significant association between IQ and caudate volume in Sample 3 ($\beta = 0.20$, $P = 0.09$). Figures 1 and 2 present zero order and residualized scatterplots (respectively) depicting the linear association between IQ and caudate volume.

Given that the effect is of almost identical magnitude in Samples 1 and 3, the lack of significance in Sample 3 is most likely Type II error, due to lack of adequate power. We tested this possibility in our second analytical step by fixing the effect of caudate volume on IQ to be equal across samples. Doing so did not significantly worsen the fit of the model, $\Delta\chi^2_{(2)} = 0.44$, $P = 0.80$, and yielded a regression weight that was significant across all three samples, $b = 0.003$, Standard Error (SE) = 0.001, $P < 0.001$. (Because variances differed across samples, the standardized regression weights were not identical even when the unstandardized weights were constrained to be equal; they ranged from $\beta = 0.21$ to $\beta = 0.24$.) In this model, caudate volume accounted for an increment in the variance of IQ, above age, sex, and total volume, ranging from 2.4% to 4.2%, depending on sample. Results were nearly identical when right or left caudate volume measurements were used in place of summed bilateral volume, hence all reported analyses utilized bilateral caudate volume. Regression results for each sample are presented in Table II. Figures 1 and 2 are present.

Although sex moderated the association of caudate with IQ in the unconstrained model for Sample 1 ($b = 0.004$, SE = 0.001, $P = 0.03$), this interaction effect was not significant in Sample 1 when the caudate effect was constrained

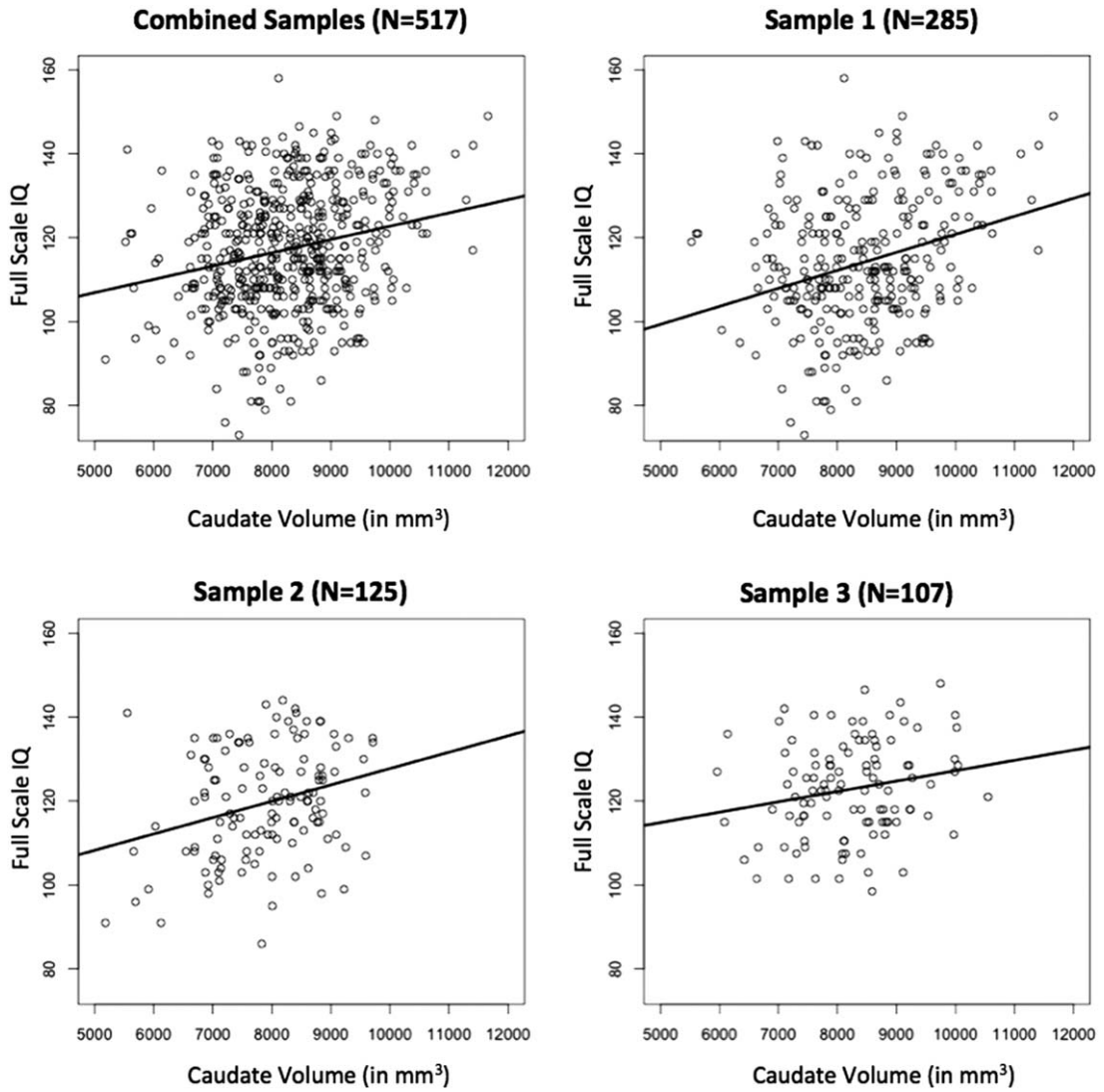

Figure 1.
IQ regressed on caudate volume (zero-order correlation).

to be equal across samples ($b = 0.003$, SE = 0.002, $P = 0.07$), nor was it significant when the interaction effect itself was constrained to be equal across samples ($b = 0.002$, SE = 0.001, $P = 0.09$), and this constraint did not significantly reduce the fit of the model, $\Delta\chi^2_{(2)} = 0.49$, $P = 0.49$. We therefore concluded that the appropriate model did not include interaction with sex.

Analyses of VIQ and PIQ appear in Tables III and IV. Regression coefficients for VIQ were very similar to those for full scale IQ. Effects for PIQ were considerably weaker, however, and nonsignificant in all three samples when estimated individually. Nonetheless, when the effect of caudate volume on PIQ was constrained to be equal across all three samples, it was just significant ($b = 0.001$, SE = 0.001, $P = 0.044$), and the fit of the model was not significantly reduced, $\Delta\chi^2_{(2)} = 0.48$, $P = 0.79$.

To determine whether the association between caudate volume and intelligence was specific to the caudate nuclei, we also examined whether the inclusion of other subcortical structures influenced model fit. In none of the samples did the inclusion of six other subcortical structures (amygdala, putamen, globus pallidus, nucleus accumbens, thalamus, hippocampus) in a second block of the regression yield a significant increase in R^2 (all $F < 1.49$, $P > 0.18$), nor was any other subcortical structure a significant predictor. Nonetheless, for the sake of completeness, partial correlations of each structure with IQ, **VIQ**, and **PIQ** (controlling for age, sex, and total brain volume) are presented in

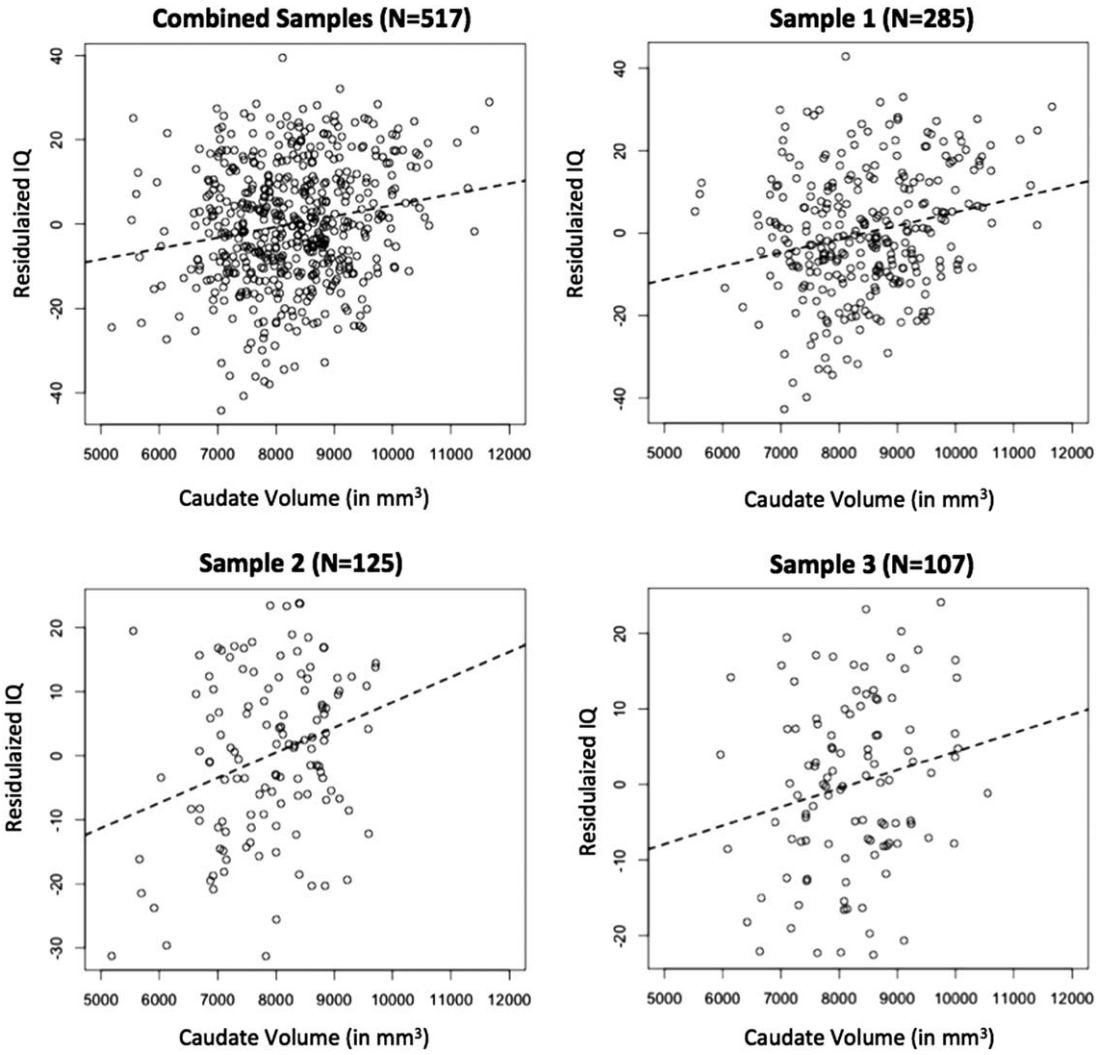

Figure 2.
Residualized IQ (controlling for sex, age, and total brain volume) regressed on caudate volume.

Table V. Note that only partial correlations for the caudate are both substantial and consistent in magnitude across all three samples.

DISCUSSION

Across three samples, bilateral caudate volume was significantly positively associated with IQ, independently of total brain volume. These results indicate that the morphology of the bilateral caudate nuclei is associated with individual differences in intelligence, and that this variation is at least partially captured by measurement of caudate volume. Although several smaller studies in special populations have suggested a role for the caudate in intelligence, and one study reported an association between caudate shape and intelligence, this is the first study to report the association of caudate volume with intelligence in a large, healthy, adult population. The three samples came from widely different areas of the country, suggesting that the finding is likely to be robust.

Our findings suggest an extension to the P-FIT, currently the most comprehensive synthesis of neuroimaging research on intelligence [Jung and Haier, 2007]. Many structural aspects of the brain have been repeatedly associated with intelligence. Cortical regions included in the P-FIT are well-summarized by Deary et al. [2010]: the extrastriate cortex and fusiform gyrus contribute to recognition and elaboration of visual input, which is then processed by parietal cortices (thought to involve abstraction and further elaboration); these parietal regions interact with the frontal cortices involved in forming a network that

TABLE II. Regression of IQ on caudate volume

	β	b	SE	t	P	R^2	F	P
Sample 1						0.11	8.56	<0.001
Caudate vol.	0.21	0.003	0.001	2.67	0.008			
(Caudate vol., constrained)	(0.21)	(0.003)	(0.001)	–	(<0.001)			
Total brain vol.	0.21	0.023	0.010	2.22	0.027			
Age	−0.04	−0.139	0.057	−0.77	0.440			
Sex	−0.15	−4.755	2.291	−2.01	0.039			
Sample 2						0.11	3.79	0.006
Caudate vol.	0.27	0.004	0.001	2.74	0.007			
(Caudate vol., constrained)	(0.22)	(0.003)	(0.001)	–	(<0.001)			
Total brain vol.	−.03	−0.003	0.014	−0.257	0.798			
Age	0.17	0.760	0.382	1.99	0.049			
Sex	0.09	2.491	2.919	0.85	0.395			
Sample 3						0.05	1.77	0.158
Caudate vol.	0.20	0.002	0.001	1.74	0.086			
(Caudate vol., constrained)	(0.24)	(0.003)	(0.001)	–	(<0.001)			
Total brain vol.	−0.02	−0.003	0.014	−0.21	0.832			
Age	−0.09	−0.222	0.232	−0.95	0.342			

supports working memory; and the anterior cingulate cortex carries out response selection and inhibition of alternative responses. Broad regions of white matter structure (as measured by diffusion imaging) are also important for intelligence, and multiple studies reveal widespread areas of white matter coherence positively associated with intelligence, especially in the centrum semiovale, the arcuate fasciculus, and the uncinate fasciculus. Although most brain structures involved in intelligence appear to be cortical, or are white matter tracts connecting different areas of cortex, the caudate may be one subcortical structure that is crucially involved in individual differences in intelligence. This would be consistent with its dense connections to prefrontal and cingulate regions that are part of the P-FIT [Voorn et al., 2004].

The effect size seen for the caudate in our study is similar to those typically seen for associations of intelligence with various cortical structures, which rarely exceed a correlation of about 0.25 [Deary et al., 2010]. This is exactly what one should expect given a MIMIC model for intelligence; MIMIC stands for "multiple indicators, multiple causes" [Kievit et al., 2012]. General intelligence contributes to performance on many different cognitive tests; hence, it is a factor indicated by a variety of test scores (the "many indicators"). However, many different brain systems and neural parameters within those systems

TABLE III. Regression of VIQ on caudate volume

	β	b	SE	t	P	R^2	F	P
Sample 1						0.08	6.18	<0.001
Caudate vol.	0.23	0.004	0.001	2.96	0.003			
(Caudate vol., constrained)	(0.20)	(0.003)	(0.001)	–	(<0.001)			
Total brain vol.	0.06	0.007	0.011	0.59	0.555			
Age	−0.11	−0.391	0.200	−1.96	0.051			
Sex	−0.13	−4.547	2.545	−1.79	0.075			
Sample 2						0.10	3.46	0.010
Caudate vol.	0.20	0.003	0.001	2.06	0.042			
(Caudate vol., constrained)	(0.22)	(0.003)	(0.001)	–	(<0.001)			
Total brain vol.	−0.11	−0.013	0.014	−0.94	0.350			
Age	0.22	0.997	0.386	2.58	0.011			
Sex	0.16	4.102	2.945	1.39	0.166			
Sample 3						0.06	2.17	0.096
Caudate vol.	0.20	0.003	0.001	1.80	0.075			
(Caudate vol., constrained)	(0.24)	(0.003)	(0.001)	–	(<0.001)			
Total brain vol.	−0.01	−0.002	−0.014	−0.11	0.913			
Age	−0.11	−0.288	0.243	−1.19	0.239			

TABLE IV. Regression of PIQ on caudate volume

	β	b	SE	t	P	R^2	F	P
Sample 1						0.10	7.99	<0.001
Caudate vol.	0.08	0.001	0.001	1.07	0.286			
(Caudate vol., constrained)	(0.12)	(0.001)	(0.001)	–	(0.044)			
Total brain vol.	0.32	0.030	0.009	3.48	0.001			
Age	0.06	0.154	0.152	1.01	0.313			
Sex	−0.14	−3.558	1.940	−1.83	0.068			
Sample 2						0.04	1.25	0.293
Caudate vol.	0.14	0.002	0.001	1.42	0.159			
(Caudate vol., constrained)	(0.10)	(0.001)	(0.001)	–	(0.044)			
Total brain vol.	0.00	0.000	0.015	0.00	0.999			
Age	0.08	0.375	0.417	0.90	0.370			
Sex	−0.18	−5.067	3.180	−1.59	0.114			
Sample 3						0.02	0.61	0.608
Caudate vol.	0.13	0.002	0.002	1.13	0.262			
(Caudate vol., constrained)	(0.10)	(0.001)	(0.001)	–	(0.044)			
Total brain vol.	0.00	−0.004	0.016	−0.25	0.807			
Age	−0.04	−0.114	0.263	−0.43	0.667			

contribute to general intelligence, and these are the "multiple causes." Variation in any one of those parameters (such as size of the caudate) should explain only a small portion of the variance in intelligence because it is merely one of many explanatory variables.

An interesting question is why the review that led to the P-FIT did not uncover an association between caudate structure and intelligence. It is somewhat surprising (in light of this study) that none of the seven whole-brain voxel-based morphometry (VBM) analyses included in the P-FIT identified regions in the caudate as relevant for individual differences in intelligence, nor did a subsequent analysis of intelligence using VBM [Colom et al., 2009]. One explanation for this dearth of findings may stem from difficulties with methodological variation and statistical validity of VBM [Henley et al., 2010].

A correlation between caudate size and intelligence is well situated in literature that supports a role for the caudate in learning, particularly in relation to the prediction-error learning signal that is transmitted by dopamine [Bromberg-Martin et al., 2010; Cools et al., 2008; Hawes et al., 2014]. Nonetheless, a limitation of the present findings is that they are purely correlational and provide no evidence regarding a mechanism for the influence of caudate volume on intelligence. Two studies hint at a possible molecular explanation for the relation of caudate size to intelligence. Dopamine D2 and D3 receptors are inhibitory autoreceptors that are densely distributed in the dorsal striatum. Availability of D2/D3 receptors in the striatum has been linked to verbal (but not performance) IQ in healthy adults [Guo et al., 2006]. In turn, D2/D3 receptor availability is positively correlated with both volume and density of bilateral caudate nuclei [Woodward et al., 2009]. Although this study did not investigate dopaminergic activity, we believe it is worth considering that the apparent cognitive benefits conferred by an increased number of available D2/D3 receptors may be involved in the association between caudate size and intelligence.

A role for dopamine in the link between caudate volume and intelligence would also be consistent with the finding that stimulation seeking at age 3 years predicted intelligence at 11 years in 1795 children [Raine et al., 2002]. Dopamine is involved in exploration and processing salience [DeYoung, 2013], and the prediction error signal in the striatum has been found to depend on the degree of stimulus saliency, even for nonrewarding stimuli, such as novel unexpected tones [Bromberg-Martin et al., 2010; Zink et al., 2006]. Heightened dopaminergic function associated with greater caudate volume may lead to better learning and, hence to higher IQ, through exploratory processes.

Although we did not develop any hypotheses about whether Verbal and Performance measures of IQ would be differentially predicted by caudate volume, we examined them separately because previous research has indicated that VIQ and PIQ have partially distinct brain correlates. Choi et al. [2008] found that VIQ was more strongly associated with structural variables, whereas PIQ was more strongly associated with variables representing neural function. Additionally, a previous study suggested that caudate volume was associated with VIQ but not PIQ [Isaacs et al., 2008]. Our results conform to this pattern: VIQ was associated with caudate volume at a similar magnitude as IQ. PIQ, however, was only weakly associated with caudate volume, and the effect only became significant when constrained to be equal across samples (thereby increasing power). Based on these results, it would appear that caudate volume may be more strongly associated with VIQ than PIQ. One speculation is that this differentiation may be due

TABLE V. Partial correlations of Full Scale IQ, Performance IQ, and Verbal IQ with each subcortical structure and total brain volume, controlling for sex, age, and total brain volume

	Sample 1 ($N = 285$)		Sample 2 ($N = 125$)		Sample 3 ($N = 107$)	
	r	*P*	*r*	*P*	*r*	*P*
Full scale IQ						
Caudate	0.16	0.01	0.24	0.01	0.17	0.09
Putamen	0.06	0.31	0.03	0.78	0.19	0.05
NAcc	−0.04	0.56	0.09	0.32	0.17	0.08
Thalamus	−0.03	0.61	−0.06	0.50	0.01	0.96
Amygdala	0.04	0.34	0.12	0.18	0.10	0.33
Hippocampus	0.06	0.31	0.07	0.44	0.11	0.26
Pallidum	−0.06	0.35	0.17	0.06	−0.01	0.95
Total brain volume	0.28	<0.001	0.04	0.64	0.08	0.42
Performance IQ						
Caudate	0.06	0.29	0.19	0.16	0.11	0.26
Putamen	0.03	0.67	0.06	0.51	0.12	0.22
NAcc	−0.07	0.27	0.11	0.25	0.11	0.26
Thalamus	−0.12	0.05	0.01	0.93	0.07	0.50
Amygdala	0.07	0.27	−0.03	0.73	0.08	0.40
Hippocampus	0.07	0.26	0.05	0.57	0.11	0.25
Pallidum	−0.15	0.01	0.09	0.31	−0.06	0.54
Total brain volume	0.3	<0.001	0.04	0.70	0.04	0.69
Verbal IQ						
Caudate	0.17	0.003	0.18	0.04	0.16	0.08
Putamen	0.09	0.14	−0.02	0.82	0.20	0.04
NAcc	0.01	0.85	0.01	0.94	0.18	0.07
Thalamus	0.04	0.52	0.01	0.95	−0.06	0.55
Amygdala	0.02	0.77	0.02	0.86	0.08	0.42
Hippocampus	0.04	0.54	0.07	0.47	0.08	0.44
Pallidum	−0.01	0.86	0.10	0.28	0.05	0.60
Total brain volume	0.18	0.003	0.04	0.69	0.10	0.34

Note. Correlations with total brain volume do not control for total brain volume.
NAcc, nucleus accumbens.

to the importance of caudate-mediated reinforcement learning during language acquisition.

Finally, our findings appear to be specific to the caudate, as no other subcortical structure was consistently related to intelligence. This was not a predicted finding, and it appears to contradict studies that have implicated the volume of other subcortical structures in intelligence [e.g., Amat et al., 2008; Schumann et al., 2007]. Findings may differ across studies for many reasons, including differing methods, differing populations, and small sample size (leading to low power and increased sampling variability). Because our sample was larger than most prior relevant studies, our study was less likely to produce false positive results. Nonetheless, we do not claim that our findings rule out the involvement of other subcortical structures in intelligence, and studies assessing brain function or other structural parameters might well establish such involvement in future research.

CONCLUSION

This study provides the first report of a positive association between bilateral caudate volume and IQ, in three large, independent, nonclinical adult samples. Constraining the effect of caudate volume to be equal across all three samples produced a well-fitting model and suggested that caudate volume accounts for somewhere between 2.4% and 4.3% of variance in IQ. Due to the fact that the present analyses are purely correlational, determining the specific mechanisms that account for the association between intelligence and caudate volume is an important goal of future research.

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