Neural sensitivity to eudaimonic and hedonic rewards differentially predict adolescent depressive symptoms over time

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The pursuit of happiness and reward is an impetus for everyday human behavior and the basis of well-being. Although optimal well-being may be achieved through eudaimonic activities (e.g., meaning and purpose), individuals tend to orient toward hedonic activities (e.g., pleasure seeking), potentially placing them at risk for ill-being. We implemented a longitudinal study and followed adolescents over 1 y to examine whether neural sensitivity to eudaimonic (e.g., prosocial decisions) and hedonic (e.g., selfish rewards and risky decisions) rewards differentially predicts longitudinal changes in depressive symptoms. Ventral striatum activation during eudaimonic decisions predicted longitudinal declines in depressive symptoms, whereas ventral striatum activation to hedonic decisions related to longitudinal increases in depressive symptoms. These findings underscore how the motivational context underlying neural sensitivity to rewards can differentially predict changes in well-being over time. Importantly, to our knowledge, this is the first study to show that striatal activation within an individual can be both a source of risk and protection.

adolescence | fMRI | depression

The pursuit of happiness and reward is an impetus for everyday human behavior and the basis of well-being (1). In the fourth century B.C., Aristotle distinguished between two aspects of well-being: hedonia (pleasure, desire) and eudaimonia (meaning and purpose, a life well-lived). Aristotle argued that optimal well-being is achieved through eudaimonia, whereas pleasure and desire can be harmful to human growth (2). Contemporary psychological research has continued to distinguish between eudaimonic well-being and hedonic well-being, (e.g., refs. 3 and 4), with empirical studies demonstrating the long-term benefits of eudaimonic pursuits and the sometimes detrimental effects of hedonic pursuits (e.g., ref. 5). Whereas the distinction between hedonic and eudaimonic rewards has received theoretical and empirical attention in adult work, we know little about how these two types of rewards are experienced during adolescence, a developmental period during which rewards take on particular salience and vulnerability for ill-being dramatically rises (6).

Neural systems involved in the generation of reward processing undergo significant changes during adolescence, resulting in a greater orientation toward rewards (6). Adolescents, more so than children or adults, show heightened activation in brain regions involved in reward processing when receiving rewards (7). Although some types of reward-seeking behaviors may be adaptive during this developmental period (e.g., engaging in meaningful social relationships), other types of reward-seeking behaviors may be detrimental (e.g., engaging in health-compromising risk taking). Therefore, the ways in which adolescents respond to different rewards may have significant implications for their well-being. In the current study, we examined how neural sensitivity to hedonic and eudaimonic rewards differentially predicts changes in adolescents' depressive symptoms over

time. Examining how alterations in reward processing to different types of rewards relate to depression is an important, but understudied avenue. Because depressive symptoms rise dramatically during adolescence, peaking around 17–18 y (8), it is essential to examine the neural antecedents that predict risk or protection for depressive symptoms during this vulnerable developmental period.

Eudaimonic rewards include helping others in need, expressing gratitude, and working toward long-term goals (5). One important type of eudaimonic behavior is the engagement in prosocial, helping behaviors. Behavioral research in adolescents and adults has found that prosocial behaviors to help strangers, friends, family members, or charities are related to feelings of happiness and meaning (9–11). Eudaimonic rewards are intrinsically meaningful, provide a sense of belonging and social connection, and therefore lead to long-term well-being (5). It is through eudaimonic activities that individuals build resources, such as feelings of mastery, competence, fulfillment, and improved social relationships (5). Thus, adolescents with high levels of eudaimonic rewards may develop long-lasting psychological and social resources, leading to more resilience and better well-being.

Hedonic rewards tend to be more extrinsically rewarding and self-focused, including food consumption, playing video games, going shopping for oneself, and musical pleasures, but also can involve risky behaviors, including sexual exploration and getting

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drunk or high (5, 12). Hedonic rewards become highly relevant during adolescence, during which time adolescents engage in more risk-taking behaviors than children or adults (13, 14), and tend to be more impulsive and oriented toward immediate hedonic rewards than to longer-term, more valuable rewards (15). Hedonic rewards provide short-term feelings of happiness and satisfaction, but such positive affect tends to dissipate more quickly than eudaimonic rewards (5, 12, 16, 17). Moreover, many theorists maintain that pleasure-seeking behaviors are not necessarily good for the individual and therefore do not promote positive, enduring well-being. In fact, in some cases, the pursuit of hedonic rewards can be detrimental to well-being, such as sensation seeking, which can result in health-compromising risky behaviors (17).

Whereas eudaimonic activities relate to higher levels of meaning and purpose in youths' and adults' daily lives, hedonic activities relate to lower levels of meaning. For example, daily diary research of adolescents (11) and adults (5) shows that meaning and purpose increase following eudaimonic activities, such as helping the family (e.g., taking care of brothers and sisters), engaging in extracurricular activities (e.g., community service), and expressing gratitude, whereas hedonic, activities—such as pleasurable leisure time (e.g., watching television or talking on phone with friends), having sex for pleasure, or getting drunk or high—relate to lower meaning and purpose (5, 11). The presence of meaning in adolescents' life is associated with a host of positive indices of well-being, including higher self-esteem, higher happiness, lower distress, lower anxiety, and greater academic motivation (11, 18). These findings underscore the importance of eudaimonic activities in youths' daily lives and the potential negative implications of hedonic activities. Although hedonic rewards are not ubiquitously negative, they do not entail meaning and purpose that provide long-term, enduring well-being.

Although hedonic and eudaimonic rewards differentially relate to well-being, adult work suggests that both types of rewards are correlated aspects of experience (5). Indeed, affective neuroscience has identified key brain mechanisms involved in the experience of reward processing, and both eudaimonic and hedonic rewards are associated with activation in the same neural circuitry, in particular, the ventral striatum, a key brain region consistently linked with the experience of pleasure or "liking" (1). Importantly, "liking" can be measured objectively through neural responses, whether or not the individual is consciously aware of their feelings of pleasure (1). For example, human and rodent research has shown that adolescents, more so than children or adults, show heightened activation in the ventral striatum following the receipt of hedonic rewards, including money, sucrose, and immediate rather than long-term rewards (7, 15, 19, 20). Moreover, during risk taking, adolescents show higher activation in the ventral striatum than younger or older individuals (21). Adolescents and adults also show heightened activation in the ventral striatum to eudaimonic rewards, such as prosocial decisions to help family, friends, or charities (22–27). Moreover, adolescents who report a greater sense of meaning from helping their family on a daily basis show heightened activation in the ventral striatum when making personal sacrifices for their family (26), highlighting how prosocial behaviors can relate to feelings of eudaimonic reward.

Rewards take on particular salience during adolescence (6). Neural regions underlying reward processing undergo significant changes, increasing susceptibility to dopaminergic dysregulation and risk for affective disorders, such as depression (28). Perhaps because of this social reorientation of the adolescent brain around the time of puberty (6), the meaning and qualitative nature of rewards changes when adolescents become increasingly motivated by more distal and abstract rewards, such as love, belonging, and status (29). Vulnerability to depression is thought to arise as a result of the unstable nature of rewards that are encoded during adolescence (29). Therefore, the ways in which

adolescents respond to rewards can have significant implications for their well-being. Longitudinal research is essential to examine whether differential neural sensitivity to eudaimonic and hedonic rewards predicts changes in depressive symptoms.

In the current study, we followed adolescents over a 1-y period to examine whether ventral striatum activation to eudaimonic and hedonic rewards differentially predicts longitudinal changes in depressive symptoms. Adolescents underwent a functional brain scan during which they completed two tasks. During the first task, participants made two types of decisions: prosocial decisions to donate money to their family (eudaimonic decisions) and selfish decisions to keep money for themselves (hedonic decisions) (Fig. 1) (27). The hedonic decisions in this task did not involve risk or uncertainty and closely approximate basic hedonic pleasure to gain known rewards for the self. In the second task, participants made risky, uncertain decisions to gain monetary rewards during a risk-taking task (Fig. 2) (30). This task allowed us to examine hedonic pleasure to uncertain rewards for the self that closely approximate risk-taking in real life, when the probabilities of risk are unknown. At the time of the scan and 1 y following the scan, adolescents completed a self-report measure of their depressive symptoms (31). We performed region of interest (ROI) analyses with the ventral striatum, which was structurally defined (Fig. 3), to examine how striatal response to prosocial eudaimonic decisions, selfish hedonic decisions, and risky hedonic decisions differentially predicted changes in adolescents' depressive symptoms over time. For whole-brain results of the main effects on each task, see the *Supporting Information*.

Results

Changes in Depressive Symptoms. Analyses examined adolescents' depressive symptoms at time 1 (T1) as well as changes in symptoms from T1 to T2 (1 y later). Participants' scores at T1 reflect their concurrent depressive symptoms. Scores at T2 after controlling for T1 (i.e., residualized score) reflect changes (increases or decreases) in participants' depressive symptoms over the following year. Adolescents did not show mean level increases or decreases in depressive symptoms from T1 (M = 14.05, SD = 8.09) to T2 (M = 13.49, SD = 9.55), $t(38) = 0.49$, not significant (ns). Depressive symptoms at T1 were highly correlated with symptoms at T2, $r(39) = 0.68$, $P < 0.001$. There was variability in this association, such that some adolescents' depressive symptoms declined whereas others' increased. The residualized scores for T2 depressive symptoms show values that range from −19.83 (decline in depressive symptoms) to +16.15 (increase in depressive symptoms).

Males (M = 13.4, SD = 8.8) and females (M = 14.6, SD = 7.0) did not differ in depressive symptoms at T1. A marginally significant sex difference emerged for changes in depressive symptoms, such that females showed slight increases in depressive
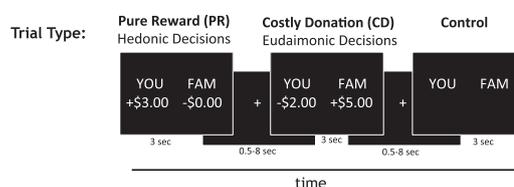
Fig. 1. Example trials from the family donation task. During PR trials, participants could choose to accept a monetary reward for themselves at no cost to their family. During CD trials, participants could choose to donate money to their family at a cost to themselves. Analyses focused on neural activation when making a donation to the family that involves self-sacrifice, a behavior that most closely approximates prosocial, eudaimonic behavior. CD trials were contrasted to PR trials, which approximate selfish hedonic rewards for the self. During control trials, participants made a button response, but no financial decisions were made.
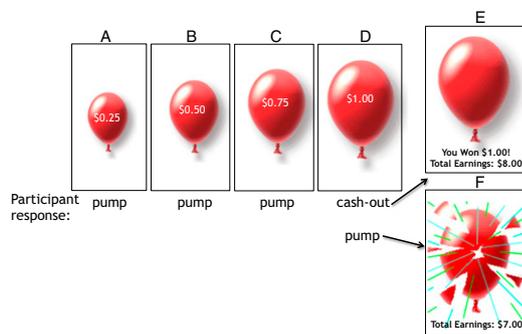
Fig. 2. Balloon Analog Risk Task. On each trial of the task, participants are shown a virtual balloon. Participants can make one of two button responses: pump or cash-out. For every decision to pump the balloon, participants earn a monetary reward (*A*–*D*). At any point the participant can choose to cash-out and keep the accumulated earnings (*E*). If the participant pumps the balloon too large, the balloon may explode, and the participant will earn no money for that trial (*F*).

symptoms from T1 to T2 (M = 1.6, SD = 6.8), whereas males showed slight decreases in depressive symptoms [M = −2.3, SD = 6.9; $t(37) = 1.78$, $P = 0.084$]. We therefore controlled for sex in all subsequent analyses.

Ventral Striatum Activation to Eudaimonic Rewards and Links to Depressive Symptoms. *Time 1 depressive symptoms.* Our first set of analyses examined striatum activation during the family donation task. Parameter estimates of signal intensity from the ventral striatum ROI during Costly Donation > Pure Reward (CD > PR) trials were regressed onto T1 depressive symptoms. Depressive symptoms were not associated with activation in ventral striatum during CD > PR decisions. In addition, when each condition was compared with the control, T1 depressive symptoms were not associated with ventral striatum activation during CD > Control or PR > Control.

Longitudinal changes in depressive symptoms. Next, we tested how ventral striatum activation during the family donation task correlated with longitudinal changes in depressive symptoms. We regressed ventral striatum activation during CD > PR trials onto the residualized scores for T2 depressive symptoms, controlling for sex. Ventral striatum activation was significantly associated with longitudinal declines in depressive symptoms ($\beta = -0.50$, $P = 0.002$). As shown in Fig. 4*A*, adolescents who demonstrated the greatest ventral striatum activation to CD decisions relative to PR decisions demonstrated the greatest declines in depressive symptoms over time.

To examine whether this protective effect was being driven by the differential effect between eudaimonic and hedonic rewards (i.e., adolescents who show greater ventral striatum activation to family donations relative to personal rewards) or whether each type of reward independently predicted changes in symptoms (i.e., higher activation in the ventral striatum to eudaimonic rewards is protective regardless of the level of activation in the ventral striatum to hedonic rewards), we examined how depressive symptoms were associated with CD and PR trials separately. In a multiple regression analysis, we regressed activation from the ventral striatum ROI to CD > Control decisions and PR > Control decisions simultaneously onto changes in depressive symptoms. Whereas adolescents who showed heightened striatal response during CD decisions showed longitudinal declines in depressive symptoms ($\beta = -0.47$, $P = 0.01$), adolescents who showed heightened activation during PR decisions showed longitudinal increases in depressive symptoms ($\beta = 0.63$, $P = 0.008$) (Fig. 4*B*).

Ventral Striatum Activation to Hedonic, Risky Rewards and Links to Depressive Symptoms. *Time 1 depressive symptoms.* Our second set of analyses examined striatal response during the risk-taking task. The analysis for risky decisions included a parametric modulator that represented the pump number, with greater pumps being linearly weighted higher, indicating greater riskiness with greater pumps. Therefore, this analysis is tracking brain activation that is linearly increasing with riskiness. Parameter estimates of signal intensity from the ventral striatum ROI during increasing risky decisions were regressed onto T1 depressive symptoms. Depressive symptoms at T1 were not associated with activation in the ventral striatum.

Longitudinal changes in depressive symptoms. Next we examined whether ventral striatum activation during the risk-taking task predicted longitudinal changes in depressive symptoms. Parameter estimates of signal intensity from the ventral striatum ROI during risky decisions were regressed onto the residualized scores for T2 depressive symptoms. Striatal response during increasing risks was significantly association with longitudinal increases in depressive symptoms ($\beta = 0.43$, $P = 0.006$) (Fig. 5).

Ventral Striatum Activation to Hedonic and Eudaimonic Rewards Independently Predict Changes in Depressive Symptoms. Finally, we examined whether adolescents' ventral striatum activation to eudaimonic and hedonic rewards shared variance in depressive symptoms or whether they uniquely contributed to changes in depressive symptoms. First, we correlated striatal activation during CD > Control, PR > Control, and risky decisions. Striatal response during CD trials was not correlated with striatal response during risky decisions ($r = 0.04$, ns) or PR trials ($r = -0.04$, ns). Striatal response during the two hedonic conditions (PR and risky decisions) were correlated ($r = 0.38$, $P = 0.04$). Next, we ran regression analyses in which we simultaneously regressed ventral striatum activation during eudaimonic rewards and ventral striatum activation during hedonic rewards onto changes in depressive symptoms. Striatal response from CD > Control, PR > Control, and risky decisions were regressed onto depressive symptoms, controlling for sex. Results show that striatal activation during each condition independently predicted changes in depressive symptoms (CD > Control: B = −5.3, SE = 1.8, $\beta = -0.42$, $P = 0.006$; PR > Control: B = 2.8, SE = 0.98, $\beta = 0.38$, $P = 0.01$; Risky Decisions: B = 5.5, SE = 2.5, $\beta = 0.30$, $P = 0.04$). Taken together these results show that ventral striatum activation to eudaimonic and hedonic rewards account for 58% of the variance in T2 depressive symptoms (controlling for T1 symptoms), with sex accounting for an additional but nonsignificant 1% of variance.

Discussion

The pursuit of rewards and attainment of well-being is perhaps the most important motivation in individuals' lives, especially during adolescence, a time when rewards take on particular salience and vulnerability for ill-being dramatically rises. Whereas optimal well-being may be achieved through eudaimonic activities
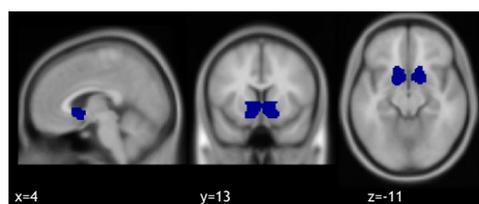

Fig. 3. Ventral striatum ROI. Statistical analyses were performed by extracting the parameter estimates of signal intensity from the ventral striatum for each contrast of interest. ROI analyses were performed at a threshold of $P < 0.05$, corrected for multiple comparisons.

Fig. 4. (*A*) Adolescents who showed greater activation in the ventral striatum when making eudaimonic decisions compared with pure hedonic decisions demonstrated longitudinal decreases in depressive symptoms over the following year. Note that negative values on the *y* axis represent declines in depressive symptoms, whereas positive values indicate increases in depressive symptoms. (*B*) Adolescents who showed heightened activation in the ventral striatum during eudaimonic decisions showed longitudinal decreases in depressive symptoms over the following year, and adolescents who showed heightened activation in the ventral striatum when making pure hedonic decisions demonstrated longitudinal increases in depressive symptoms over the following year.

(2), individuals tend to engage in more hedonic activities, potentially placing them at risk for ill-being (5). In the present study, we used brain imaging techniques and demonstrated that ventral striatum activation to eudaimonic decisions predicted longitudinal declines in depressive symptoms, whereas ventral striatum activation to hedonic decisions predicted longitudinal increases in depressive symptoms. These findings underscore how the motivational context underlying neural sensitivity to rewards can differentially predict changes in well-being over time.

We found that adolescents who showed stronger activation in the ventral striatum when making prosocial decisions for their family showed longitudinal declines in depressive symptoms. Interestingly, striatal response to eudaimonic decisions was not associated with depressive symptoms at T1. Therefore, neural sensitivity to eudaimonic rewards does not relate to immediate well-being but, rather, predicts changes in depressive symptoms over time. Thus, our striatal response to eudaimonic rewards may represent a motivational orientation toward engaging in inherently meaningful activities that may increase feelings of value, meaningfulness, and intrinsic reward, therefore providing psychological and social resources and leading to better well-being over time. This finding is consistent with theories of eudaimonic well-being, which suggest that through eudaimonic activities, individuals build resources, such as feelings of mastery, competence, fulfillment, and improved social relationships, and are more likely to develop enduring well-being (5).

In contrast, we found that ventral striatum activation during both pure rewards and uncertain risky rewards related to longitudinal increases in depressive symptoms. Although striatal responses during each type of hedonic reward were correlated, they each independently predicted increases in depressive symptoms, highlighting that they are tapping unique and important psychological processes. Therefore, the experience of pleasure during the receipt of pure rewards and risk taking may not be connected to deeper psychological processes, and striatal response to such immediate rewards may represent a poor long-term strategy for achieving enduring well-being (5). Taken together, our findings suggest that well-being may depend on attending to higher values related to family, culture, and morality, rather than to immediate, selfish pleasure (1). Given the differential, yet independent, nature of eudaimonic and hedonic rewards, finding ways for adolescents to engage in meaningful, eudaimonic activities could provide protection against developing ill-being, even if they are also oriented toward hedonic activities. Adolescents may not be able to consciously control the degree to which they experience pleasure from

eudaimonic versus hedonic pursuits. Rather, the ways in which they respond to rewards may function at an unconscious and uncontrollable level or may be fixed by one's genes, gene expression, or other aspects of one's current biological milieu (e.g., inflammation). Therefore, providing more opportunities for adolescents to engage in activities that cultivate eudaimonic feelings, rather than attempting to change how adolescents process rewards, may be a promising direction by which to reduce ill-being in adolescents. It is important to note that we did not find an association between eudaimonic and hedonic rewards, which is likely a byproduct of the experimental tasks, and less reflective of real-world experiences, as empirical and theoretical work in adults suggests that the two types of rewards are correlated aspects of experience (5).

Interestingly, we found that ventral striatum activation to eudaimonic and hedonic rewards was not associated with depressive symptoms at T1 but rather to changes in long-term well-being. These findings suggest that the neural responses are likely

Fig. 5. Adolescents who showed heightened activation in the ventral striatum during increasing hedonic risky decisions demonstrated longitudinal increases in depressive symptoms over the following year. Note that the *x* axis represents ventral striatum activation during risk taking, where the level of risk is parametrically modulated and mean centered. Values around 0 on the *x* axis therefore represent striatal response to the mean level of risk, positive scores indicate striatal response to higher than average risk, and negative scores indicate striatal response to lower than average risk.

not capturing trait-level personality characteristics but rather individual differences in long-term behavioral strategies that lead to changes in symptomology. For example, adolescents who show heightened activation in the ventral striatum during eudaimonic decisions likely experience a sense of reward from supporting their family and may therefore show increases in the time they spend helping their family. We have previously found that adolescents who help their family more and report a greater sense of meaning and happiness from that support show heightened activation in the ventral striatum when making eudaimonic decisions for their family (26). Thus, consistent with theories of eudaimonic well-being (5), by engaging in and experiencing reward from eudaimonic pleasures, adolescents can build resources, such as feelings of meaning, happiness, and improved social relationships, and are therefore more likely to develop enduring well-being.

Recently, attention has been paid to the meaning of reward-related neural sensitivity during adolescence: Is more or less activation good (32)? Although traditional views suggested that heightened reward sensitivity in adolescence places youth at risk for negative developmental outcomes, some recent work has demonstrated the potential protective role that striatal activation can serve (e.g., refs. 27 and 33). The current findings highlight the importance of the context in which reward-related neural activation occurs. Heightened striatal response in the context of risk taking or the attainment of personal monetary rewards may be maladaptive, relating to increases in depressive symptoms, whereas heightened striatal response in the context of prosocial family decisions can be adaptive, relating to declines in depressive symptoms. These findings are consistent with models suggesting that reward-related neural regions undergo significant changes during adolescence, resulting in a greater sensitivity to the attainment of rewards (6). Rather than this reward sensitivity being monolithically negative, our findings highlight that the ways in which adolescents respond to different types of rewards can have significant implications for their health and attainment of well-being. Future research should continue to pay close attention to the social and motivational context in which neural activation occurs. A strong striatal response may be a risk factor in one context but a protective factor in another. Finally, it is important that future research replicate these findings in a larger sample size as well as across other tasks that tap other aspects of eudaimonic and hedonic rewards.

In summary, to our knowledge this is the first study to test the differential roles of eudaimonic and hedonic sensitivity in youth. We identified a potential neural mechanism by which adolescents may develop or be protected from developing ill-being over time. Rewards are salient and important during adolescence, and the ways in which youth respond to different rewards can have significant implications for their attainment of well-being over time.

Methods

Participants. Adolescents provided written assent and their primary caregiver provided written consent in accordance with the University of California, Los Angeles Institutional Review Board. The present study used a longitudinal design across 2 y in high school. At Time 1 (T1), 47 adolescents ranging in age from 15 to 17 y (M_{age} = 16.3 y; 20 males, 27 females) completed measures of their depressive symptoms and underwent a brain scan during which they completed a family donation task and a risk-taking task. One year later (T2), 39 adolescents (M_{age} = 17.1 y, 16 males, 23 females) completed the self-report measure of their depressive symptoms again.

Depressive Symptoms. Adolescents completed the internalizing symptoms subscale of the Youth Self-Report form of the Child Behavior Checklist (31), a widely used measure to examine depressive symptoms in youth. At both time points, adolescents rated 31 items on a 3-point scale (0 = not true of me, 1 = somewhat or sometimes true of me, 2 = true or often true of me) tapping anxious, somatic, and withdrawn symptoms (e.g., "I cry a lot," "I worry a lot," "I don't have much energy").

Functional MRI Paradigms. *Family donation task.* To examine ventral striatum activation to prosocial, eudaimonic rewards, we used a family donation task (27). Participants could earn money for themselves and their families by responding to a series of financial offers that varied in terms of whether they represented gains or losses for the participants and their families. During PR trials, participants could choose to gain money without a cost to their family (e.g., YOU earn $3.00, FAMILY loses $0.00). During CD trials, participants could choose to donate money to their family at a cost to themselves (e.g., YOU lose $1.00, FAMILY earns $2.00). There were also Pure-Donations and Costly Rewards, which we don't report in this study. We focused on the contrast between CD and PR, which allowed us to focus on neural activation when making a donation to the family that involves self-sacrifice, a behavior that most closely approximates prosocial, eudaimonic behavior. CDs were contrasted to PRs, which approximate selfish hedonic rewards for the self.

Participants played two runs of the family donation task, which included 56 unique payment trials presented once per run, totaling 112 payment trials (40 costly donations, 24 pure donations, 24 pure rewards, 24 costly rewards). In addition, there were 24 trials to control for the visual and motor aspects of the task, in which YOU and FAM were presented without a financial gain or loss. For these control trials, participants were instructed to press either button, and it would not affect their payments. Trial order was randomized for each participant. Each payment offer was presented for 3 s, followed by a fixation for an intertrial period that was jittered, lasting 3 s on average (range = 0.5–8 s). The financial values of the offers ranged in value from −$3.00 to +$7.00, as well as in the ratio of loss:gain to reduce heuristic responding and fatigue (22, 34). Participants were not shown the running total of their own or their family's earnings. Participants who accepted fewer than seven trials for any condition were excluded from the analyses because of low statistical power (n = 7). At the end of the task, participants and their family were paid their earnings in cash. [Note that the main effects of this task have been reported previously, as well as links to externalizing symptoms (27).]

Risk-taking task. To examine ventral striatum sensitivity to hedonic, risk-taking behaviors, participants completed the Balloon Analog Risk Task (BART) (31). On each trial of the task, participants were shown a virtual balloon and given the option to inflate the balloon, which can either grow larger or explode. The larger the balloon is inflated, the greater the monetary reward but the higher the probability of explosion. Participants pressed one of two buttons to either inflate the balloon or "cash-out." Each trial began with the presentation of a balloon and ended when the balloon either exploded or the participant chose to cash-out. The participant received a cash payoff (25 cents) for each pump on which the balloon was successfully inflated and could stop inflating the balloon at any point and keep the accumulated payoff. If the balloon exploded before cashing out, the participant received no payoff for that trial, but earnings from the previous trials were not affected. The number of inflations before explosion varied probabilistically according to a Poisson distribution, which models the unpredictable rewards and punishments that characterize real-world risky behaviors. As pumping progressed during a trial, explosion probability increased exponentially. The explosion point of each balloon was drawn from a uniform distribution from 1 to 12 pumps. Thus, with increasing pumps, each decision became more and more risky. The task was self-paced, and was performed during one 9-min run. Participants received their total earnings in cash at the end of the task. [Note the main effects of this task have been reported previously, as well as links to family values (35) and sleep (36).]

Functional MRI Data Acquisition and Analysis. *Functional MRI data acquisition.* Imaging data were collected using a 3 Tesla Siemens Trio MRI scanner. The family donation and risk-taking tasks were completed in counterbalanced order across participants. The family donation task consisted of 342 functional T2*-weighted echoplanar images (EPI) (slice thickness = 4 mm; 34 slices; TR = 2 s; TE = 30 ms; flip angle = 90°; matrix = 64 × 64; FOV = 200 mm; voxel size 3 × 3 × 4 mm^3). A T2*weighted, matched-bandwidth (MBW), high-resolution, anatomical scan and magnetization-prepared rapid-acquisition gradient echo (MPRAGE) scan were acquired for registration purposes (TR = 2.3; TE = 2.1; FOV = 256; matrix = 192 × 192; sagittal plane; slice thickness = 1 mm; 160 slices). The orientation for the MBW and EPI scans was oblique axial to maximize brain coverage.

Functional MRI data preprocessing and analysis. Neuroimaging data were preprocessed and analyzed using Statistical Parametric Mapping (SPM8; Wellcome Department of Cognitive Neurology, Institute of Neurology, London, United Kingdom). Preprocessing for each participant's images included spatial realignment to correct for head motion (no participant exceeded 2 mm of maximum image-to-image motion in any direction). The realigned

functional data were coregistered to the high-resolution MPRAGE, which was then segmented into cerebrospinal fluid, gray matter, and white matter. The normalization transformation matrix from the segmentation step was then applied to the functional and T2 structural images, thus transforming them into standard stereotactic space as defined by the Montreal Neurological Institute and the International Consortium for Brain Mapping. The normalized functional data were smoothed using an 8-mm Gaussian kernel, full-width-at-half maximum, to increase the signal-to-noise ratio.

Statistical analyses were performed using the general linear model in SPM8. Each trial was convolved with the canonical hemodynamic response function. High-pass temporal filtering with a cutoff of 128 s was applied to remove low-frequency drift in the time series. Serial autocorrelations were estimated with a restricted maximum-likelihood algorithm with an autoregressive model order of 1. The family donation task was modeled as an event-related design with linear contrasts comparing CD to PR for each participant. Events were modeled with a 3-s duration beginning with the appearance of the payment screen. The BART was modeled as an event-related design and included multiple regressors for each event type: pumps, cash-outs, and explosions. For the pumps, we analyzed the adjusted pumps, which represent the number of pumps on balloons that did not explode. This approach is preferable to examining pumps on balloons that did explode, because the number of pumps is necessarily constrained on balloons that explode (30). Pumps, cash outs, and explosions were modeled with a parametric regressor that tested for the linear relationship between brain activation and the magnitude of pumps, reward, or loss. We used pump number as a parametric modulator, with each pump in a trial assigned a weight that increased linearly across pumps within a trial. On cash-out trials, and explosions, this number represented how many pumps occurred before the cash-out or explosion. The number of pumps was demeaned by subtracting the mean number of pumps from each pump number within the trial. Because the task was self-paced, the duration of each trial represented the reaction time for that trial. For both tasks, null events, consisting of the jittered intertrial intervals, were not explicitly modeled and therefore constituted an implicit baseline.

The individual subject contrasts were submitted to random-effects, group-level analyses. At the group-level, we ran ROI analyses focusing on the ventral striatum, a brain region that has consistently been associated with reward processing in adolescence (7). Moreover, we have previously reported in the same sample of participants using each of the tasks in the current study that prosocial family donations and risky decisions engage the ventral striatum (27, 35). The striatum was anatomically defined using the WFU Pick Atlas (37–39). As shown in Fig. 2, the ventral striatum was defined as the medial portion of the ventral striatum which was defined below $z = 2$, and medial of $x = -13$ to $+13$. Statistical analyses were performed by extracting the parameter estimates of signal intensity from the ventral striatum for each contrast of interest using the MarsBaR ROI analysis tool in SPM8 (MARSeille Boîte À Région d'Intérêt) (40), in which the activations for each of the voxels within the ROI were averaged to produce a single estimate of activity for each participant. ROI analyses were performed at a threshold of $P < 0.05$, corrected for multiple comparisons.

Analyses examining ventral striatum activation during the family donation task included 40 participants at T1 (seven participants were excluded due to too few trials for analysis), and 32 participants at T2 (an additional eight participants did not provide T2 data). Analyses examining ventral striatum activation during the risk taking task included all 47 participants at T1 and 39 participants at T2 (nine participants did not provide T2 data). Each set of analyses described below used all participants available for the analysis. Analyses examining only those with complete data for all measures and tasks ($n = 32$) did not differ. Therefore, whenever possible we report results for the more complete sample.

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