esized that endophytes may protect their host plants by scavenging the damaging reactive oxygen species (ROS) generated by the plant defense mechanisms in response to environmental stress (*15*). The leaves of nonsymbiotic plants generated detectable ROS when stressed with heat, whereas those of symbiotically colonized plants did not (table S1). However, there was no difference in the ROS response to heat between plants inoculated with the virus-free and the CThTV-infected isolates of *C. protuberata*.

Complex tripartite symbioses have been found among arthropods, bacteria, and mutualistic bacteriophages (*16*, *17*). This study reports a three-way mutualistic symbiosis involving a virus, a fungal endophyte, and either a monocot or eudicot plant.

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Materials and Methods
Figs. S1 to S5
Table S1
References

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The Neural Basis of Loss Aversion in Decision-Making Under Risk

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People typically exhibit greater sensitivity to losses than to equivalent gains when making decisions. We investigated neural correlates of loss aversion while individuals decided whether to accept or reject gambles that offered a 50/50 chance of gaining or losing money. A broad set of areas (including midbrain dopaminergic regions and their targets) showed increasing activity as potential gains increased. Potential losses were represented by decreasing activity in several of these same gain-sensitive areas. Finally, individual differences in behavioral loss aversion were predicted by a measure of neural loss aversion in several regions, including the ventral striatum and prefrontal cortex.

Many decisions, such as whether to invest in the stock market or to accept a new job, involve the possibility of gaining or losing relative to the status quo. When faced with such decisions, most people are markedly risk averse. For instance, people typically reject gambles that offer a 50/50 chance of gaining or losing money, unless the amount that could be gained is at least twice the amount that could be lost (e.g., a 50/50 chance to either gain $100 or lose $50) (*1*). Prospect theory, the most successful behavioral model of decision-making under risk and uncertainty (*1*, *2*), explains risk aversion for "mixed" (gain/loss) gambles using the concept of loss aversion: People are more sensitive to the possibility of losing objects or money than they are to the possibility of gaining the same objects or amounts of money (*1*, *3*–*5*). Thus, people typically require a potential gain of at least $100 to make up for exposure to a potential loss of $50 because the subjective impact of losses is roughly twice that of gains. Similarly, people demand substantially more money to part with objects that they have been given than what they would have been willing to pay to acquire those objects in the first place (*6*). Loss aversion also has been used to explain a wide range of economic behaviors outside the laboratory (*7*, *8*). Further, loss aversion is seen in trading behavior of both children as young as age five (*9*) and capuchin monkeys (*10*), which suggests that it may reflect a fundamental feature of how potential outcomes are assessed by the primate brain.

Previous neuroimaging studies of responses to monetary gains or losses have focused on activity associated with the anticipation of immediate outcomes ("anticipated" utility) (*11*, *12*) or the actual experience of gaining or losing money ("experienced" utility) (*11*, *13*, *14*) rather than specifically investigating which brain systems represent potential losses versus gains when a decision is being made ("decision" utility). Behavioral researchers have shown that anticipated, experienced, and decision utilities often diverge in dramatic ways, which raises the possibility that the corresponding brain systems involved may also differ (*15*). In the current study, we aimed to isolate activity associated with the evaluation of a gamble when choosing whether or not to accept it (i.e., decision utility) without the expectation that the gamble would be immediately resolved. This allowed us to test whether neural responses during the evaluation of potential outcomes are similar to patterns previously reported in studies of anticipated and experienced outcomes.

One fundamental question for the study of decision-making is whether loss aversion reflects the engagement of distinct emotional processes when potential losses are considered. It has been suggested that enhanced sensitivity to losses is driven by negative emotions, such as fear or anxiety (*16*). This notion predicts that exposure to increasing potential losses should be associated with increased activity in brain structures thought to mediate negative emotions in decision-making [such as the amygdala or anterior insula; compare with (*17*, *18*)]. Alternatively, loss aversion could reflect an asymmetric response to losses versus gains within a single system that codes for the subjective value of the potential gamble, such as ventromedial prefrontal cortex (VMPFC)/orbitofrontal cortex (OFC) and ventral striatum (*11*, *19*, *20*).

To examine the neural systems that process decision utility, we collected functional magnetic resonance imaging (fMRI) data while partici-

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pants decided whether to accept or reject mixed gambles that offered a 50/50 chance of either gaining one amount of money or losing another amount (Fig. 1A) (*21*). To encourage participants to reflect on the subjective attractiveness of each gamble rather than to rely on a fixed decision rule, we asked them to indicate one of four responses to each gamble (strongly accept, weakly accept, weakly reject, and strongly reject). In order to allow for separate estimates of neural responses to gains and losses, the sizes of the potential gain and loss were manipulated independently, with gains ranging from $10 to $40 (in increments of $2) and losses ranging from $5 to $20 (in increments of $1). We chose these ranges because previous studies indicate that people are, on average, roughly twice as sensitive to losses as to gains (*1*, *5*); thus, we expected that, for most participants, this range of gambles would elicit a wide range of attitudes, from strong acceptance to indifference to strong rejection. To introduce incentive-compatible payoffs, we endowed participants with $30 one week before scanning and told participants that one decision from each of three scanning runs would be honored for real money.

We assessed behavioral sensitivity to gains and losses by fitting a logistic regression to each participant's acceptability judgments collected during scanning, using the size of the gain and loss as independent variables. Based on this analysis, we computed a measure of behavioral loss aversion λ as the ratio of the (absolute) loss response to the gain response, which yielded a median $\lambda = 1.93$ (range: 0.99 to 6.75). This finding is consistent with the observations that participants were, on average, indifferent to gambles in which the potential gain was twice the amount of the potential loss (Fig. 1B) and that participants were slower to decide whether or not to accept these gambles (Fig. 1C). These behavioral data also accord well with previous findings (*1*, *5*).

We first analyzed the imaging data to identify brain regions whose activation correlated with the size of the potential gain or loss, using parametric regressors (*21*). This analysis isolated a set of regions responsive to the size of potential gains when evaluating gambles (averaging over levels of loss) (Fig. 2 and fig. S2). The gain-responsive network included regions previously shown to be associated with the anticipation and receipt of monetary rewards, including the dorsal and ventral striatum, VMPFC, ventrolateral PFC, anterior cingulate cortex (ACC), OFC, and dopaminergic midbrain regions. There were no regions that showed decreasing activation as gains increased.

If loss aversion is driven by a negative affective response (e.g., fear, vigilance, discomfort), then one would expect increasing activity in brain regions associated with these emotions as the size of the potential loss increases. Contrary to this prediction, no brain regions showed significantly increasing activation during evaluation of gambles as the size of the potential loss increased (averaging over all levels of gain). Instead, a group of brain regions including the striatum, VMPFC, ventral ACC, and medial OFC, most of which also coded for gains, showed decreasing activity as the size of the potential loss increased (Fig. 2 and fig. S3). A conjunction analysis between increasing activity for gains and decreasing activity for losses demonstrated joint sensitivity to both gains and losses in a set of regions, including the dorsal and ventral striatum and VMPFC (Fig. 3 and table S1).

In order to ensure that potential loss–related responses were not being obscured by the overall positive expected value of the gambles, we compared activity evoked by the worst possible gambles (gain: $10 to $16; loss: $17 to $20) and the best possible gambles (gain: $34 to $40; loss: $5 to $8). In a whole-brain analysis, there were no regions that showed significantly more activity for the worst gambles as compared to that for the best gambles (corrected $P > 0.4$ in all voxels by means of randomization tests). Given the specific prediction regarding loss-related activity in the amygdala and insula based on previous studies of experienced utility and risk aversion (*11*, *18*), we performed further analyses that focused on these areas. Even at a very liberal uncorrected threshold of $P < 0.01$, there were no significant voxels in the amygdala and only two single unconnected voxels in the insula. By comparison, at the same threshold, there were large clusters of activation for the best versus the worst

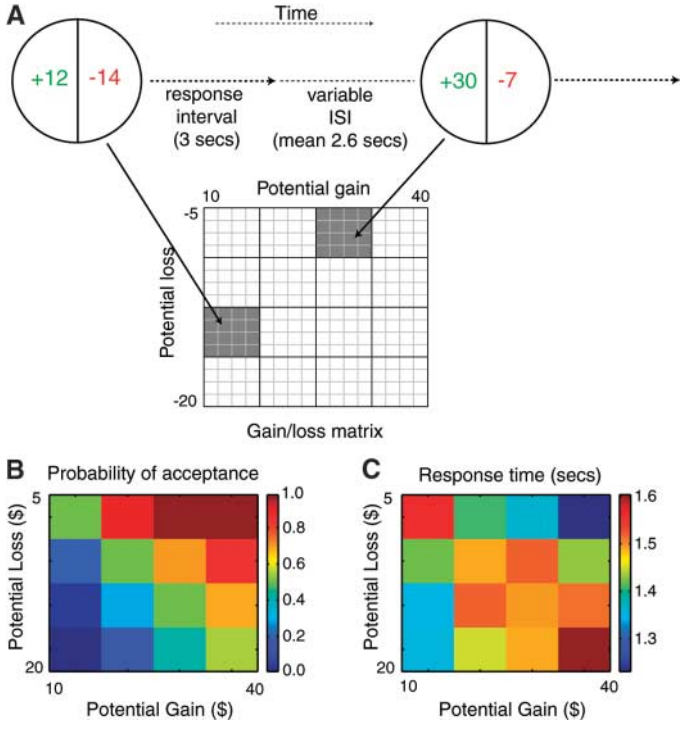

Fig. 1. (**A**) An illustration of the event-related task design. During each trial, the participant was presented for 3 s with a display showing the size of the potential gain (in green) and loss (in red). After the accept or reject response, a variable interval was presented to allow for optimal deconvolution of fMRI responses to each trial (*27*). Gambles were not resolved during scanning. The values of gain and loss for each trial were sampled from the gain/loss matrix, as shown here for two example gambles; a gamble from each cell in this 16 × 16 matrix was presented during scanning, but the data were collapsed into a 4 × 4 matrix for analysis. All combinations of gains and losses were presented. ISI, interstimulus interval. (**B**) Color-coded heatmap of probability of gamble acceptance at each level of gain/loss (red indicates high willingness to accept the gamble, and blue indicates low willingness to accept the gamble). (**C**) Color-coded heatmap of response times (red indicates slower response times, and blue indicates faster response times).

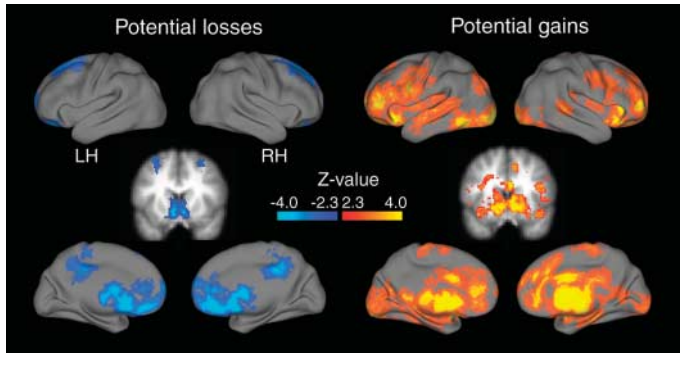

Fig. 2. Whole-brain analysis of parametric responses to size of potential loss (left) or gain (right). Statistical maps were projected onto an average cortical surface with the use of multifiducial mapping in CARET software (*28*); coronal slices ($y = 10$) are included to show ventral striatal activation. All maps are corrected for multiple comparisons at the whole-brain level by means of cluster-based Gaussian random field correction (*29*) at $P < 0.05$. LH, left hemisphere; RH, right hemisphere.

gambles in the ventral striatum and VMPFC. Although null results in fMRI must be interpreted with caution, these results are consistent with the conclusion that losses and gains are coded by the same mechanism rather than by two separate mechanisms. Moreover, this aggregate representation of decision utility appears to be represented by the same neural circuitry that is engaged by a range of experienced rewards (*11*). These results support previous studies showing increased and decreased activity in the striatum for experienced monetary gains and losses, respectively (*11*, *13*).

We next investigated whether individual differences in brain activity during decision-making were related to individual differences in behavior, using whole-brain analyses to identify regions where the neural response to gains or losses was correlated with behavioral loss aversion. Unexpectedly, greater behavioral loss aversion was associated with greater neural sensitivity not only to losses but also to gains. For increasing gains, we observed a significant correlation with behavioral loss aversion in the sensorimotor cortex and superior frontal cortex (fig. S4). On the other hand, as potential losses increased, an extensive set of areas showed a more rapidly decreasing response to mounting losses among individuals who were more loss averse (fig. S5). Notably, these regions encompassed many of the areas that showed an overall decrease in neural activity with increasing potential loss. The association of decreased behavioral loss aversion with decreased neural responses to both losses and gains during decision-making is consistent with the long-standing notion that some forms of risk taking may have their roots in sensation seeking by individuals who have a diminished physiological response to stimulation (*22*).

Examination of regions of interest in the striatum and VMPFC from the gain/loss conjunction analysis (Fig. 3) revealed that these regions exhibited a pattern of "neural loss aversion"; that is, the (negative) slope of the decrease in activity for increasing losses was greater than the slope of the increase in activity for increasing gains in a majority of participants (striatum: loss > gain for 14 out of 16 participants, $P = 0.004$; VMPFC: loss > gain for 13 out of 16 participants, $P = 0.021$). In order to more directly assess the relationship between neural loss aversion and behavioral loss aversion, we performed a whole-brain robust regression analysis with these measures (*21*). This analysis revealed significant correlations between behavioral and neural loss aversion in several regions, including bilateral ventral striatum (Fig. 4), bilateral lateral and superior PFC (pre-supplementary motor area), and right inferior parietal cortex (figs. S6 and S7 and table S2). These results demonstrate that differences in behavior were strongly predicted by differences in neural responses.

The present study replicates the common behavioral pattern of risk aversion for mixed gambles that offer a 50/50 chance of gaining or losing money and shows that this pattern of behavior is directly tied to the brain's greater sensitivity to potential losses than gains. These results provide evidence in favor of one of the fundamental claims of prospect theory (*1*, *2*), namely that the function that maps money to subjective value is markedly steeper for losses than gains [see also (*4*)]. Moreover, mediation analysis (*21*) suggests that individual differences in behavioral loss aversion (as inferred by willingness to accept mixed gambles) are driven primarily by individual differences in neural sensitivity to potential losses. Although the present study focuses on loss aversion in the context of mixed gambles, recent work has found that the coefficient of loss aversion (i.e., the ratio of sensitivity to losses versus gains) is highly correlated across risky and riskless contexts (*23*). Therefore, we surmise that a similar mechanism may contribute to other manifestations of loss aversion.

Previous studies have shown that anticipated or experienced losses give rise to activation in regions that have been associated with negative emotions, such as the amygdala or anterior insula (*11*, *17*, *18*). In contrast, the present study demonstrates that, in the context of decision-making, potential losses are represented by decreasing activity in regions that seem to code for subjective value rather than by increasing activity in regions associated with negative emotions. This difference between present and previous results reinforces the importance of distinguishing among experienced, anticipated, and decision utility in economic theories of choice (*15*). It is possible that amygdala engagement for experienced losses reflects negative prediction error (*11*, *24*) rather than negative value, whereas the lack of immediate outcomes in the present study (which was designed to isolate decision utility) precludes the computation of prediction errors.

The neural basis of decision under risk was investigated in a recent study by De Martino *et al*. (*25*), who found that amygdala activity correlated with choices of risky gambles framed as losses and sure outcomes framed as gains. However, the reflection in risk attitudes when moderate-probability gambles are framed as losses versus gains has been attributed in prospect theory primarily to the reflection in curvature of the value function for losses versus gains (*2*) and secondarily to distortions in probability weighting rather than to loss aversion. In contrast, we asked participants in the present study to evaluate balanced (50/50) gain/loss gambles, which allowed us to isolate the role of loss aversion. Thus, although amygdala activation may play a role in some decisions under risk, it does not appear to be a necessary component in loss aversion.

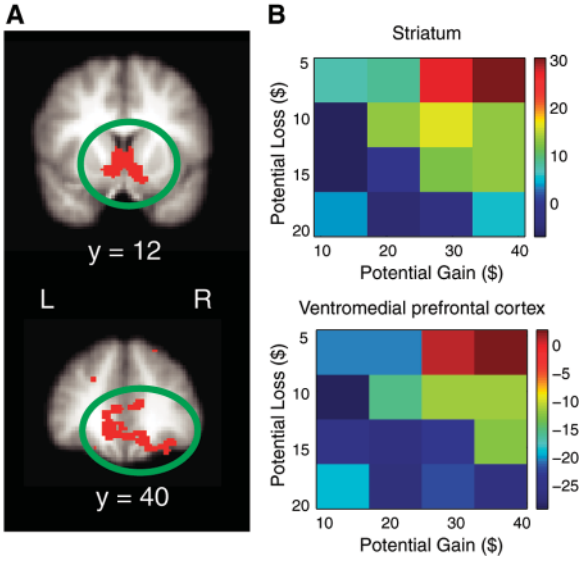

Fig. 3. Conjunction analysis results. (**A**) Map showing regions with conjointly significant positive gain response and negative loss response ($P < 0.05$, whole-brain corrected, in each individual map) (see also table S1). Red pixels indicate regions showing significant conjunction; green circles highlight clusters included in the respective heatmaps to the right. L, left; R, right. (**B**) Heatmaps were created by averaging parameter estimates versus baseline within each cluster in the conjunction map for each of the 16 cells (of 16 gambles each) in the gain/loss matrix; color coding reflects strength of neural response for each condition, such that dark red represents the strongest activation and dark blue represents the strongest deactivation.

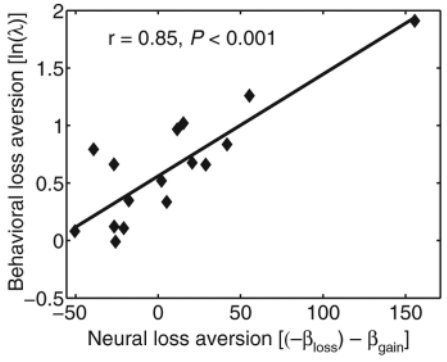

Fig. 4. Scatterplot of correspondence between neural loss aversion and behavioral loss aversion in ventral striatum [Montreal Neurological Institute coordinates (*x*, *y*, *z*): 3.6, 6.3, 3.9; center of gravity in millimeters]. Regression line and *P* value were computed with the use of robust regression by iteratively reweighted least squares to prevent the influence of outliers; however, this regression also remained highly significant ($P = 0.004$) when the extreme data point (top right-hand corner) was removed from the analysis. β_{loss} and β_{gain} are the unstandardized regression coefficients for the loss and gain variables, respectively.

The present results illustrate how neuroimaging can be used to directly test predictions stemming from behavioral theories: in this case, the prediction from prospect theory that risk aversion for mixed gambles can be attributed to enhanced sensitivity to losses. Neural loss aversion was observed throughout, though not strictly limited to, the targets of the mesolimbic and mesocortical dopamine (DA) systems. It is tempting to speculate that individual differences in behavioral and neural loss aversion observed in the present study may be related to naturally occurring differences in DA function, though the relationship between genetic variation in the DA system and personality traits such as impulsivity and risk taking remains largely unknown (*26*). Further, the diminished neural sensitivity to losses among individuals who were less loss averse (i.e., more risk seeking) may shed light on a number of neuropsychiatric and behavioral disorders, such as substance abuse, pathological gambling, and antisocial personality disorder, that are associated with increased risk taking and impulsive behavior. This suggests that studies integrating methods from behavioral economics and cognitive neuroscience may provide greater insight into the nature of these disorders.

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Materials and Methods
Figs. S1 to S7
Tables S1 and S2
References

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Asymmetric Inheritance of Mother Versus Daughter Centrosome in Stem Cell Division

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Adult stem cells often divide asymmetrically to produce one self-renewed stem cell and one differentiating cell, thus maintaining both populations. The asymmetric outcome of stem cell divisions can be specified by an oriented spindle and local self-renewal signals from the stem cell niche. Here we show that developmentally programmed asymmetric behavior and inheritance of mother and daughter centrosomes underlies the stereotyped spindle orientation and asymmetric outcome of stem cell divisions in the *Drosophila* male germ line. The mother centrosome remains anchored near the niche while the daughter centrosome migrates to the opposite side of the cell before spindle formation.

Adult stem cells maintain populations of highly differentiated but short-lived cells throughout the life of the organism. To maintain the critical balance between stem cell and differentiating cell populations, stem cells have a potential to divide asymmetrically, producing one stem and one differentiating cell (*1*). The asymmetric outcome of stem cell divisions can be specified by regulated spindle orientation, such that the two daughter cells are placed in different microenvironments that either specify stem cell identity (stem cell niche) or allow differentiation (*2*, *3*).

Drosophila male germline stem cells (GSCs) are maintained through attachment to somatic hub cells, which constitute the stem cell niche. Hub cells secrete the signaling ligand Upd, which activates the Janus kinase–signal transducer and activator of transcription (JAK-STAT) pathway in the neighboring germ cells to specify stem cell identity (*4*, *5*). *Drosophila* male GSCs normally divide asymmetrically, producing one stem cell, which remains attached to the hub, and one gonialblast, which initiates differentiation. This stereotyped asymmetric outcome is controlled by the orientation of the mitotic spindle in GSCs: The spindle lies perpendicular to the hub so that one daughter cell inherits the attachment to the hub, whereas the other is displaced away (*6*).

The stereotyped orientation of the mitotic spindle is set up by the positioning of centrosomes during interphase (Fig. 1A) (*6*). GSCs remain oriented toward the niche throughout the cell cycle. In G_1 phase, the single centrosome is located near the interface with the hub. When the duplicated centrosomes separate in G_2 phase, one stays next to the hub, whereas the other migrates to the opposite side of the cell. Centrosomes in the GSCs separate unusually early in interphase, rather than at the G_2-prophase transition, so it is common to see GSCs with fully separated centrosomes without a spindle (of >500 GSCs in the 0- to 3-day-old males counted, ~40% of the GSCs had two centrosomes that were separated to opposite sides of the cell, but no spindle was yet assembled) (*6*).

Differences between the mother and daughter centrosomes underlie the stereotyped behavior of the centrosomes in *Drosophila* male GSCs. The mother centrosome normally remains anchored to the hub-GSC interface and is inherited by the GSC, whereas the daughter centrosome moves away from the hub and is inherited by the cell that commits to differentiation. Mother and daughter centrosomes were differentially

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