Research Article

The Wick in the Candle of Learning

Epistemic Curiosity Activates Reward Circuitry and Enhances Memory

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ABSTRACT—Curiosity has been described as a desire for learning and knowledge, but its underlying mechanisms are not well understood. We scanned subjects with functional magnetic resonance imaging while they read trivia questions. The level of curiosity when reading questions was correlated with activity in caudate regions previously suggested to be involved in anticipated reward. This finding led to a behavioral study, which showed that subjects spent more scarce resources (either limited tokens or waiting time) to find out answers when they were more curious. The functional imaging also showed that curiosity increased activity in memory areas when subjects guessed incorrectly, which suggests that curiosity may enhance memory for surprising new information. This prediction about memory enhancement was confirmed in a behavioral study: Higher curiosity in an initial session was correlated with better recall of surprising answers 1 to 2 weeks later.

Curiosity is the complex feeling and cognition accompanying the desire to learn what is unknown. Curiosity can be both helpful and dangerous. It plays a critical role in motivating learning and discovery, especially by creative professionals, increasing the world's store of knowledge. Einstein, for example, once said, "I have no special talents. I am only passionately curious" (Hoffmann, 1972, p. 7). The dangerous side of curiosity is its association with exploratory behaviors with harmful consequences. An ancient example is the mythical Pandora, who opened a box that unleashed misfortunes on the world. In modern times, technology such as the Internet augments both good and bad effects of curiosity, by putting both enormous amounts of information and potentially dangerous social encounters a mouse-click away.

Despite the importance of human curiosity, its psychological and neural underpinnings remain poorly understood. Philosophers and psychologists have described curiosity as an appetite for knowledge, a drive like hunger and thirst (Loewenstein, 1994), the hunger pang of an "info-vore" (Biederman & Vessel, 2006, p. 247), and "the wick in the candle of learning" (William Arthur Ward, cited by Wikiquote, 2008). In reinforcement learning, a novelty bonus is used to motivate the choice of unexplored strategies (Kakade & Dayan, 2002). Curiosity can be thought of as the psychological manifestation of such a novelty bonus.

A theory guiding our research holds that curiosity arises from an incongruity, or information gap—a discrepancy between what one knows and what one wants to know (Loewenstein, 1994). This theory assumes that the aspired-to level of knowledge increases sharply with a small increase in knowledge, so that the information gap grows with initial learning. When one is sufficiently knowledgeable, however, the gap shrinks, and curiosity falls. If curiosity is like a hunger for knowledge, then a small "priming dose" of information increases the hunger, and the decrease in curiosity from knowing a lot is like being satiated by information.

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In the information-gap theory, the object of curiosity is an unconditioned rewarding stimulus: unknown information that is anticipated to be rewarding. Humans (and other species, such as cats and monkeys) will expend resources to find out information they are curious about, much as rats will work for a food reward (Loewenstein, 1994). On the basis of this observation, we hypothesized that the striatum would be linked to curiosity because a growing body of evidence suggests that activity in the human striatum is correlated with the level of reward signals (Hare, O'Doherty, Camerer, Schultz, & Rangel, 2008; Knutson, Westdorp, Kaiser, & Hommer, 2000; McClure, York, & Montague, 2004; O'Doherty, 2004).

Guided by these ideas, we explored the neural correlates of curiosity in one study and tested the hypotheses derived from its findings in two additional studies. In all studies, subjects were presented with a series of trivia questions chosen to create a mixture of high and low *epistemic* curiosity[1] (Fig. 1a). Subjects read each question, guessed the answer, rated their curiosity about the question, and rated how confident they were that they knew the answer (P). Then the question was presented again, followed by the correct answer (Fig. 1b).

In the first experiment, subjects read the questions during functional magnetic resonance imaging (fMRI). In the second experiment, they performed the same task without scanning, and their memory for answers was tested in a follow-up session 1 to 2 weeks later. In the third experiment, we behaviorally tested whether curiosity is indeed a form of reward anticipation.

EXPERIMENT 1

Method

Participants and Task
Nineteen Caltech students were scanned (average age = 21.7 ± 3.5 years; 14 males, 5 females; 18 right-handed, 1 left-handed). They earned $20 for participation. Informed consent was obtained using a consent form approved by the internal review board at Caltech. The stimuli used in the task were 40 trivia questions on various topics (these and other materials can be viewed in Experimental Materials in the Supporting Information available on-line; see p. 973). They were designed to measure curiosity about semantic knowledge, and pretesting indicated that they evoked a range of curiosity levels (for sample questions, see Fig. 1a). Participants were instructed that after reading each question, they should silently guess the answer and indicate their curiosity about the correct answer and their confidence in their guess. Then the question was presented again, followed by the correct answer (for a time line, see Fig. 1b). Curiosity ratings were on a scale from 1 to 7, and for all the analyses that follow, the raw curiosity ratings were individually normalized (i.e., the individual's mean curiosity was subtracted from each rating, and the resulting value was divided by that individual's standard deviation). The confidence scale ranged from 0 to 100%, but was rescaled to range from 0 to 1. Verbal or typed responses are not easy to collect in a scanner, so subjects provided their initial guesses outside of the scanner upon completion of the task.
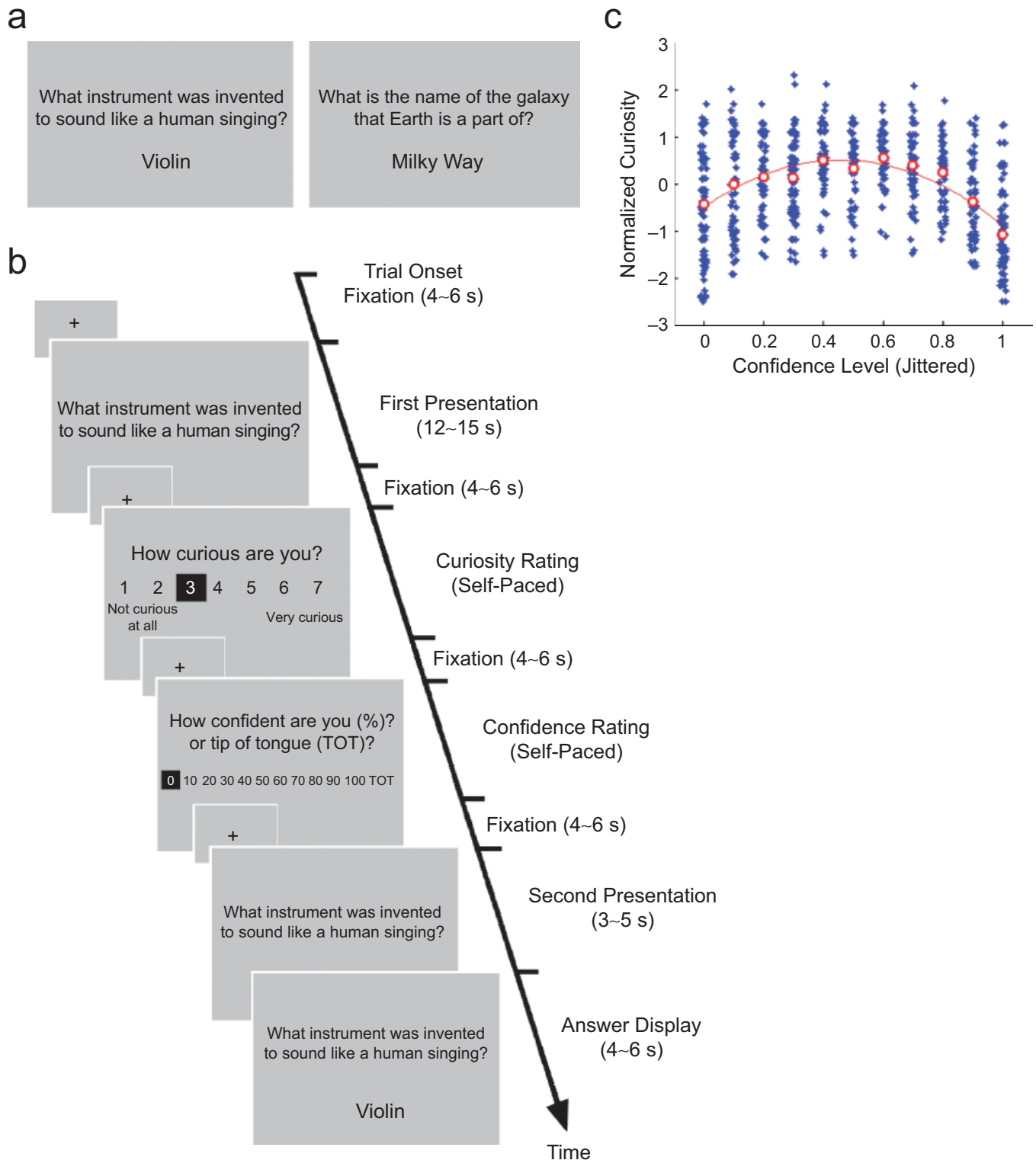
fMRI Acquisition and Analysis
Data were acquired using a 3-T Siemens (Erlangen, Germany) Trio scanner at Caltech. A set of high-resolution ($0.5 \times 0.5 \times 1.0$ mm^3) T1-weighted anatomical images was first acquired to enable localization of functional images. Whole-brain T2*-weighted echo-planar images with blood-oxygenation-level-dependent (BOLD) contrast were acquired in 32 axial slices (64×64 voxels; 3-mm thickness and 3-mm in-plane resolution) at a repetition time of 2,000 ms and echo time of 30 ms. The scan sequences were axial slices approximately parallel to the anterior commissure–posterior commissure axis. The fMRI data were preprocessed using SPM2 (Wellcome Department of Imaging Neuroscience, Institute of Neurology, London, United Kingdom). Functional scans were first corrected for slice timing via linear interpolation. Motion correction of images was performed using a six-parameter affine transformation followed by nonlinear warping using basis functions (Ashburner & Friston, 1999). Finally, images were smoothed with a Gaussian kernel of 8-mm full-width at half-maximum. The data analysis was conducted using the random-effects general linear model (GLM) for event-related designs in SPM2.

Curiosity Median-Split Analysis. Each subject's trials were split into two conditions (high or low) according to where they fell relative to that individual's median curiosity level. Then all five epochs in each trial (first presentation, curiosity rating, confidence rating, second presentation, and answer display) were classified as being in the high- or low-curiosity condition according to the condition to which the whole trial had been assigned. Thus, there were two curiosity conditions for each epoch, resulting in a total of 10 separate regressors of interest. Each regressor was time-locked to stimulus presentation. A GLM including these 10 regressors plus regressors of no interest was estimated. The 10 regressors of interest were modeled using box-car functions with the length of each epoch (e.g., the presentation time for the first answer) as the corresponding box-car duration. We then calculated contrasts to compare the effects of high versus low curiosity.

Curiosity Modulator Analysis. We also examined whether the brain activations identified in the median-split analysis increased linearly with curiosity level, rather than being associated with two levels (high or low) of curiosity. We estimated a GLM in which normalized curiosity was a parametric modulator for each of the five epochs.

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[1]Epistemic curiosity refers to a desire to acquire knowledge and applies mainly to humans (Loewenstein, 1994).

a

What instrument was invented to sound like a human singing?	What is the name of the galaxy that Earth is a part of?
Violin	Milky Way

c

b

Fig. 1. Experimental protocol and behavioral results in Experiment 1: (a) sample questions, (b) trial sequence, and (c) distribution of curiosity ratings as a function of confidence. The questions in (a) are examples of items with relatively high (left; average score = 5.72) and low (right; average score = 2.28) curiosity ratings. For the scatter plot (c), all confidence ratings were jittered by adding random numbers $U \sim [-0.01, 0.01]$, to convey data density. There was also a ''tip of the tongue'' response option, but there were too few of these responses to analyze, so they were excluded. The large, unfilled circles indicate mean curiosity at each confidence level. Diamonds indicate individual observations. The solid curve is the regression line of curiosity against confidence, P, and $P(1 - P)$. The estimated regression was calculated as follows: curiosity $= -0.49 - 0.39P + 4.77P(1 - P) +$ residual curiosity.

Residual Curiosity Analysis. Finally, we investigated the effect of curiosity that is dissociated from confidence level, P, and uncertainty, $P(1 - P)$.[2] To do this, we first regressed curiosity on P and $P(1 - P)$ (with a constant) and then took the residuals from this regression to construct a new variable, the residual curiosity. Further, to study the interaction between residual curiosity and correctness, we divided the answer-display epochs into correct- and incorrect-guess conditions. This procedure resulted in a total of six conditions of interest: first presentation, curiosity rating, confidence rating, second presentation, answer display preceded by a correct guess, and answer display preceded by an incorrect guess. We then estimated a GLM in which P, $P(1 - P)$, and residual curiosity were parametric modulators for each of these six conditions.

Results

Curiosity and Confidence Ratings

The information-gap theory predicts that curiosity should increase with statistical uncertainty, $P(1 - P)$ (because people who know very little have not had their curiosity piqued, and those who know a lot are satiated). Reported curiosity was indeed an inverted-U-shaped function of P, reaching its maximum when P was around .50 (Fig. 1c). Curiosity correlated positively with $P(1 - P)$, $r = .44$, $p < .0005$, $p_{rep} > .99$. Most subjects showed this relation; estimated peak curiosity was at values of P between .45 and .55 in three quarters of the subjects (see Table S1 in the Supporting Information available on-line).

Curiosity and Brain Activity

In this section, we first focus on brain activity when questions were initially presented and then discuss brain activity when answers were presented. Results are reported for brain areas with significant activity; unless noted otherwise, our criteria for significance were an uncorrected p value of less than .001, $p_{rep} > .99$, and a minimum cluster size (k) of 5.

The first question-presentation epoch was associated with the high- or low-curiosity condition according to the individualized median curiosity level. We created a contrast that identified regions whose activity was greater in response to high curiosity than in response to low curiosity. Significantly activated regions

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[2]Uncertainty, $P(1 - P)$, measures a subject's uncertainty about a guess. A guess is a random variable (more specifically, a Bernoulli random variable) with two outcomes, correct or incorrect; the two outcomes have probabilities of P (confidence level) and $1 - P$, respectively. The uncertainty associated with the random variable (or uncertainty about which outcome will occur) is measured by the entropy, which in this case is a monotonic function of the variance $P(1 - P)$. $P(1 - P)$ is a quadratic function with a maximum at $P = .5$ and minima at $P = 0$ and 1. For example, suppose that you are 100% (or 0%) sure about your guess. In this case, your confidence level, P, is 1 (or 0). Your uncertainty about the outcome will be minimal. In contrast, if your confidence level about your guess is .5, then you are most uncertain about which outcome will occur because the two outcomes are equally likely.

included the left caudate; bilateral prefrontal cortex (PFC), including inferior frontal gyrus (IFG); and parahippocampal gyri (PHG; Table 1). Activations in the putamen ($x = 21$, $y = 9$, $z = 9$), $t(18) = 3.15$, $p_{rep} > .99$, and the globus pallidus ($x = 12$, $y = -6$, $z = 0$), $t(18) = 3.94$, $p_{rep} > .99$, were significant at $p < .005$ (uncorrected), $p_{rep} = .98$, but no activation was found in the nucleus accumbens. The area of significant activation in the left caudate overlapped with areas of significant activity identified by the models using subject-normalized linear curiosity and residual curiosity as the regressors (Fig. 2). This finding is consistent with the view of curiosity as anticipation of rewarding information.

When the answers were revealed, activations in areas linked to learning and memory were much stronger if the subject's prior guess had been incorrect, rather than correct. Areas differentially activated when subjects guessed incorrectly included the bilateral putamen (right: $x = -24$, $y = -9$, $z = 6$; left: $x = 24$, $y = -9$, $z = 12$), $t(18) = 4.63$, $p_{rep} > .99$, and $t(18) = 4.77$, $p_{rep} > .99$, respectively, and left IFG ($x = -54$, $y = 24$, $z = 18$; Broca's area, Brodmann's area 44/45), $t(18) = 6.64$, $p_{rep} > .99$ (Fig. 3a). Further, curiosity level modulated the activations during the answer display. After an incorrect guess, left PHG ($x = -24$, $y = -27$, $z = -6$) and left IFG ($x = -54$, $y = 9$, $z = 24$) activations during the answer display were positively correlated with residual curiosity, $t(18) = 4.69$, $p_{rep} > .99$, and $t(18) = 4.48$, $p_{rep} > .99$, respectively (Fig. 3b). Bilateral midbrain regions (left: $x = -12$, $y = -24$, $z = -6$; right: $x = 12$, $y = -21$, $z = -18$), $t(18) = 3.37$, $p_{rep} > .99$, and $t(18) = 3.97$, $p_{rep} > .99$, respectively, were also activated at $p < .005$ (uncorrected), $p_{rep} = .98$ (see Fig. S1 in the Supporting Information available on-line), as was the hippocampus ($x = -27$, $y = -33$, $z = -6$), $t(18) = 3.2$. The identified area in left IFG was dorsal to areas identified in the analyses of the question epoch (Fig. 2) and was part of Broca's area, which is important for language comprehension (Bookheimer, 2002). When subjects guessed correctly, residual curiosity did not correlate with activity in any of the identified regions.

Because memory-related regions were differentially activated in response to answers presented after incorrect guesses, and the activity was modulated by curiosity, we hypothesized that curiosity would be associated with memory enhancement for new information (in this paradigm, a correct answer is new information if it follows an incorrect guess). That is, we hypothesized that after guessing incorrectly, people would be more likely to remember the answer to a question if they were curious to know it.

The findings from this fMRI study suggested that curiosity is anticipation of rewarding information and that it may enhance learning of new information. We tested these hypotheses in separate experiments. We first describe the experiment that tested the memory-enhancement hypothesis and then report the experiment that tested the reward-anticipation hypothesis.

Brain Regions Exhibiting Greater Activation on High-Curiosity Trials Than on Low-Curiosity Trials During the First Presentation of the Question

Region	Hemisphere	Coordinates			Spatial extent (voxels)	$t(18)$
		x	y	z		
Caudate	Left	−9	3	3	10	4.04
Inferior frontal gyrus/Brodmann's area 45	Left	−54	24	21	112	5.71
Inferior frontal gyrus/Brodmann's area 45	Right	48	24	21	5	4.01
Parahippocampal gyrus	Left	−33	−39	−12	21	4.04
Parahippocampal gyrus	Right	36	−30	−18	5	4.46
Medial frontal gyrus	Left	−12	36	48	26	4.49
Middle frontal gyrus, premotor cortex	Left	−27	15	57	70	5.71
Lingual gyrus	Right	18	−63	−3	11	4.57
Cerebellum	Right	36	−69	−36	34	4.67

Note. All locations are reported in Montreal Neurological Institute coordinates.

EXPERIMENT 2

Method

Participants and Task

Sixteen Caltech students (11 males, 5 females) participated. Informed consent was obtained using a consent form approved by the internal review board at Caltech. The task, questions, and time line were identical to those in Experiment 1 except for some minor changes: The order of questions was fully randomized across the experiment, no fixation screens were presented, each question was presented for a fixed duration of 10 s, and a countdown screen showing every second was presented for the 5 s before the answer.

Upon completing the task, subjects were surprised with a request to return within 11 to 16 days for a follow-up study. Twelve returned and provided data used in the analyses. At the follow-up session, subjects were shown the same questions and asked to recall the correct answers (earning $0.25 for each correct answer, in addition to $15 for participation). (See Experimental Materials in the Supporting Information available on-line for the instructions given to subjects.)

Measures

For the first session, the measured variables were identical to those of Experiment 1 except that subjects' guesses were recorded during the task (as a check on postscanner overreporting of correct guesses in Experiment 1; the percentage of correct guesses was not significantly different between the experiments), as was pupil dilation response (PDR) before and after the answer display. The second session provided a new recall measure.
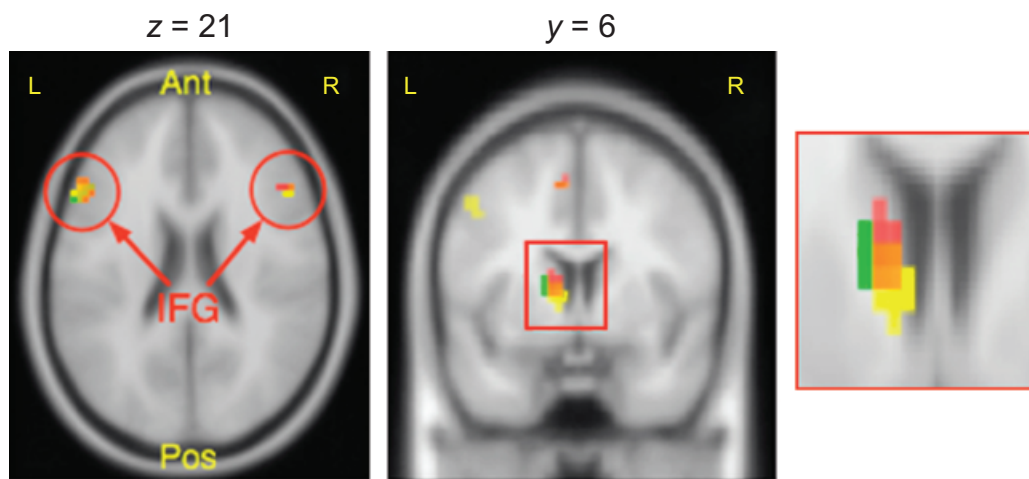
Fig. 2. Brain regions that showed differential activity in high- versus low-curiosity trials during the first question presentation in Experiment 1 ($p < .001$ uncorrected, $p_{rep} > .99$, extent threshold ≥ 5). Colored areas showed greater activation on high-curiosity trials in the median-split analysis (red), the modulator analysis (yellow), and the analysis of residual curiosity (green). The illustration at the right is a close-up view of the overlapping caudate activations. Ant = anterior; Pos = posterior; L = left; R = right; IFG = inferior frontal gyrus.
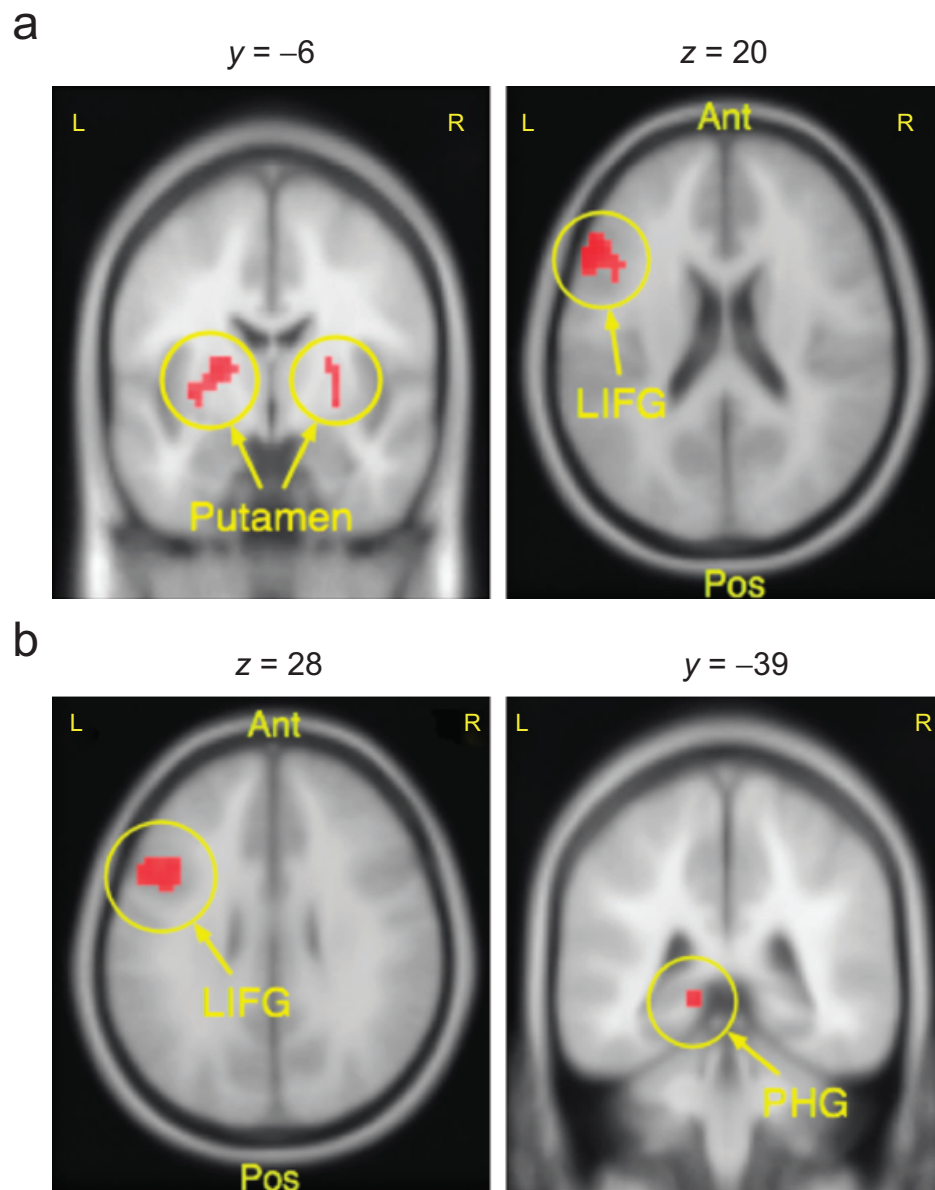
Fig. 3. Brain areas that showed differential activation during the answer displays in Experiment 1: (a) regions that were more active after incorrect guesses than after correct guesses (bilateral putamen and left inferior frontal gyrus, or LIFG) and (b) regions whose activity after incorrect guesses correlated with curiosity (LIFG and parahippocampal gyri, or PHG). Ant = anterior; Pos = posterior; L = left; R = right.

PDR was recorded using a Mobile Eyelink II eye tracker (SR Research, Osgoode, Ontario, Canada) at 250 Hz. The two sessions in Experiment 2 were conducted and analyzed in Matlab (Mathworks, Inc., Natick, MA) using the Psychophysics Toolbox (Brainard, 1997) and the Eyelink Toolbox (Cornelissen, Peters, & Palmer, 2002). Blinks were treated as missing data and removed. We focused on the time interval from 4.8 s before to 4.8 s after the onset of the answer display. After normalization, we split the pupillary data collected over this interval according to the level of curiosity reported: high, middle, or low. Within each curiosity level, the data were averaged across subjects for every 400-ms interval.

Results

Pupil Dilation

On high-curiosity trials, PDRs ramped up 1 to 2 s before the onset of the answer display, peaked after 800 ms, and then dropped back to baseline around 2 s after the onset of the display (Fig. 4a). Average PDR during anticipation (1 s before the onset of the answer) was significantly higher for high-curiosity items than for middle-curiosity items, $t(164.3) = 2.04$, $p < .03$ (one-tailed), $p_{rep} = .92$, $d = 0.23$, and was modestly higher for middle-curiosity compared with low-curiosity items, $t(294.8) = 1.15$, $p = .13$ (one-tailed), $p_{rep} = .79$, $d = 0.11$. When the
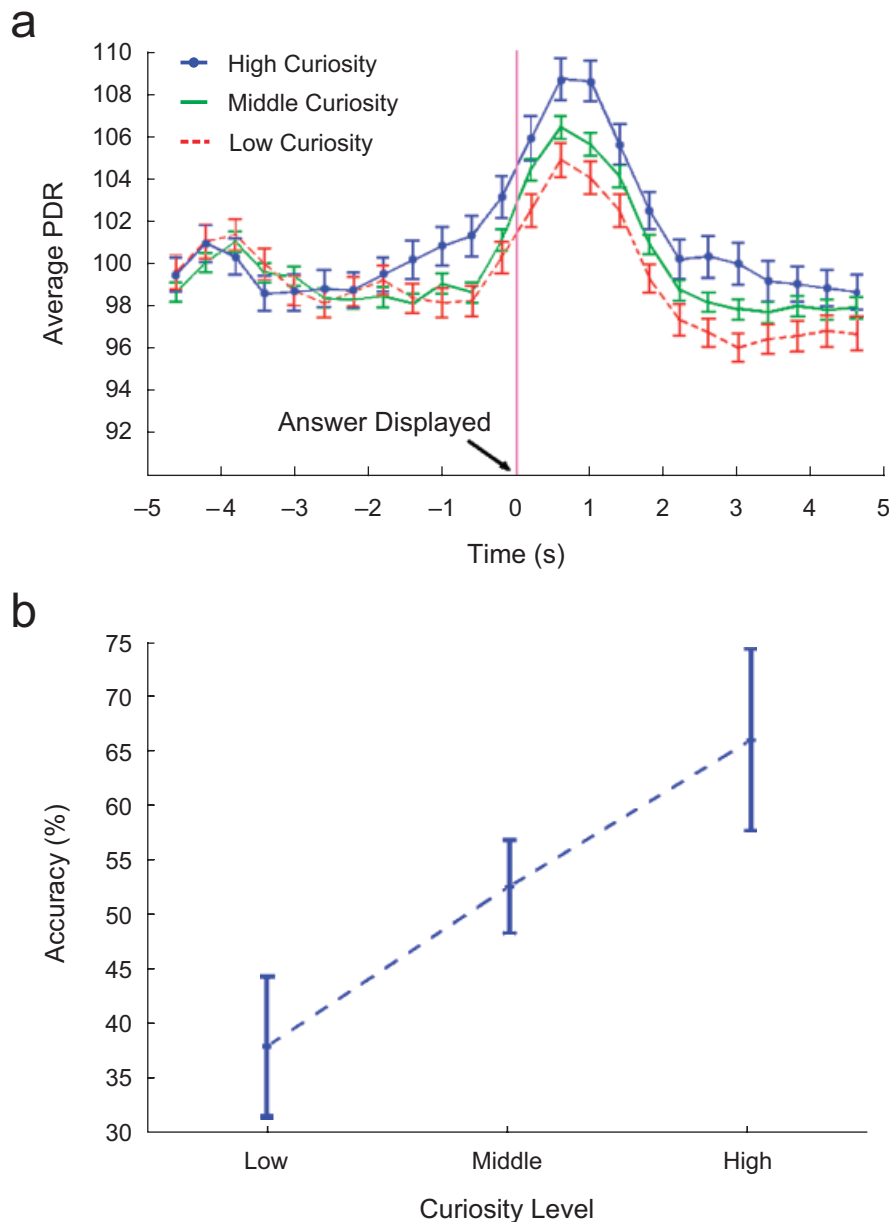
Fig. 4. Results from Experiment 2: (a) average pupil dilation response (PDR) as a function of time interval (Time 0 = onset of the answer display) and (b) percentage accuracy on the memory test for trials on which subjects initially guessed incorrectly. In (a), PDR was individually normalized to 100 ($n = 16$). Results in both graphs are shown separately for high-curiosity trials (top tercile for a given individual), middle-curiosity trials (middle tercile), and low-curiosity trials (bottom tercile). Error bars denote standard errors.

answer appeared (0–1,000 ms after the onset of the answer), the average PDR differed significantly across the three trial types, $p < .03$ (one-tailed), $p_{rep} \geq .91$, $d \geq 0.18$.

Curiosity and Memory
Curiosity expressed in the initial session had a strong effect on subsequent recall of the answers to the questions that were initially guessed incorrectly (Fig. 4b). The accuracy rates differed significantly between high- and middle-curiosity items,

$t(10) = 2.10$, $p < .05$, $p_{rep} = .91$, $d = 0.61$; middle- and low-curiosity items, $t(12) = 2.37$, $p < .02$, $p_{rep} = .93$, $d = 0.74$; and high- and low-curiosity items, $t(10) = 3.13$, $p < .01$, $p_{rep} = .97$, $d = 1.11$ (all $ps < .05$, paired one-tailed t tests). These results support the hypothesis that higher curiosity levels lead to better recollection. When we repeated the analysis using residual curiosity, and including control variables P and $P(1 - P)$, we again found a main effect of curiosity on recall. Consistent with the fMRI findings, these findings suggest that curiosity activates
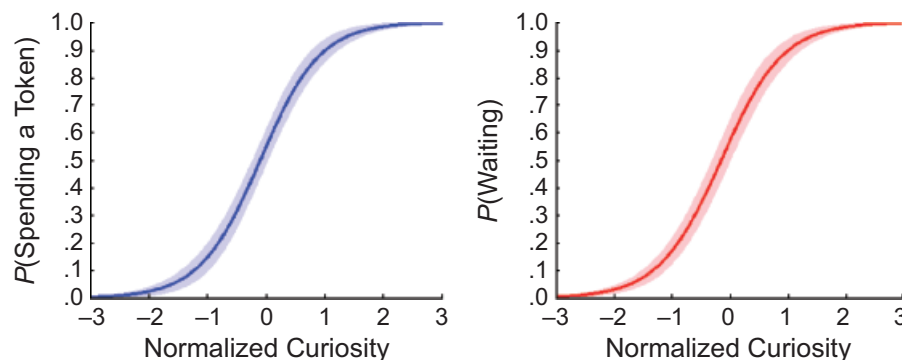
Fig. 5. Results from Experiment 3: Group logistic curves relating normalized curiosity to the probability of spending a token or waiting time to learn the answer to a trivia question. The dependent variables, whether to spend a token (left panel) or to spend assigned waiting time (right panel), were regressed on subject-normalized curiosity ratings and a constant. For each condition, we pooled the data across subjects. The shaded areas around the plotted lines indicate the 95% confidence intervals.

memory regions differentially in response to surprising (incorrectly guessed) answers, resulting in greater accuracy of subsequent memory for the correct answers.

EXPERIMENT 3

Method

Participants
Participants in this follow-up experiment were assigned to one of two conditions: a token condition (10 Caltech students; mean age $= 23.4 \pm 3.3$ years; 5 males, 5 females) and a time condition (20 Caltech students; mean age $= 19.9 \pm 2.2$ years; 12 males, 8 females). Informed consent was obtained using a consent form approved by the internal review board at Caltech.

Task and Measures
The task and time line were like those of Experiments 1 and 2 except for two features: Subjects had to spend scarce tokens or time to learn answers, and 10 questions were added to the original 40 questions (see Experiment 3 Procedure, Experimental Materials, and Fig. S2 in the Supporting Information available on-line). A reward is an object or event that elicits approach and is worked for (Wise, 2004). Requiring subjects to spend tokens or time measured their willingness to pay for information they were curious about. The different conditions tested the robustness of the effect of curiosity to changes in the type of resource that was spent.

In the token condition, subjects had to spend 1 of their 25 experimental tokens to find out the answer to a question. Subjects read each question, reported their curiosity and confidence levels, and typed their guess. After guessing, they could pay 1 token to see the answer immediately. The tokens did not have cash value, but because there were 25 tokens and 50 questions,

spending a token on an answer meant skipping another answer. Given our previous finding that high curiosity was correlated with activity in the striatal region, we hypothesized that when subjects were more curious, they would anticipate higher reward from learning information, so they would be more likely to spend a token. Other results were possible, however. Subjects could allocate tokens on the basis of their confidence in their guesses, impatiently use all their tokens in the beginning, alternate spending and saving, or exhibit some other pattern unrelated to curiosity.

The second condition imposed a different cost: After guessing, subjects had to wait until the answer appeared. They were told that the waiting time would vary randomly from trial to trial and that any amount of time from 5 to 25 s would be equally likely. Subjects could quit waiting and skip to the next question at any time, but then they would not get to see the correct answer to the preceding question. We hypothesized that subjects would be more likely to spend time, to wait longer, for the answers that they were more curious about.

Results
Logistic regressions showed that spending tokens (1 if a token was spent; 0 otherwise) and spending time (1 if a subject waited until the answer appeared; 0 otherwise) were both strongly correlated ($p < .001$, $p_{rep} > .99$) with curiosity (Fig. 5). We obtained the same significant pattern of results when P and $P(1 - P)$ were included in the equations, and when residual curiosity was used as the predictor. At the individual-subject level, correlations between curiosity and spending were significant, $p < .01$, $p_{rep} = .97$, for 28 of the 30 subjects (see Fig. S3 in the Supporting Information available on-line). A regression analysis showed that subjects waited for an additional 3.7 s as their normalized curiosity level increased by 1 standardized unit.

DISCUSSION

In turn-of-the-century psychology, curiosity was considered an important drive, but research on it subsequently waned (Loewenstein, 1994). With this study, we have attempted to revive interest in curiosity, measuring it by self-report and using fMRI to study neural correlates of reported curiosity. The findings suggest hypotheses about memory and reward anticipation.

The correlations between reported curiosity and both lateral PFC and caudate activity are consistent with the information-gap hypotheses that curiosity is linked to anticipation of information, and that information is a secondary reinforcer. Curiosity was correlated with activity in the caudate when a question was first presented. It is well established that the caudate is involved in reward anticipation, or reward learning, across a wide variety of primary and secondary reinforcers (Delgado, Locke, Stenger, & Fiez, 2003; Delgado, Nystrom, Fissell, Noll, & Fiez, 2000), including social rewards such as benevolent reciprocity (Fehr & Camerer, 2007; King-Casas et al., 2005), social cooperation (Rilling et al., 2002), altruistic punishment (de Quervain et al., 2004), and winning an auction (Delgado, Schotter, Ozbay, & Phelps, 2008).

Previous studies have found that the expectation of feedback is sufficient for activation of the caudate (Aron et al., 2004). Our experimental design included feedback in the form of the correct answers presented to the subjects. If there is brain activity in anticipation of positive feedback, it should be modulated by confidence level, P (the more confident one is in being right, the more positive feedback one expects). The parametric design of the analysis (correlating activity with curiosity levels and then with residual curiosity) precludes the possibility that the observed caudate activation was driven solely by expectation of feedback from accurate guesses (because residual curiosity and confidence were uncorrelated by construction). The finding that activity in the left PFC is correlated with curiosity is also consistent with the idea that curiosity is associated with an intrinsic value of learning, because neurons in the left PFC receive input from neurons in the substantia nigra via the dorsal striatum. The dorsal striatum responds to magnitude of primary rewards and reward prediction (Leon & Shadlen, 1999; Rogers et al., 1999) and shows sustained phasic activations during reward expectation (Watanabe, 1996).

There are also studies that have reported striatal activations in response to negatively valenced stimuli (Knutson, Adams, Fong, & Hommer, 2001) or during nonreward activity such as working memory and motor preparation (Cairo, Liddle, Woodward, & Ngan, 2004; Simon et al., 2002). Because our task did involve working memory and motor preparation, the striatal activation we found could have been due to increased attention, incentive salience, or other activities (as some studies suggest). Given that people tend to be more attentive to an object that is more rewarding, the fMRI evidence alone cannot rule out these interpretations in favor of the reward-anticipation interpretation.

Therefore, we investigated the reward-anticipation interpretation further in a separate behavioral study. In Experiment 3, subjects were allowed to either spend a token or wait to see the answer to a question. Both actions incurred a cost—a lost opportunity or lost time. People are generally willing to spend time and resources to obtain objects that they find rewarding. Thus, enhanced willingness to spend resources to find out the answers to more curiosity-provoking questions is consistent with the reward interpretation and not with the idea that the fMRI results indicate only effects of attention or incentive salience.

Recent computational neural network models suggest another compatible interpretation involving memory (Frank, Loughry, & O'Reilly, 2001; O'Reilly & Frank, 2006). Question stimuli trigger differing levels of curiosity; the basal ganglia may send out a stronger signal to enable the lateral PFC to update, maintain, and internally represent questions eliciting higher curiosity, whose answer may be anticipated to be more rewarding. This internal representation in the lateral PFC, particularly in the left IFG, is a crucial component of long-term memory consolidation and is critical in the learning of new information (Paller & Wagner, 2002).

The PHG and left IFG were activated in response to wrong guesses, and the level of activation was correlated with the level of curiosity. These regions are thought to be involved in successful verbal memory encoding (Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998; Paller & Wagner, 2002; Wagner et al., 1998). In conjunction with the caudate and left PFC activations when questions were first presented, this activity suggests that curiosity strengthens memory of correct answers when people initially make incorrect guesses—that is, that curiosity is linked to the reward value of information and also enhances learning from new information.

This conjecture led to Experiment 2, in which we measured PDR and memory. Because pupil dilation is known to be linked to arousal, attention, interest, and cognitive effort (Beatty, 1982; Hess & Polt, 1960), and because anticipatory pupillary responses increase following a stimulus that predicts rewards (O'Doherty, Dayan, Friston, Critchley, & Dolan, 2003), the observed correlation of curiosity with pupil dilation is consistent with both reward anticipation and learning of novel information. The finding that curiosity enhanced later recall of novel information suggests that curiosity helps to consolidate novel information in memory. Having established that curiosity is a form of reward anticipation, we can also tie this research to the work of Adcock, Thangavel, Whitfield-Gabrieli, Knutson, and Gabrieli (2006), who showed that anticipated monetary rewards modulate activations in the mesolimbic and parahippocampal regions and promote memory formation prior to learning. Our results complement theirs by showing that endogenous internal motivation manifested in curiosity recruits neural circuits similar to those that are recruited by exogenous incentives, and has a similar effect on learning.

We also found bilateral putamen activation during the answer display after incorrect guesses. Although no explicit reward or punishment was involved, subjects might have perceived guessing incorrectly as an unexpected inherent, or self-, punishment, and the severity of this punishment might have been based on confidence in the answer (e.g., subjects would have felt worse about an incorrect guess if they had been very confident about that guess than if they had not been confident). The differential putamen activations we found might reflect this "internal punishment" aspect of guessing incorrectly. This interpretation is consistent with the recent finding that unexpected punishments and unexpected rewards produce very similar BOLD responses in the putamen at the time of outcomes (Knutson et al., 2000; Seymour, Daw, Dayan, Singer, & Dolan, 2007).

The exploratory nature of our study did not allow us to examine all possible aspects of curiosity separately. It is certainly likely that curiosity works differently in different sensory and knowledge domains. The trivia questions we used evoke what is often called *specific epistemic curiosity* (Berlyne, 1954). This kind of curiosity is the desire for a particular piece of information and is often associated with motivations for academic achievement and scientific discovery. This type of curiosity is probably different from the sensation driven by stimulus novelty or the desire to avoid boredom or sensory deprivation. The latter type of curiosity is called *diversive perceptual curiosity* and can be found in various animals (Berlyne, 1954). The curiosity we measured included a desire to learn new information and anticipation of the rewarding information to be learned (because subjects received feedback). A study without feedback would isolate pure curiosity absent anticipation and learning, though it would not permit study of the response to right and wrong guesses. Further studies could also show whether curiosity is different for visual stimuli, semantic narratives (e.g., page-turner novels), social information (e.g., gossip), and subjects of "morbid curiosity."

Understanding the neural basis of curiosity has important substantive implications. Note that although information seeking is generally evolutionarily adaptive (Panksepp, 1998), modern technologies magnify the amount of information available, and hence the potential effects of curiosity. Understanding curiosity is important for selecting and motivating knowledge workers who gather information (e.g., scientists, detectives, and journalists). The production of engaging news, advertising, and entertainment is also, to some extent, an attempt to create curiosity. The fact that curiosity increases with uncertainty (up to a point) suggests that a small amount of knowledge can pique curiosity and prime the hunger for knowledge, much as an olfactory or visual stimulus can prime a hunger for food; this observation might suggest ways for educators to ignite the wick in the candle of learning.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the on-line version of this article:

Experimental Materials
Experiment 3 Procedure
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Figure S1
Figure S2
Figure S3

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