A memory-enhancing emotionally arousing narrative increases blood glucose levels in human subjects

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To examine the contribution of glucose to the memory-enhancing effects of emotional arousal, we determined whether a memory-enhancing emotional narrative would increase blood glucose levels. Blood glucose was measured before and after participants viewed slides accompanied by a neutral or an emotionally arousing narrative. Prior to the slide show, the participants drank a beverage containing either glucose or saccharin. Participants who heard the emotionally arousing narrative had better memory of the narrative and slide show 2 weeks later than did participants who heard the neutral narrative. Blood glucose levels increased after the emotionally arousing narrative, but not after the neutral narrative. Glucose administration produced a larger increase in blood glucose levels than did the emotionally arousing narrative and prevented the memory-enhancing effect of emotional arousal. These findings indicate that small increases in blood glucose levels may contribute to the memory-enhancing effects of emotional arousal, whereas larger glucose increases may prevent its effects.

Extensive evidence from studies of rodent learning indicates that emotional arousal is associated with enhanced memory (see Gold & McGaugh, 1975; McGaugh, 1989). In humans, retention is enhanced by inducing arousal through muscular contraction (Nielson & Jensen, 1994) or by increasing the emotional content of information that is to be remembered (Burke, Heuer, & Reisberg, 1992; Cahill & McGaugh, 1995; Cahill, Prins, Weber, & McGaugh, 1994; Heuer & Reisberg, 1990). These findings support the possibility that emotional arousal, which is typically produced by significant situations, serves as an important signal to promote memory storage (Gold, 1992b; Gold & McGaugh, 1975; McGaugh, 1990).

Although it is well established that arousing events are easily remembered, the biological mechanisms that make such events so memorable are not fully understood. It is known that the catecholamine stress hormones epinephrine and norepinephrine, which are released into the blood from the adrenal gland during times of high arousal, par-

ticipate in the memory-enhancing effect of emotion (McGaugh, 1989, 1990). In rodents, endogenous levels of adrenal catecholamines are correlated with memory (Gold & McCarty, 1981), and exogenous administration of these stress hormones enhances memory in a variety of situations (Gold & Van Buskirk, 1975; Introini-Collison & McGaugh, 1986, 1991; Izquierdo & Dias, 1983). Moreover, drugs that block the actions of epinephrine and norepinephrine impair memory (Gold & Van Buskirk, 1978; Introini-Collison & McGaugh, 1991). In humans, such drugs prevent the memory-enhancing effects of arousal (Cahill et al., 1994; Nielson & Jensen, 1994; van Stegeren, Everaerd, Cahill, McGaugh, & Gooren, 1998). For example, Cahill et al. (1994) found that long-term memory was enhanced in college students when the emotional content of a narrative was increased. Importantly, the memory-enhancing effects of emotional arousal were prevented by the beta-adrenergic antagonist propranolol.

Since adrenal catecholamines do not easily enter the brain (Weil-Malherbe, Axelrod, & Tomchick, 1959), it is likely that they influence memory indirectly by activating one or more secondary signals. One physiological action of epinephrine is to increase circulating blood glucose levels, largely via the release of glucose from hepatic stores (Ellis, Kennedy, Eusebi, & Vincent, 1967; Saccà, Vigorito, Cicala, Corso, & Sherwin, 1983). As in the case of epinephrine, glucose administration enhances memory in rodents (see Gold, 1991, 1992a, 1995a, 1995b; Korol & Gold, 1998; Messier & Gagnon, 1996; Wenk, 1989; White, 1991). Also, evidence from rodents indicates that natural

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increases in circulating glucose levels observed after some training experiences are related to better memory for those experiences (Gold & Stone, 1988; Hall & Gold, 1986). In humans, glucose administration enhances verbal declarative memory in young adults, healthy elderly participants, and participants with Alzheimer's disease or Down's syndrome (Benton & Owens, 1993; Benton, Owens, & Parker, 1994; Benton & Sargent, 1992; Craft, Murphy, & Wenstrom, 1994; Craft et al., 1996; Craft, Zallen, & Baker, 1992; Hall, Gonder-Frederick, Chewing, Silveira, & Gold, 1989; Korol & Gold, 1998; Manning, Hall, & Gold, 1990; Manning, Honn, Stone, Jane, & Gold, 1998; Manning, Parsons, Cotter, & Gold, 1997; Manning, Parsons, & Gold, 1992; Manning, Ragozzino, & Gold, 1993; Manning, Stone, Korol, & Gold, 1998; Parsons & Gold, 1992). These findings indicate that glucose is a key component of a system that influences memory formation and that deficits in this system may contribute to cognitive impairments seen in some patients. Furthermore, these findings suggest that beta-adrenergic antagonists may prevent the memory-enhancing effect of emotional arousal in humans (Cahill et al., 1994; Nielson & Jensen, 1994; van Stegeren et al., 1998), at least in part, by preventing an epinephrine-induced increase in glucose levels. However, the recent finding that a peripherally acting beta-adrenergic antagonist (nadolol) does not prevent the memory-enhancing effects of emotional arousal suggests that adrenergic mechanisms influence memory through central, rather than peripheral, mechanisms (van Stegeren et al., 1998). This finding must be interpreted cautiously, however, because only the effects of one dose of nadolol were examined.

Collectively, the evidence reviewed above raises the possibility that increases in blood glucose levels, which may follow the release of epinephrine in response to arousing events, are part of the biological mechanism that allows emotional arousal to enhance memory (Gold, 1991, 1992b, 1995a; Korol & Gold, 1998; Wenk, 1989). The purpose of the present experiment was to determine whether memory-enhancing, emotionally arousing stimuli would increase circulating blood glucose levels in college students. We used the same stimuli as Cahill et al. (1994), who found that beta-adrenergic antagonists blocked the memory-enhancing effect of emotional arousal. A second goal was to examine the effects of glucose administration on the memory-enhancing effects of emotional arousal.

METHOD

Participants

The participants were 41 college students (mean age, 19.7 years; 26 males and 15 females) recruited through advertisements posted at the University of Virginia Reserve Officer Training Corps program facilities. The participants were paid \$29 (U.S.) for participating in the experiment. They signed a consent form explaining the procedure and filled out a medical questionnaire. Participants with a familial history of diabetes or those taking prescribed med-

ications other than antibiotics, acne medication, or birth control pills were excluded from participation in the experiment.

Materials and Apparatus

The narratives and slides were originally developed by Heuer and Reisberg (1990; Burke et al., 1992) and recently modified by Cahill and his colleagues (Cahill & McGaugh, 1995; Cahill et al., 1994). Evidence based on the use of these stimuli suggests that emotional arousal enhances memory and that this memory-enhancing effect of emotional arousal involves the actions of stress hormones (Cahill et al., 1994). There were a total of 11 slides in the slide show. Each slide was presented for 15 sec and was accompanied by a one-sentence tape-recorded narration. Both narratives were presented with flat, unemotional voices. The beginnings and ends of the two narratives were similar, and the content of the middle phase was made more emotionally arousing by including a description of a car accident and injury (see Table 1).

Blood glucose levels were measured with a Lifescan One Touch Basic blood glucose monitor. The participant's finger was pricked with a sterile pen lancet to obtain a single drop of blood. The drop of blood was applied to an enzyme pad and read by a reflectance meter, and the concentration of glucose in the drop was digitally displayed on the glucose monitor.

Procedure

The participants were told that this was an experiment in which the effects of mood and nutrients on physiological responses were examined; no mention of a memory test was made. They were asked to avoid food and beverages other than water after midnight on the night before scheduled appointments. All the participants were tested individually between 7:00 and 9:00 a.m. the following morning. A between-subjects experimental design was used in which different groups of participants were given lemonade that contained either glucose or saccharin and viewed a slide show that was accompanied by either an emotionally arousing or a relatively neutral narrative. Ten participants were in the saccharin-neutral group, 10 in the saccharin-arousal group, 10 in the glucose-neutral group, and 11 in the glucose-arousal group.

After the participants signed the consent form and answered the medical questionnaire, a baseline blood glucose measure was obtained, and then the participants were asked to consume a beverage that contained either dextrose anhydrous (glucose; 50 g/8 oz lemonade) or saccharin (23.7 mg). This dose of glucose was selected on the basis of previous reports indicating that it enhanced verbal declarative memory (Hall et al., 1989; Manning et al., 1990; Manning et al., 1997). The saccharin dose was based on previous reports indicating that it produced a comparably sweet taste and did not change blood glucose levels (Manning et al., 1990; Manning et al., 1997). The participants were blind to the beverage they received and were only told that it might contain a common nutrient. Fifteen min after the beverage was consumed, a blood glucose measure was obtained, and then the participants viewed the slide show. All the participants viewed the same slide show; however, half of the participants heard a neutral narrative accompanying the slide show, and the other half heard a closely matched, but more emotionally arousing, narrative (see Table 1). Immediately after viewing the slide show, the participants were asked to rate the emotionality of the narrative, using a scale from 0 to 10. A score of 0 indicated *not emotional*, and a score of 10 indicated *highly emotional*. The participants were also asked to rate their comprehension of the narrative on a scale from 0 to 10, where a score of 0 indicated *no understanding*, and a score of 10 indicated *complete understanding*. Blood glucose measures were obtained immediately following the slide show, 15 min later, and 30 min later.

The participants returned 2 weeks later, expecting to repeat the same experiment in the absence of fasting. Instead, they were ad-

Table 1
Content of the Narratives That Accompanied Each Slide

Slide	Narrative	
	Neutral	Emotionally Arousing
1	A mother and her son are leaving home in the morning.	Same as neutral
2	She is taking him to visit his father's workplace.	Same as neutral
3	The father is the chief laboratory technician at a nearby hospital.	Same as neutral
4	They check before crossing a busy road.	Same as neutral
5	While walking along, they pass the scene of a minor accident, which the boy finds interesting.	While crossing the road, the boy is struck by a runaway car, which critically injures him.
6	At the hospital, staff are preparing for a practice disaster drill, which the boy will watch.	At the hospital, the staff prepare the emergency room, to which the boy is rushed.
7	All morning long, surgeons practiced the standard disaster drill procedures.	All morning long, surgeons struggled to save the boy's life.
8	Special make-up artists were able to create realistic injuries on actors for the drill.	Specialized surgeons were able to successfully re-attach the boy's severed feet.
9	After the drill, while the father stayed with the boy, the mother left to phone her other child's pre-school.	After the surgery, while the father stayed with the boy, the mother left. . . .
10	Running late, she phones the preschool to tell them she will soon pick up her child.	Feeling distraught, she phones the preschool. . . .
11	Heading to pick up her child, she hails a taxi at the number nine bus stop.	Same as neutral

ministered an oral recall test, and then they were asked 76 multiple-choice questions that tested their recognition memory of both visual and narrative elements of the slide show. The questions were presented orally by the experimenter, and for each question, one correct and three incorrect but plausible choices were presented. The participants were instructed to guess for those questions in which they did not know the answer. At the end of the session, the participants were debriefed as to the intent of the study and were asked whether they were expecting a memory test at any time. All the participants indicated that they had not expected a memory test. They were then asked to avoid discussing the experiment with other potential participants.

Statistical Analyses

For purposes of analysis, the recall and recognition data were divided into three phases. Phase 1 was defined as the portion of the narrative that occurred prior to the presentation of the emotionally arousing information, Phase 2 was the portion of the narrative in which the emotionally arousing information was presented, and Phase 3 was the portion of the narrative that occurred following the emotionally arousing manipulation. The recognition data were scored for percent total recognition and percent recognition by phase. The recall data were scored by condensing sentences into meaningful segments. For example, the sentence "A mother and son are leaving home," which accompanied slide one (see Table 1), was divided into two segments: (1) *a mother and son* and (2) *are leaving home*. The recall data were scored for total recall and recall by phase.

The data were analyzed in two ways. The first set of analyses were omnibus analyses of variance conducted with two between-subjects factors of beverage (saccharin vs. glucose) and narrative (neutral vs. emotionally arousing). Dependent variables consisted of recall and recognition memory measures and circulating blood glucose levels (both absolute and relative to baseline). The second set of analyses addressed comparisons that were specific to the goals of the study—namely, the relationship between memory for emotionally arousing information and circulating blood glucose levels and the effect of glucose administration on memory. For the first goal, the memory measures used in the omnibus analyses were compared for the two saccharin groups and were related to circulating blood glucose levels. To address the second goal, memory measures obtained from participants given saccharin and glucose

were compared for the neutral narrative and then for the emotionally arousing narrative. All the tests were one-tailed, and an alpha level of .05 was used as a criterion of statistical significance.

RESULTS

Memory measures were initially analyzed in sets of omnibus analyses of variance including between-subjects factors of both beverage (saccharin vs. glucose) and narrative (neutral vs. arousal). The omnibus analyses were not statistically significant, although interesting trends were observed, as is shown in Figure 1, which illustrates percent recognition of information as a function of narrative phase. In general, participants in the saccharin condition who heard the emotionally arousing narrative demonstrated greater recognition memory, particularly for information from the neutral first phase and the emotionally arousing second phase of the narrative. The participants in the other three conditions demonstrated remarkably similar recognition memory, even for the differing information in Phase 2 of the narrative. Also, the participants in the glucose condition who heard the neutral narrative tended to have impaired recognition memory for information from the final phase of the narrative, although this effect was not statistically significant.

Given the strong trends and our original hypothesis regarding the effects of the emotionally arousing narrative on memory and blood glucose levels, we conducted the separate analyses reported below, which address the specific goals of our study.

The Effects of Memory-Enhancing, Emotionally Arousing Stimuli on Blood Glucose Levels

The primary goal of this study was to determine whether circulating blood glucose levels increase in as-

Figure 1. Recognition memory for the neutral and emotionally arousing narratives as a function of beverage and phase of the narrative.

sociation with memory-enhancing, emotionally arousing stimuli. Consequently, recognition memory data for the participants in the saccharin condition were analyzed, and then the effects of the narratives on blood glucose levels were examined.

Ratings. The emotionally arousing narrative was rated as being more emotional than the neutral narrative [$t(18) = 4.19, p < .01$]. The mean ($\pm SEM$) emotional rating was $2.5 (\pm 0.45)$ for the neutral narrative versus $5.7 (\pm 0.62)$ for the emotionally arousing narrative. The narratives were rated as equally understandable [$t(18) = 0.90$], with means of $9.2 (\pm 0.29)$ and $9.5 (\pm 0.17)$ for the neutral and emotionally arousing narratives, respectively.

Recognition memory. The results of the forced multiple-choice test were analyzed for percent correct of total information recognized, as well as for percent correct as a function of narrative phase. Total recognition was greater for participants who heard the emotionally arousing narrative than for subjects who heard the neutral story [$t(18) = 1.89, p < .05$]. Furthermore, as is shown in Figure 2, this enhanced recognition was restricted to the middle phase of the narrative, which is the phase in which the emotionally arousing information was presented [$t(18) = 1.78, p < .05$]. Although there was a tendency for enhanced memory for information presented in Phase 1 for

the participants who heard the emotionally arousing narrative, this effect was not statistically significant [$t(18) = 1.41$].

Free recall. There were no differences between the total amount of information recalled by participants who heard the neutral narrative and participants who heard the emotionally arousing narrative [$t(18) = 0.28$]. Mean recall was $9.9 (\pm 1.57)$ and $9.3 (\pm 1.46)$ units of information for participants in the neutral and the emotional arousal conditions, respectively. Consistent with the findings obtained with recognition memory, the participants in the emotional arousal condition recalled significantly more information from the emotionally arousing middle phase of the narrative than did subjects who heard the neutral narrative [$t(18) = 1.95, p < .05$].

Circulating blood glucose levels. Circulating blood glucose levels were expressed and analyzed as percent change from baseline. Baseline levels were determined as the average of the first two blood glucose measurements, obtained prior to showing the slide show. Figure 3 shows percent change in circulating blood glucose for participants in the saccharin condition who heard the emotionally arousing or the neutral narrative. As is shown in the figure, relative to baseline measures, there was an increase in circulating blood glucose levels immediately and 15 min

Figure 2. Recognition memory for the neutral and emotionally arousing narratives for participants in the saccharin condition as a function of the phase of the narrative.

after viewing the emotionally arousing narrative ($z = 3.10$ and 2.48 , $p < .05$); this effect was maintained 30 min after the slide show ($z = 1.65$, $p < .05$). The blood glucose levels of participants who viewed the neutral story showed no change from baseline; indeed, although not statistically significant, circulating blood glucose levels tended to drop below baseline by the end of the session ($z = 1.23$, $p < .07$).

Effects of Glucose Administration on Memory

A second goal of this study was to examine the effects of glucose administration on memory of the narratives.

Ratings. No differences were obtained in ratings of emotionality of the neutral or the emotionally arousing narrative as a function of glucose administration. The mean emotionality ratings for participants who heard the neutral narrative was $2.5 (\pm 0.45)$ in the saccharin group and $1.9 (\pm 0.43)$ in the glucose group [$t(18) = 0.95$]. Similarly, the mean emotionality ratings for participants who heard the emotionally arousing narrative was $5.1 (\pm 0.46)$ in the glucose group and $5.7 (\pm 0.62)$ in the saccharin group [$t(19) = 0.80$]. Glucose administration also did not affect comprehension ratings. The mean comprehension rating for participants who heard the neutral narrative was $9.2 (\pm 0.29)$ in the saccharin group and $9.3 (\pm 0.34)$ in the glucose group [$t(18) = 0.22$]. Likewise, the mean com-

prehension rating for participants who heard the emotional narrative was $9.5 (\pm 0.17)$ in the saccharin group and $9.6 (\pm 0.20)$ in the glucose group [$t(19) = 0.51$].

Circulating blood glucose levels. Glucose administration significantly increased circulating blood glucose levels [$F(4,76) = 41.81$, $p < .0001$]. Circulating blood glucose levels increased across time periods, from a mean of $83.8 (\pm 2.1)$ mg/dl at baseline to a mean of $113.3 (\pm 4.2)$ mg/dl 15 min after consuming the glucose beverage, to a mean of $124.4 (\pm 4.3)$ mg/dl immediately after viewing the slide show, reaching a maximum mean of $134.4 (\pm 5.6)$ mg/dl approximately 35 min after consuming the beverage (15 min after the slide show), and then decreasing to a mean of $126.6 (\pm 5.0)$ mg/dl 15 min later [$t(20) = 6.93, 3.86, 3.28$, and -2.3 , $p < .05$, comparing each time with the subsequent time].

There were no differences in blood glucose levels as a function of type of narrative for participants administered glucose [$F(1,19) = 0.30$], nor was there an interaction between type of narrative and circulating blood glucose levels [$F(4,76) = 0.51$].

As is shown in Figure 4, relative to baseline, blood glucose levels remained consistently above baseline throughout the experiment (z s ranging from 16.26 to 19.63 , $ps < .05$).

Figure 3. Percent change in circulating blood glucose levels as a function of narrative type for participants in the saccharin condition.

Effects of Glucose Administration on Memory of the Neutral Narrative

Recognition memory. Comparisons between the saccharin and the glucose conditions were made for percent total information correctly recognized, as well as for percent correct recognition for each phase of the narrative. The results of this analysis indicated that there were no significant differences between the saccharin and the glucose participants for any of the recognition measures, although there was a tendency for glucose to decrease percent recognition for the final part of the narrative [$t(18) = 1.67$, p (one-tailed) $< .07$].

Free recall. The participants in the saccharin condition tended to recall more information from the neutral narrative than did the participants in the glucose condition [$t(18) = 1.76$, p (one-tailed) $< .06$]. Mean recall was 9.9 (± 1.57) for the participants in the saccharin condition and 6.5 (± 1.13) for the participants in the glucose condition. There was no overall effect of phase of the narrative on free recall by the participants in the saccharin and glucose groups [$F(1,18) = 2.26$]; however, a phase-by-phase analysis revealed that the participants in the glucose condition had less recall than did the participants in the saccharin condition for the last phase [$t(18) = 0.62$ and

0.72, for Phase 1 and Phase 2, respectively, and $t(18) = 2.45$, $p < .05$, for Phase 3].

Effects of Glucose Administration on Memory of the Emotionally Arousing Narrative

Recognition memory. There were no significant effects of glucose administration on total amount of information recognized. The participants given glucose tended to have less total recognition than did the participants in the saccharin condition [$t(19) = 1.55$, $p < .07$]; mean recognition was 61% ($\pm 2\%$) and 55% ($\pm 4\%$) for the saccharin versus the glucose condition.

The recognition-by-phase results indicated that glucose administration prevented the memory-enhancing effect of the emotionally arousing manipulation for the middle phase of the narrative (see Figure 5). The participants in the glucose condition recognized less information from the emotionally arousing middle part of the narrative than did the participants in the saccharin condition [$t(19) = 1.90$, $p < .05$]; there were no differences in recognition for the other phases [$t(19) = 1.41$ and 0.37, for Phase 1 and Phase 3, respectively]. Although percent recognition-by-phase for participants in the saccharin condition demonstrated a significant quadratic effect [$F(1,18) =$

Figure 4. Percent change in circulating blood glucose levels as a function of narrative type for participants in the glucose condition.

11.97, $p < .05$], the percent recognition-by-phase of participants in the glucose condition demonstrated a linear effect [$F(1,20) = 5.67$, $p < .05$]. Thus, these analyses indicate that recognition of the emotionally arousing, middle phase of the narrative was significantly enhanced in the saccharin condition, but not in the glucose condition.

Free recall. The participants in the glucose condition tended to recall less information (6.5 ± 1.48) than did the participants in the saccharin condition (9.3 ± 1.46), although there were no statistically significant differences for this [$t(19) = 1.32$] or any of the recall measures.

DISCUSSION

The findings of the present experiment indicate that blood glucose levels increased in college students after they heard a narrative with high emotional content but did not change in participants who heard a narrative with low emotional content. Furthermore, this increase in blood glucose levels was paralleled by better memory for the emotionally arousing information. Our results also demonstrate that giving participants glucose, at a dose that produces greater increases in blood glucose levels than did

presenting the emotionally arousing narrative alone, prevented the enhancing effects of the emotionally arousing narrative on memory.

Inasmuch as all the participants viewed the same slide show and because both narratives were presented with similar tones of voice, our findings demonstrate that a person's own cognitive reactions to emotionally arousing information lead to increases in blood glucose levels. These results are consistent with those obtained from animal studies, which indicate that glucose is released in rodents following emotionally arousing situations (de Boer, Koopmans, Slangen, & van der Gugten, 1990; Gold & Stone, 1988; Hall & Gold, 1986). These findings are also in agreement with research findings from humans that show that brief exposure to emotional stimuli increases neuroendocrine secretions, including levels of epinephrine, adrenocorticotrophic hormone, beta-endorphin, growth hormone, and cortisol (Gerra et al., 1996). Our findings are also consistent with those of Armario and colleagues (Armario, Marti, Molina, de Pablo, & Valdes, 1996), who observed an increase in plasma glucose levels in college students prior to writing college exams. However, the magnitude of the blood glucose increase we observed

Figure 5. Recognition memory for the emotionally arousing narrative as a function of beverage and phase of the narrative.

(4%–6%) was smaller than that observed in the experiment by Armario and colleagues (approximately 28%). This difference may be due to the fact that participants in the latter experiment had not fasted and thus would be likely to have higher baseline levels of endogenous glucose stores than did the participants in our experiment. The differences in magnitude may also be related to differences in the intensity of the emotionally arousing stimuli that were used. It is probable that the emotional arousal produced by the anticipation of writing a real-life exam is greater than that produced by watching a slide show in an experimental situation.

The present findings replicate previous results that indicated that the emotionally arousing narrative preferentially enhanced memory for Phase 2, which is the phase of the narrative in which the emotionally arousing information was presented (Burke et al., 1992; Cahill, Babin-sky, Markowitsch, & McGaugh, 1995; Cahill et al., 1994). We also obtained comparable ratings of the emotionality of the narratives. As in the study by Cahill et al. (1994), we found that the emotionality ratings were not affected by pharmacological manipulations (beta-adrenergic antagonist in their study, glucose in ours). We have extended their findings by demonstrating that the memory-enhancing emotionally arousing narrative elevates blood glucose levels. Furthermore, we have shown that larger increases in blood glucose levels, which were produced by

the exogenous administration of glucose, prevented the enhancing effect of emotion on memory. This finding is also in agreement with those of Cahill et al. (1994), who found that a beta-adrenergic antagonist selectively impaired memory of the emotionally arousing narrative. The magnitude of the increase in blood glucose levels produced by glucose in the present experiment is comparable with that observed in other studies that administered the same dose of glucose to a young adult population (see Korol & Gold, 1998). The present findings indicate that glucose administration did not enhance memory of the neutral narrative. Unlike the findings with aged adults, glucose administration does not typically enhance memory in young adults, although it will do so when task difficulty is increased (Korol & Gold, 1998). Thus, it is possible that glucose did not affect memory of the neutral narrative in the present experiment because the mnemonic requirements were not sufficiently demanding.

The findings of the present experiment indicate that the enhancing effect of emotional arousal on memory is associated with small increases in blood glucose levels, whereas large increases prevent the enhancement. Such findings add to the existing evidence that indicates that the memory-modulating abilities of glucose are dose dependent. In rats, lower doses of glucose enhance memory, whereas higher doses impair it (Gold, 1986). In experimentally induced diabetes, deficits in water maze are as-

sociated with severe but not with moderate hyperglycemia (Biessels et al., 1996). In aged humans, doses of glucose that are optimal for producing memory enhancement increase blood concentrations to values near 160–185 mg/dl (see Parsons & Gold, 1992). Larger increases typically have no effect, although, in one report, increases to approximately 225 mg/dl impaired memory (Craft et al., 1993). This inverted-U-shaped dose–response curve is typical of many memory-modulating drugs. For example, epinephrine enhances memory at low doses and impairs it at high doses, and the enhancing and impairing effects of epinephrine are mediated via different mechanisms. Specifically, epinephrine enhances through influences on a central noradrenergic system but impairs through activation of a central opioid peptidergic system (McGaugh, 1989). We have obtained evidence in rats that suggests that the memory-impairing effects of hyperglycemia may involve an interaction with the GABAergic neurotransmitter system (Parent & Gold, 1997; Parent, Laurey, Wilkniss, & Gold, 1997). Our findings raise the possibility that memory may be impaired in experimental and clinical cases of hyperglycemia via a mechanism that involves an interaction between glucose and the GABAergic neurotransmitter system. However, the mechanism through which glucose prevented the enhancing effect of emotional arousal on memory in the present experiment remains unclear. One possibility is that the effects of the emotionally arousing stimuli on blood glucose levels summed with the effects of the exogenously administered glucose to produce memory-impairing concentrations of glucose. This possibility is not supported, however, by the finding that there were no differences between the blood glucose levels of participants given glucose who heard the neutral narrative and those of participants who heard the emotionally arousing narrative.

To our knowledge, this is the first report examining the interaction between glucose and emotional memory in human participants. Thus, there are questions that will need to be addressed in future studies. For example, our study did not determine whether increases in blood glucose observed following the emotionally arousing narrative directly contributed to the memory-enhancing effects of emotional arousal. Thus, it will be essential to determine whether glucose, given at doses that produce increases in blood glucose levels comparable with those produced by the emotionally arousing narrative, will enhance memory of the neutral narrative. It would also be interesting to know whether the increase in blood glucose levels is associated with the valence of the emotion (i.e., positive or negative) and/or the degree of arousal produced by the stimuli (Bradley, Greenwald, Petry, & Lang, 1992; Hamann, Cahill, & Squire, 1997). Also, to characterize the interactions between the peripheral stress hormones and glucose, it will be important to determine whether the emotionally arousing narrative elevates blood glucose levels in participants that are given beta-adrenergic antagonists.

It is likely that the enhancing effect of emotional arousal observed in the present experiment involves acti-

vation of the amygdala. Extensive evidence from studies of animal learning and memory indicates that the amygdala is critically involved in emotional memory processes (Davis, 1992; LeDoux, 1992; McGaugh, Introini-Collison, Cahill, Kim, & Liang, 1992). In human participants, imaging studies indicate that the amygdala is activated by and involved in the encoding of negative emotional visual stimuli (Cahill et al., 1996; Irwin et al., 1996; Morris et al., 1996). Furthermore, participants with selective damage to the amygdala have impaired memory of emotional information (Adolphs, Cahill, Schul, & Babinsky, 1997; Babinsky et al., 1993; Bechera et al., 1995; Cahill et al., 1995; Markowitsch et al., 1994). Of particular interest are the findings from patients with bilateral amygdala damage who were tested with the same stimuli as those used in the present experiment (Adolphs et al., 1997; Cahill et al., 1995). Although these patients had intact memory for the first phase of the story, they did not have enhanced memory for the emotionally arousing portion of the narrative.

In conclusion, the findings of the present experiment indicate that a memory-enhancing emotionally arousing narrative increases blood glucose levels. Also, glucose administration, at doses that produce much larger increases in blood glucose levels, prevents the enhancing effect of emotion on memory. Our findings suggest that increases in circulating blood glucose levels that occur during emotionally arousing events may make memory for those events especially profound. In addition, it is possible that the responses of this system contribute to intense memories of stressful events and, in exaggerated form, perhaps the unfortunately indelible memories observed in post-traumatic stress disorder. Finally, these results demonstrate that findings and theories based on rodent studies of learning and memory apply to humans.

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