Rationality and emotionality: serotonin transporter genotype influences reasoning bias

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INTRODUCTION

Humans are not perfectly rational. We display biases leading to errors in reasoning and decision making (Tversky and Kahneman, 1974). One common type of bias in deductive reasoning is when one accepts or rejects a conclusion based on one’s knowledge about the world (hereafter termed beliefs) rather than logical validity (Evans et al., 1983). In relational reasoning tasks, one must evaluate whether a conclusion follows logically from the premises, regardless of the believability of the content. For example, given the premises, ‘Cars are bigger than motorcycles’ and ‘Motorcycles are bigger than airplanes’, the conclusion ‘Cars are bigger than airplanes’ is logically valid but unbelievable, as cars are not bigger than airplanes in the real world. Participants tend to be slower or less accurate in accepting unbelievable conclusions as logically valid and also in accepting believable conclusions that are logically invalid (Roberts and Sykes, 2003). Thus, accepting conclusions that are incongruent with our beliefs interferes with logical reasoning. Conversely, when the validity and believability of the conclusion are congruent (valid, believable or invalid, unbelievable), participants are faster or more accurate in evaluating the conclusion. Reduced performance for incongruent than congruent conclusions, termed the belief-bias effect, indexes how much our beliefs interfere with reasoning and has been demonstrated using categorical syllogisms and conditional and relational reasoning problems (Byrne and Tasso, 1999; Goel and Dolan, 2003; Roberts and Sykes, 2003).

In addition to our beliefs, emotion also influences deductive reasoning. Two lines of evidence indicate that manipulation of emotional processing hinders the reasoning process. First, affective state (pre-existing or induced) reduces logical reasoning performance. Patients with anxiety disorders made more errors on a conditional reasoning task (Wason Selection Task) than healthy controls when reasoning with anxiety-provoking material (de Jong et al., 1997). In healthy participants, experimentally inducing negative or positive mood resulted in more errors on the Wason Selection Task than without mood manipulation (Oaksford et al., 1996). Second, affective content (pre-existing or conditioned) reduces reasoning performance relative to neutral content. Given logically identical reasoning problems, participants made more errors when problems comprised emotionally charged statements (e.g. ‘If there is danger, then one feels nervous’) than neutral statements (e.g. ‘If one is in a library, then one sees books’) for conditional (Blanchette and Richards, 2004; Blanchette, 2006) and categorical (Leflfd, 1946) reasoning problems. Reduced reasoning accuracy was also observed for neutral words associated with negative or positive emotional pictures relative to those associated with neutral pictures (Blanchette and Richards, 2004; Blanchette, 2006). Thus, neutral content with experimentally acquired emotional valence also reduced deductive reasoning performance. Together, these findings indicate that emotional state and content influence logical reasoning.

If emotional processing influences logical reasoning, then individual differences in emotional reactivity ought to influence reasoning performance. One source of individual differences in emotional reactivity is a polymorphism in the promoter region of the serotonin transporter gene (5-HTTLPR) that results in short (S) and long (L) variants. The S allele is linked to lower expression of serotonin transporter mRNA (Hu et al., 2006). Further, the L allele contains an A to G single-nucleotide polymorphism (SNP, rs25531) that influences transcriptional efficiency, rendering the L allele functionally similar to the S allele (Hu et al., 2006). Findings of studies comparing S carriers (SS alone or with SL) with homozygous L carriers (e.g. LL or LLA) suggest that the S allele is associated with higher emotional reactivity. Specifically, S allele carriers were overrepresented in patients with affective disorders (Caspi et al., 2003), exhibited more depressive and anxiety-related behaviors despite being healthy (Lesch et al., 1996; Gonda et al., 2009) and showed a stronger bias towards emotional content in spatial attention (Beers et al., 2009) and interference (Koizumi et al., 2010) tasks. Further, the amygdala, a critical brain region underlying emotional behavior, is more responsive to negative stimuli in healthy S carriers (Munafo et al., 2008). Together, these findings indicate that S (and L) carriers differ in emotional reactivity from L carriers (and L alone). No study has examined whether these allelic differences influence emotional processing in the context of logical reasoning.

We investigated the effect of 5-HTTLPR genotype on belief-bias in relational reasoning problems with and without emotional content. In light of evidence indicating functional similarity between the S and L carriers (Hu et al., 2006), we included L carriers in the S group as done...
in past work (Armbruster et al., 2009). Other heterozygous carriers (SLA, LALG) were excluded in order to maximize observed allelic differences (Roiser et al., 2009). We predicted that carriers of the 5-HTTLPR S or L allele (SS, LSL) would demonstrate increased belief-bias relative to homozygous carriers of the LA allele (LALG) during reasoning with emotional, but not non-emotional, content. This prediction is based upon findings of increased sensitivity to negative affective stimuli in S (and L) carriers, which ought to make suppression of beliefs with emotional content more difficult relative to LA carriers. Such a finding would indicate that serotonin-related differences in emotional reactivity influence cognitive control during deductive reasoning. Furthermore, in light of past findings relating the S allele to increased anxiety, we also examined the association between the 5-HTTLPR genotype, trait anxiety and belief-bias for emotional material.

METHODS
Participants
One hundred and sixty-nine Georgetown University undergraduates (65 males) of primarily European descent without history of psychiatric diagnosis or medication, who were native English speakers or fluent by age 10 years, participated for course-credit or payment. Consent was acquired according to Institutional Review Board guidelines. Participants provided a saliva sample that was analysed for 5-HTTLPR and the rs25531 SNP in the serotonin transporter gene (SLC6A4). Genotype frequencies were in Hardy-Weinberg equilibrium ($\chi^2 = 2.45, df = 1, P > 0.1$). For SLC6A4, after excluding LA and LS/LG genotypes, our final sample included two groups, LAL and SLSL. The LALG group ($N = 44$; 44% males; 85% European descent; age: $M = 19.4$, s.d. = 1.2) did not differ from the SS/SL group ($N = 34$; 41% males; 74% European descent; age: $M = 19.1$, s.d. = 1.1) in age ($P > 0.4$), gender ($P > 0.8$) or ethnicity ($P > 0.2$). The SS/SL group was composed of SS ($n = 22$) and SLSL ($n = 12$) carriers. No participants had the rare LALG genotype.

Genotyping
Saliva samples (Oragene, Canada) were analyzed for 5-HTTLPR using a two-step process. First, the long (L) and short (S) variants were determined. The repeat polymorphism in the promoter region of the 5-HT gene was typed by PCR as previously described (Lesch et al., 1996) using the following primers at concentrations of $10 \mu M$; forward: 5'-GGCGTTGCCGCTCTGAATGC-3'; reverse: 5'-GAGGGA

Table 1
| Trial type | Emotional | Non-emotional |
|------------|-----------|---------------|
| Congruent | Cockroaches are smaller than snakes. | Adults are younger than children. |
| Incongruent | Cockroaches are bigger than maggots. | Children are older than infants. |

Stimulus materials
Stimuli consisted of 96 three-term relational reasoning problems (e.g. A > B, B > C, therefore A > C) that varied by emotion and congruency (Table 1). Words for the reasoning problems were selected from the Affective Norms for English Words database (ANEW; Bradley and Lang, 1999), which provides ratings for arousal and valence on a 10-point scale. Emotional problems contained primarily negative (<4 = negative, 84.7% >7 = positive valence, 15.3%) and highly arousing (>3.5; mean: 5.9) words, whereas non-emotional problems contained words that were neither positive nor negative (4–7 valence) and low in arousal (<5.5; mean: 4.2).

Problems also varied on belief-logic congruence. For congruent problems, the validity of the conclusion was in accordance with semantic beliefs (valid, believable and invalid, unbelievable). For incongruent problems, the validity of the conclusion was in conflict with semantic beliefs (valid, unbelievable and invalid, believable). The 96 logic problems varied by Emotional content (emotional, non-emotional) and Congruency (congruent, incongruent), creating four conditions, 24 problems each: Emotional Congruent, Emotional Incongruent, Non-emotional Congruent and Non-emotional Incongruent. Conditions were equated for conclusion believability (12 believable, 12 unbelievable), validity (12 valid, 12 invalid), determinacy (18 deterministic, 6 indeterminate) and content type (13 non-living, 6 living, 5 abstract).

Procedure
Practice
Following task description and explanation of the task (what constitutes a logical conclusion), participants completed 14 practice problems where they determined if the conclusion followed logically from the premises by basing the decision on logical form and not on the factual truth or falsity of the conclusion. Participants were given unlimited time and were asked to re-think the problem if they made errors and to correct the error until all problems were correctly solved.

Reasoning task
Problems were presented on a computer screen in pre-determined random order held constant across participants. Participants were
instructed to press the 'F' key if a problem was 'logical' and 'J' key if it was 'not logical', as quickly as possible. Premise 1 appeared on the screen for 3s, followed by Premise 2 below it for 3s, and then the conclusion below it, after which all three remained on the screen for 6s. Participants had 6s to respond, and the next problem appeared immediately after their response or after the 6s. No feedback was provided.

**Belief questionnaire**

The questionnaire measured whether the participant’s beliefs matched those of the experimenters. Forty-eight conditions (half believable, half unbelievable) were selected randomly, including 12 problems from each of the four experimental conditions. Participants were asked to mark each conclusion as 'True', 'False' or 'Don’t Know', based on their own knowledge.

**Working memory**

Participants completed a verbal N-back task, consisting of six alternating 1.2-min blocks of two- and three-back conditions (‘low’ and ‘high’ working memory load, respectively). Each block comprised 24 trials preceded by an instruction screen stating the type of trial in the block, for example, ‘2-back’ or ‘3-back’. For all conditions, one letter was presented on the screen at a time (for 0.5s followed by a 2.5-s inter-trial interval), and the participant was instructed to press a button with their right index finger on the keyboard when the letter on the screen was the same as the one presented n trials previously. In the two-back condition, participants were instructed to press the button if the letter was the same as 2 before it (e.g. ‘R’ then ‘L’ then ‘R’); in the three-back condition, participants were instructed to press the button if the letter was the same as 3 before it (e.g. ‘M’ then ‘K’ then ‘M’). The number of target responses was identical across trial conditions. Stimuli comprised consonants only; vowels were omitted to prevent encoding series of letters as pronounceable strings.

**Trait anxiety**

Participants completed the STAI (Spielberger et al., 1983), a self-report measure of state and trait anxiety. Scores of trait but not state anxiety were used in further analysis in order to examine the influence of a stable rather than situational characteristic of emotionality.

**RESULTS**

**Belief questionnaire**

For each participant, responses were coded based upon the match with the experimenter as agree (true/false by both), disagree (true/false mismatch between the two) or uncertain (‘don’t know’). Mean agreement revealed no genotype differences. Mean percentage of ‘agree’ responses was emotional: congruent (L ALA: M 6.9; SS/SLG: M 7.3; SS/SLG: M 4.8%; s.d. 2.8; SS/SLC: M 4.8%; s.d. 2.9; P > 0.3) were collapsed across conditions.

| Table 2 Mean (s.d.) accuracy and reaction time for relational reasoning problems with emotional and non-emotional content in SS/SLC and L Ala carriers |
|-----------------------------------------------|
| **Short (SS/SLC, N = 34)** | **Long (L Ala, N = 41)** |
| **Accuracy** | | |
| Emotional Congruent | 85.57% (10.31) | 85.88% (10.19) |
| Incongruent | 73.93% (14.01) | 80.74% (10.82) |
| Non-emotional Congruent | 85.06% (11.54) | 88.27% (8.19) |
| Incongruent | 77.94% (12.59) | 80.67% (10.75) |
| **Reaction time** | | |
| Emotional Congruent | 2482 ms (718) | 2411 ms (572) |
| Incongruent | 2850 ms (584) | 2700 ms (468) |
| Non-emotional Congruent | 2586 ms (546) | 2447 ms (528) |
| Incongruent | 2785 ms (588) | 2676 ms (521) |

**Reasoning task**

A response was scored as ‘correct’ if it was consistent with the logical validity of the problem and ‘incorrect’ if it was not consistent with logical validity or if there was no response within 6s (timed-out; M = 7% of problems). For each participant, mean accuracy (% correct) and mean reaction time (ms) for correct responses were computed for congruent and incongruent problems with and without emotional content (Table 2). Mixed ANOVAs with genotype (SS/SLC vs L Ala) as a between-subject factor and congruency (congruent vs incongruent) and emotion (emotional vs non-emotional content) as within-subjects factors were computed separately for accuracy and reaction time. Controlling for ethnicity and for working memory performance (3-back accuracy) did not change the significance of any reported results.

**Accuracy**

A main effect of congruency [F(1, 73) = 65.99, P < 0.001, η2 = 0.47] indicated a significant belief-bias effect as participants were more accurate for belief-logic congruent (M = 85.19%, s.d. = 8.77%) than incongruent (M = 78.32%, s.d. = 10.83%) problems. While no other main effects or two-way interactions reached significance (P > 0.10), the genotype × congruency × emotion interaction was significant [F(1, 73) = 6.28, P = 0.014, η2 = 0.08]. Planned comparisons testing for group differences indicated that accuracy was lower in SS/SLC (M = 73.93%, s.d. = 14.01) relative to L Ala (M = 80.74%, s.d. = 10.82) participants, only for problems in the emotional incongruent condition [t(73) = 2.37, P = 0.020]; genotype groups did not differ in other conditions (P > 0.20). Further, planned comparisons showed that each genotype group exhibited belief-bias (congruent > incongruent) for both emotional (SS/SLC: t(33) = 6.31, P < 0.001; L Ala: t(40) = 3.240, P < 0.001) and non-emotional (SS/SLC: t(33) = 3.71, P = 0.001; L Ala: t(40) = 5.50, P = 0.002) conditions.

As expected based on the three-way interaction, a genotype × emotion ANOVA on the amount of belief bias (Congruent minus Incongruent) revealed an interaction [F(1, 73) = 6.28, P = 0.014, η2 = 0.08], such that SS/SLC carriers (M = 11.64%, s.d. = 10.75) had higher belief-bias relative to L Ala carriers (M = 5.14%, s.d. = 10.16) for emotional problems [t(33) = 2.68, P = 0.009; Figure 1]. Amount of belief-bias did not differ by genotype for non-emotional problems (SS/SLC: M = 7.12%, s.d. = 11.19; L Ala: M = 7.60%, s.d. = 9.18; P > 0.8). Further, SS/SLC carriers had higher belief-bias for emotional (M = 11.64%, s.d. = 10.75) relative to non-emotional (M = 7.12%, s.d. = 11.19) problems [t(33) = 2.234, P = 0.032]; belief-bias in L Ala
carriers did not differ by emotional content \((P > 0.2)\). No main effects reached significance \((P’s > 0.1)\).

**Reaction time**
A main effect of congruency \([F(1, 73) = 64.86, P < 0.001, \eta^2 = 0.47]\) showed that participants were faster to evaluate conclusions of congruent \((M = 2477 \text{ ms}, \text{s.d.} = 555)\) than incongruent \((M = 2747 \text{ ms}, \text{s.d.} = 505)\) problems. Thus, participants’ response latencies exhibited a belief-bias effect. No other main effects or interactions reached significance \((P’s > 0.1, \text{Table 2})\).

**Working memory**
A between-subject ANOVA showed that mean accuracy for two-back \((L_A L_A; M = 92.78\%, \text{s.d.} = 7.89; \text{SS/SLG}; M = 91.84\%, \text{s.d.} = 9.82)\) and three-back \((L_A L_A; M = 88.03\%, \text{s.d.} = 14.11; \text{SS/SLG}; M = 82.17\%, \text{s.d.} = 17.89)\) working memory conditions did not differ between groups \((P’s > 0.1)\). Furthermore, neither two-back \((P = 0.51)\) nor three-back \((P = 0.20)\) accuracy correlated with emotional belief-bias scores. Including three-back accuracy as a covariate did not change any significance value in our belief-bias ANOVAs or correlational analyses.

**Trait anxiety**
A between-subject ANOVA showed that mean standard scores were higher in \(\text{SS/SLG} (M = 50.48, \text{s.d.} = 8.07)\) than \(L_A L_A (M = 46.32, \text{s.d.} = 7.56)\) participants \([F(1,71) = 5.25, P = 0.025, \eta^2 = 0.07]\). Further, anxiety scores correlated positively with the amount of belief-bias for problems with emotional \((r = 0.24, P = 0.04)\) but not non-emotional \((r = 0.03, P = 0.789)\) content (Figure 2). Thus, individuals with higher trait anxiety were more biased towards their beliefs during reasoning with emotional content alone.

**OLS linear regression**
In light of the association between anxiety and emotional belief-bias and higher anxiety in \(\text{SS/SLG}\) carriers, we examined the role of genotype in the relationship between anxiety and emotional belief-bias. A simple regression model with anxiety scores as the sole independent variable revealed that the estimated association between anxiety and emotional belief-bias was 0.32 with an associated standard error (s.e.) of 0.15 \((P = 0.04; \text{standardized } \beta = 0.24, \text{replicating the bivariate correlation})\). This association was reduced to non-significance \((P > 0.1)\) upon adding 5-HTTLPR genotype to the model. This reduction suggests that the positive association between anxiety and emotional belief-bias is explained by the covariance between both behavioral variables (anxiety and emotional belief-bias) and genotype. Moreover, genotype was significantly associated with emotional belief-bias even with anxiety held constant \((b = 5.61, \text{s.e.} = 2.46, P = 0.02). The unstandardized coefficient of 5.61 indicates that the \(\text{SS/SLG}\) group scored 5.61% points higher on emotional belief-bias than the \(L_A L_A\) group, even with anxiety held constant. With 5-HTTLPR and anxiety included, the model accounted for 12% of variance in emotional belief-bias.

**DISCUSSION**
A polymorphism of the 5-HTTLPR genotype influenced the extent to which beliefs interfered with deductive reasoning, selectively for emotional content. Overall, participants exhibited belief-bias, defined by more errors and slower evaluation of conclusions of relational reasoning problems in which beliefs and logical structure were in conflict relative to congruent. However, the amount of belief-bias was larger in carriers of the \(S/L_G\) alleles relative to the \(L_A\) allele, for problems with highly arousing and emotionally valenced content but not for those with less arousing, less emotional content. Further, trait anxiety correlated positively with belief-bias for emotional problems, and the 5-HTTLPR genotype accounted significantly for the variance in this
relationship. Thus, individual variation in deductive reasoning, a higher cognitive ability, depends upon an interaction between semantic content and serotonin-based genetic differences in emotional reactivity.

It has been argued that reasoning with meaningful content involves inhibiting one’s semantic knowledge in order to process the logical structure (Houde et al., 2000; Handley et al., 2004; Prado and Noveck, 2007; De Neys et al., 2008; Luo et al., 2008; De Neys and Franssens, 2009). Behaviorally, suppression of one’s beliefs is effortful as reflected in failures or slower speed of reasoning for problems where beliefs and logic conflict, as observed in this study. Support for the involvement of inhibitory processing during deductive reasoning comes from two sources. First, inhibitory control abilities are associated with the amount of belief-bias. Children with higher response inhibition (as measured by the stop signal task) had lower belief-bias in conditional and relational reasoning tasks (Handley et al., 2004). Second, functional brain imaging studies show that a brain region known to support inhibitory control, right inferior frontal cortex (IFC; [Aron et al., 2004]) was consistently activated during belief-bias [e.g. incongruent vs congruent and neutral problems (Goel et al., 2000; Stollstorff et al., 2012); logical vs belief-based responses for incongruent problems (Goel and Dolan, 2003)] and increased activity of this region but not its left-hemisphere homologue was associated with less belief-bias (Tsujii and Watanabe, 2010). Further, disruption of neural activity in the right, but not left, IFC with transcranial magnetic stimulation reduced accuracy for incongruent, but not congruent, syllogisms, thereby increasing belief-bias relative to a control group (Tsujii et al., 2010). Together, these findings suggest that successful logical reasoning requires the inhibition of interference from semantic knowledge.

Our findings suggest that inhibiting emotionally valenced semantic knowledge was selectively effortful for carriers of the 5-HTTLPR short allele. Overall, reasoning abilities were similar across genotype groups, as their accuracy did not differ on either incongruent or congruent problems without emotional content [consistent with Gong et al. (2011), who found no relation between analogical reasoning ability and 18 functional genetic variants influencing neurotransmitter function, including several that influence 5-HT function]. Thus, greater interference from beliefs in S carriers was specific to reasoning with emotional material. Logic problems in this study included primarily negatively valenced words, with only a few highly arousing positive words. Thus, our results cannot be examined by valence, but should be in future studies in light of past findings of the 5-HTTLPR polymorphism. Specifically, S/Lc carriers showed a higher attentional bias towards negative faces, whereas L/La carriers showed a higher attentional bias towards happy faces in an emotional dot-probe task (Beever et al., 2009)]. These findings together with the observed interaction between emotional valence and 5-HTTLPR genotype serve to elucidate past problems without emotional content [consistent with Gong et al. (2011)]. Our findings suggest that inhibiting emotionally valenced semantic knowledge was selectively effortful for carriers of the 5-HTTLPR short allele. Overall, reasoning abilities were similar across genotype groups, as their accuracy did not differ on either incongruent or congruent problems without emotional content [consistent with Gong et al. (2011), who found no relation between analogical reasoning ability and 18 functional genetic variants influencing neurotransmitter function, including several that influence 5-HT function]. Thus, greater interference from beliefs in S carriers was specific to reasoning with emotional material. Logic problems in this study included primarily negatively valenced words, with only a few highly arousing positive words. Thus, our results cannot be examined by valence, but should be in future studies in light of past findings of the 5-HTTLPR polymorphism. Specifically, S/Lc carriers showed a higher attentional bias towards negative faces, whereas L/La carriers showed a higher attentional bias towards happy faces in an emotional dot-probe task (Beever et al., 2009)]. These findings together with the observed interaction between emotional valence and 5-HTTLPR genotype serve to elucidate past problems without emotional content [consistent with Gong et al. (2011)].

Enhanced belief-bias from emotional content in S carriers who are known to be more emotionally reactive may result from two sources: Parallel to findings from emotional Stroop-like tasks [e.g. color-word and face-word (Koizumi et al., 2010)], S carriers’ increased attention to negative emotional content could have increased inhibitory demands making its suppression more difficult than that of non-emotional information. Another possibility is that the emotional content, which was primarily negative, could have temporarily evoked a negative mood state. Indeed, past findings indicate that S carriers have a higher propensity for negative mood (Lesch et al., 1996; Gonda et al., 2009). Thus, negative emotional material may draw more attention and induce a negative affective state, two factors known to impede reasoning (Oakford et al., 1996; Blanchette and Richards, 2004). Together, they may serve to reduce reasoning accuracy for emotional problems with belief-logic conflict, only in participants with higher emotional reactivity.

Trait anxiety, one property of emotional reactivity, was higher in SS/Sc than Lc/La carriers, consistent with previous reports (Lesch et al., 1996; Lonsdorf et al., 2009). Past studies using the emotional Stroop task found greater interference from threat-related words in patients with anxiety disorder (Becker et al., 2001) as well as healthy participants with high anxiety (Dresler et al., 2009). Further, belief-bias during reasoning with social-anxiety-provoking statements was higher in healthy participants with higher levels of social anxiety (Vroeling and de Jong, 2009). Similarly, belief-bias for emotional problems was higher in participants with higher trait anxiety in the present study. However, multiple regression analysis revealed that 5-HTTLPR genotype accounted for the relationship between anxiety and emotional belief-bias. Indeed, mediation analysis indicated that anxiety was not a significant mediator between 5-HTTLPR and emotional belief-bias. We suggest that the S-allele leads to a pre-disposition to negative emotional reactivity, which in turn leads to higher anxiety and emotional belief-bias. In contrast, N-back working memory performance did not differ between groups and did not correlate with emotional belief-bias, indicating 5-HTTLPR effects found in the present study have some specificity, acting through emotional rather than general cognitive processing mechanisms. Thus, a more anxious temperament due to 5-HTTLPR genotype was related to reduced inhibitory control during reasoning selectively with emotional material.

The ability to make rational decisions relates to success in various aspects of contemporary society. Superior deductive reasoning ability predicts higher academic achievement. Specifically, children showing less belief-biased reasoning errors had higher math and reading performance (Handley et al., 2004). Furthermore, relational reasoning is also important for social functioning (Maclean et al., 2008). For example, if Johnny knows that his older sibling Pat is stronger than him based on previous experience and that Mark, the new kid in school, is stronger than Pat, the ability to infer that Mark is therefore stronger than Johnny without having to directly test this hypothesis can be highly beneficial. Interestingly, 5-HTTLPR genotype relates to a variety of social functions, including establishment of social dominance and aggression in animals that live in social groups (Neumann et al., 2010). The present findings show that genotypic differences in the functioning of the serotonin transporter lead some individuals to be more vulnerable to the influence of emotion and its deleterious effects on reasoning, an important ability for academic and social success.

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