REPORTS

- M. Tranter, M. Skidmore, J. Wadham, *Hydrol. Process.* 19, 995 (2005).
- 29. J. C. Priscu et al., Science 286, 2141 (1999).
- J. L. Kirschvink, in *The Proterozoic Biosphere*,
 J. W. Schopf, C. Klein, Eds. (Cambridge Univ. Press, Cambridge, 1992), pp. 51–52.
- 31. P. F. Hoffman, D. P. Schrag, Terra Nova 14, 129 (2002).
- 32. D. E. Canfield *et al., Science* **321**, 949 (2008); published online 16 July 2008 (10.1126/science.1154499).
- 33. J. A. Mikucki, thesis, Montana State University (2005).
- 34. G. Eischeld and S. Fawcett assisted with oxygen isotope measurements, A. Masterson assisted with sulfur isotope measurements, and G. Gordon assisted with iron isotope

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Supporting Online Material

www.sciencemag.org/cgi/content/full/324/5925/397/DC1 Materials and Methods Fig. S1 Tables S1 to S4 17 October 2008; accepted 5 March 2009 10.1126/science.1167350

Recursive Processes in Self-Affirmation: Intervening to Close the Minority Achievement Gap

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A 2-year follow-up of a randomized field experiment previously reported in *Science* is presented. A subtle intervention to lessen minority students' psychological threat related to being negatively stereotyped in school was tested in an experiment conducted three times with three independent cohorts (N = 133, 149, and 134). The intervention, a series of brief but structured writing assignments focusing students on a self-affirming value, reduced the racial achievement gap. Over 2 years, the grade point average (GPA) of African Americans was, on average, raised by 0.24 grade points. Low-achieving African Americans were particularly benefited. Their GPA improved, on average, 0.41 points, and their rate of remediation or grade repetition was less (5% versus 18%). Additionally, treated students' self-perceptions showed long-term benefits. Findings suggest that because initial psychological states and performance determine later outcomes by providing a baseline and initial trajectory for a recursive process, apparently small but early alterations in trajectory can have long-term effects. Implications for psychological theory and educational practice are discussed.

hether and how psychological interventions produce lasting positive consequences are critical questions for scientists and policy-makers. This report presents evidence of how interventions, even brief or subtle, can produce lasting benefit when targeted at important psychological processes. It does so by focusing on the long-term impact of a psychological intervention designed to reduce the racial achievement gap through the lessening of academic underperformance.

The achievement gap between academically at-risk minority students and European American students has long concerned the educational community (1). In a society where economic success depends heavily on scholastic accomplishment, even partial remediation of this gap would be consequential. This is especially true for low-achieving students, given the societal, institutional, and personal costs of academic failure.

Research shows the importance of psychological factors in intellectual achievement (2-4).

Situations where one could be judged or treated in light of a negative stereotype can be stressful and thus undermine performance (5–7). For African Americans in school, the concern that they or another African American could be seen as confirming a negative stereotype about their group's intelligence can give rise to stress and depress performance (5–8).

Findings of two randomized field experiments addressing this psychological threat in the classroom were reported in Science (8). These tested a values-affirmation intervention. Beginning early in seventh grade, students reflected on an important personal value, such as relationships with friends and family or musical interests, in a series of structured writing assignments. Such selfaffirmations reduce psychological threat and stress (9-11) and can thus improve performance. The intervention should benefit students from groups subjected to threat pervasive enough to undermine their average performance-in this case, negatively stereotyped minority students. As predicted, relative both to a control group and to historical norms, one or two administrations of the intervention improved the fall-term grades of African Americans and lowered the psychological availability of the stereotype. European Americans were unaffected (8).

A 2-year follow-up is now reported. We assess whether the affirmation buffers minority students from the effects of psychological threat over the long term, leading to academic benefits beyond the short-term ones of a single academic term previously found. Generally, psychological processes and their consequences are examined for relatively brief periods, often in experimental studies lasting 30 min or an hour. By contrast, because the present study spans 2 years, its findings speak to how an apparently brief psychological intervention triggers processes that affect performance and psychological outcomes over considerable periods of time. Given the multitude of factors that could mute the effects of such processes in the classroom, the findings address the longevity and real-world significance of these processes. This is particularly important given that the effects of interventions and psychological manipulations often decay and may even reverse over time for reasons that are little understood (12, 13).

Because chronic evaluation is a key aspect of school and work environments, performance in these settings can be self-reinforcing. A recursive cycle, where psychological threat lowers performance, increasing threat and lowering performance further, in a repeating process, can magnify early performance differences among students (*14*). Early outcomes set the starting point and initial trajectory of a recursive cycle and so can have disproportional influence. For instance, the low self-confidence of students who experience early failure, even by chance, is surprisingly difficult to undo (*15*). A well-timed intervention could provide appreciable long-term performance benefits through early interruption of a recursive cycle.

Results encompass the original two student cohorts and a third cohort run after the original two experiments. The cohorts were observed for a period running from the first term of seventh grade to the end of eighth grade, typically covering ages 12 to 14. Although the period involves the last 2 years of middle school, for clarity these will henceforth be referred to as Year 1 and 2, respectively. Individual students were randomly assigned to the affirmation condition or the control condition. The former completed affirmation exercises, the latter neutral exercises. The treatment consisted of variations on the original affirmation exercise in which students wrote about the personal importance of a self-defining value (16). The control exercises consisted of variations on the original control exercise in which students wrote about an unimportant value or a similarly

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neutral topic like their morning routine. The experimental manipulation, given three to five times in the seventh grade, occurred at roughly equal intervals throughout the year.

With the exception of a treatment dosage manipulation introduced at the beginning of Year 2, all original condition assignments were preserved (16). At the start of Year 2, 50% of the affirmed students were randomly assigned to a booster condition. These students received between two and four additional affirmations in Year 2. All remaining participants completed control exercises. This would determine whether long-term intervention effects, if present, rested on the treatment's continued administration or were triggered by its early effects.

The key outcome was grade point average (GPA) in core academic courses (science, social studies, math, and English), as the intervention was administered in different courses over 2 years and its effect was found across core courses in the original studies (δ). To increase statistical power, we combined data from the three cohorts, because the intervention's effect, if found, was expected to be small and was found to be consistent across cohorts (16).

Complete GPA data for 2 years were obtained for 93% of the original participants (N =385). Attrition did not vary by experimental condition either overall or within racial group (*16*). Degrees of freedom are greater for earlier out-

Fig. 1. Mean GPA in core courses, as a function of student group (African American versus European American), experimental condition, and pre-intervention level of performance of African Americans (an average of the prior year's GPA and pre-intervention seventhgrade performance). Data from participants with complete data are presented. Error bars represent standard errors. African Americans were categorized into low and high performers based on a median split within their racial group, reflecting their relative standing within their group. Year 1, Term 1 represents the first term after the initiation of the intervention. (Left) Raw means and error terms. (Right) Means and error terms adjusted for baseline covariates and students' assigned teacher team. The scale reflects the grade metric, ranging from 0 (= F) to 4.33 (= A+).

comes because of attrition. Multiple regression tested treatment effects (16). A positive effect of affirmation on average 2-year GPA emerged for African Americans but not for European Americans. As with short-term grades, a group \times experimental condition interaction emerged for the new long-term data [B = 0.33, t(321) = 3.59, t(321) = 3.59]P < 0.001] (table S1). African Americans earned a higher 2-year GPA in the affirmation condition than in the control condition [B = 0.24, t(144) =3.45, P = 0.001]. No treatment effect was found for European Americans [B = -0.07, t(170) = -1.19, t(170) = -1.19]P = 0.236]. The treatment effect for African Americans emerged for GPA in both outcome years. The group × treatment interaction and treatment effect for African Americans was significant for each year [Year 1: interaction B =0.25, t(344) = 2.73, P = 0.007, treatment B =0.18, t(162) = 2.69, P = 0.008; Year 2: interaction B = 0.39, t(321) = 3.25, P = 0.001, treatment B =0.27, t(144) = 3.03, P = 0.003].

If the intervention interrupts a recursive process, its effects should be larger for initially low-achieving African Americans, because low performance should trigger worsening performance. Affirmation should make their prior performance less predictive of subsequent achievement. A three-way interaction between racial group, condition, and a continuous measure of pre-intervention performance on average 2-year GPA shows this [B = -0.32, t(319) =



-2.59, P = 0.010] (16). A two-way interaction between condition and pre-intervention performance emerged for African Americans [B = -0.21, t(144) =-2.49, P = 0.014], not European Americans [B = 0.10, t(170) = 1.10, P = 0.274]. Regardless of previous performance level, European Americans were unaffected by the intervention. However, the affirmation effect was significant for lowperforming African Americans, those at the 25th percentile of pre-intervention performance for their racial group [B = 0.41, t(144) = 4.41, P < 0.41]0.001]. Although the affirmation effect was present in the first term for high-performing African Americans, those at the 75th percentile of pre-intervention performance for their group [Fig. 1; B = 0.19, t(160) = 2.30, P = 0.019], it decayed and did not reach significance on 2-year GPA for them [B =0.15, t(144) = 1.67, P = 0.096]. At mean or moderate pre-intervention performance, treatment effects were virtually identical to those in the overall analysis (16).

Affirmed African Americans should be more likely to maintain their performance over time if the intervention interrupted a recursive process of worsening performance. Indeed, the downward trend in performance commonly found in middle school (17) was less steep for these students than for African Americans in the control condition, not just for one term but across 2 years. Although all children performed progressively worse with time (Fig. 1), the linear decline in annual GPA was smaller among affirmed than nonaffirmed African Americans [F(1, 146) = 7.36, P = 0.007](16). The decline among European Americans did not vary by condition [F(1,172) = 1.37, P =0.24; group × condition × measure interaction, F(1,323) = 7.41, P = 0.007]. Figure 2 illustrates how the performance trajectory of low-achieving African Americans angles upward after the intervention, keeping the gap between them and European Americans from widening with time.

Although the initial treatment had long-term performance effects, the dosage manipulation did not moderate the treatment effect on Year 2 GPA for either racial group or for any pre-intervention performance subgroup [| t's | < 1.3, P's > 0.20]. This further supports the presence of a recursive process, as the intervention's early effects suffice to explain its long-term effects (16). All students, including African Americans, tended to perform relatively worse in Year 2 if they had performed poorly in Year 1, even controlling for pre-intervention performance (16). That the treatment effect on Year 2 GPA was significantly mediated by Year 1 GPA suggests that this natural performance cycle could have carried forward the intervention's early impact (SOM Text).

The intervention's impact on students' psychological environment is indicated by data suggesting that it buffered African Americans against the impact of early poor performance on their long-term perceptions of adequacy. A survey assessed students' self-perceived ability to fit in and succeed in school—their adaptive adequacy in the academic environment (16). These data indicate

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that the intervention uncoupled African Americans' long-term perceptions of adequacy from early poor performance. African Americans who had performed poorly early in the school year, and then received the affirmation, maintained a sense of their ability to fit and succeed in school over time. They had similar levels of selfperceived adequacy at the beginning and end of the year [paired |t| < 0.2]. For them, as for European Americans, early poor performance bore little relationship to their perceptions of adequacy at year's end, controlling for baseline perceptions [B's < 0.04, |t's| < 1]. By contrast, for African Americans in the control condition, performing poorly before the manipulation predicted more negative perceptions of adequacy later [B =0.23, t(155) = 3.79, P < 0.001]. They had lower self-perceived adequacy at the end of the year than they had had at the beginning [paired t(40) =-2.45, P=0.019]. Low-performing African Americans thus ended the year with a lower sense of personal adequacy in the control condition than in the affirmation condition [B = 0.31, t(155)] =3.30, P = 0.001], with the latter not differing from European Americans [|t| < 1]. A mid-year assessment, which due to pragmatic constraints involved a shorter scale and only the first two cohorts, yielded the same results. Without intervention, early poor performance for minority students

Fig. 2. Mean GPA in core courses for each term over 2 years, as a function of student group (African American versus European American), experimental condition, and preintervention level of performance of African Americans (an average of the prior year's GPA and pre-intervention seventh-grade performance). Data from participants with complete data are presented. African Americans were categorized into low and high performers based on a median split within their racial group, reflecting their relative standing within their group. Because European Americans in the two conditions did not differ significantly. their data were combined. (Left) Raw means. (Right) Means adjusted for baseline covariates and students' assigned teacher team.

appeared to deliver a lasting blow to their sense of adequacy (18).

Although end-of-year adequacy correlated with higher GPA [R = 0.23, P < 0.001], statistical evidence that it mediated the treatment effect on GPA was not found (16). This suggests that the intervention might have discrete effects on a host of education-relevant psychological and behavioral outcomes. Here the intervention weakened the relationship not only between past and future performance, but also between past performance and later psychological state.

We also explored the effect of the intervention on students' assignment by their school to two major performance tracks-whether students were placed in remediation (assigned to a remedial program or held back in their grade), and whether they received advanced placement in math (16). Of the 13 students in the sample placed in remediation after the intervention, 11 were in the control condition (6%, versus 1% in the affirmation condition). Because counts for European Americans receiving the intervention were zero, we tested main effects of affirmation and racial group separately (16) (fig. S1). Logistic regression yielded a condition effect, with fewer affirmation-treated students placed in remediation $[\Delta \chi^2 (1) = 14.06]$, P < 0.001]. Additionally, fewer European Americans (2%) were placed in remediation than Afri-



can Americans (6%) [χ^2 (1) = 4.03, P = 0.045]. However, fewer affirmed African Americans were so classified than nonaffirmed African Americans [3% versus 9%; $\Delta\chi^2$ (1) = 9.31, P = 0.002]. This condition effect was confined to previously lowperforming African Americans [5% versus 18%] (*16*). Condition effects were virtually identical in a rare events logistic regression (*19*).

Evidence of a positive treatment effect regarding assignment to advanced placement in math was found for African Americans (SOM Text) (16).

A values-affirmation intervention closed the achievement gap not only over one school term, but throughout African Americans' tenure in middle school. It also decreased the number of African Americans identified as at-risk and enrolled in remediation. Moreover, the intervention benefited those most in need and often least affected by traditional intervention—low-achieving students (20).

In chronically evaluative settings such as school, performance issues from self-reinforcing or recursive processes. A feedback loop, with psychological threat and poor performance reinforcing one another, can create worsening performance over time. Students' poor performance may also cause them to be seen as less able by their teachers and less worthy of attention and mentoring, increasing the likelihood of lower performance (21). The ability of the intervention to interact with recursive processes lies at the heart of how its effects persisted for 2 years. Because initial psychological states and early performance establish the starting point and initial trajectory of a recursive cycle, they can have disproportionate influence on long-term outcomes. When such recursive cycles are interrupted early, baseline outcomes and the long-term performance trajectories following from them can be changed. That a new starting point and trajectory for the recursive cycle was introduced by the affirmation is suggested by its weakening of the relationship between early poor performance and later performance and felt adequacy.

The following findings provide evidence for the intervention's interruption of a recursive cycle. First, early poor performance was less predictive of later performance and psychological state for affirmed African Americans than for nonaffirmed ones, suggesting that the intervention reset the starting point of a recursive cycle. Second, the affirmation not only benefited GPA, but also lifted the angle of the performance trajectory and thus lessened the degree of downward trend in performance characteristic of a recursive cycle. Third, the affirmation's benefits were most evident among low-achieving African Americans. These are the children most undermined by the standard recursive cycle with its worsening of performance and magnifying of initial differences in performance. Fourth, the affirmation prevented the achievement gap from widening with time. Fifth, treatment boosters were not needed to sustain its impact into Year 2. This indicates that processes triggered by the intervention in Year 1 suffice to explain its effect in Year 2. That the intervention's first-year impact mediated much of this effect further supports this notion.

Finally, students' psychological state sheds light on how affirmation processes interact with the recursive cycle. African Americans, a stereotyped group, displayed greater psychological vulnerability to early failure. For them, early failure may have confirmed that the stereotype was in play as a stable global indicator of their ability to thrive in school. By shoring up self-integrity at this time, the affirmation helped maintain their sense of adequacy and interrupted the cycle in which early poor performance influenced later performance and psychological state. Students' performance and psychological trajectory can be strongly influenced by timely actions, even when apparently small, that alter or reset the trajectory's starting point.

Other factors, such as teachers' expectancies of their students, could contribute to the longevity of the treatment's effect (21). For instance, that fewer affirmed children were assigned to remediation suggests that the intervention's effects were not only noted by the academic system, but acted upon by it.

The findings demonstrate how initial psychological processes, triggered by an apparently subtle intervention, can have psychological and pragmatic effects that perpetuate themselves over extended time spans, in the present case 2 years (6, 13). They demonstrate the role of such processes in long-term intellectual achievement and also suggest a practical strategy for addressing the achievement gap. Effective psychological interventions depend on the presence of positive and sufficient structural, material, and human resources. Together with such resources and other educational programs, psychological interventions can help individuals perform to their potential and produce lasting positive changes in equity and opportunity.

References and Notes

- 1. C. Jencks, M. Phillips, *The Black-White Test Score Gap* (Brookings Institution, Washington, DC, 1998).
- A. Bandura, Social Foundations of Thought and Action: A Social Cognitive Theory (Prentice Hall, Englewood Cliffs, NJ, 1986).
- 3. C. S. Dweck, C. Chiu, Y. Hong, Psychol. Inq. 6, 267 (1995).
- 4. E. Zigler, E. C. Butterfield, Child Dev. 39, 1 (1968).
- C. M. Steele, S. J. Spencer, J. Aronson, in Advances in Experimental Social Psychology, M. P. Zanna, Ed. (Academic Press, San Diego, CA, 2002), pp. 379–440.
- J. Aronson, C. B. Fried, C. Good, J. Exp. Soc. Psychol. 38, 113 (2002).
- G. L. Cohen, J. Garcia, J. Pers. Soc. Psychol. 89, 566 (2005).
 G. L. Cohen, J. Garcia, N. Apfel, A. Master, Science 313, 1307 (2006).
- 9. J. D. Creswell et al., Psychol. Sci. 16, 846 (2005).
- C. M. Steele, in Advances in Experimental Social Psychology, L. Berkowitz, Ed. (Academic Press, New York, 1988), pp. 261–302.
- D. K. Sherman, G. L. Cohen, in *Advances in Experimental Social Psychology*, M. P. Zanna, Ed. (Academic Press, San Diego, CA, 2006), pp. 183–242.
- R. Schulz, B. H. Hanusa, J. Pers. Soc. Psychol. 36, 1194 (1978).
- L. Ross, R. Nisbett, *The Person and the Situation* (McGraw-Hill, New York, 1991).

- T. D. Wilson, P. W. Linville, J. Pers. Soc. Psychol. 49, 287 (1985).
- M. R. Lepper, L. Ross, R. Lau, J. Pers. Soc. Psychol. 50, 482 (1986).
- 16. Materials and methods are available as supporting material on *Science* Online.
- 17. J. S. Eccles, S. Lord, C. Midgley, Am. J. Educ. 8, 520 (1991).
- 18. For the adequacy outcome, the racial group × condition × prior performance interaction was significant [B = -0.31, t(328) = -2.54, P = 0.011], indicating that while there was no condition × prior performance interaction among European Americans [B = 0.11, [$I \ t \ < 1.1$], there was such an interaction among African Americans [B = -0.20, t(155) = -2.75, P = 0.007].
- M. Tomz, G. King, L. Zeng, RELOGIT: Rare events logistic regression, v. 1.1; Harvard Univ., Cambridge, MA, 1 October 1999, http://gking.harvard.edu/.
- 20. S. J. Ceci, P. B. Papierno, Am. Psychol. 60, 149 (2005).
- 21. R. Rosenthal, Curr. Dir. Psychol. Sci. 3, 176 (1994).
- 22. We thank the student participants and their parents, the teachers, staff, and administrators of the school district for their involvement in the project. We also thank E. Zigler, D. Green, C. Steele, E. Pronin, D. Sherman, G. Walton, J. Correll, C. Judd, J. Cook, E. Paluck, S. Taborsky-Barba, S. Tomassetti, and S. Wert for their help and feedback. This research was supported primarily by grants from the William T. Grant Foundation and the Russell Sage Foundation. Additional support was provided by the Nellie Mae Education Foundation and the Institute for Social and Policy Studies of Yale University.

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Fig. S1

Table S1

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Mirror Neurons Differentially Encode the Peripersonal and Extrapersonal Space of Monkeys

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Actions performed by others may have different relevance for the observer, and thus lead to different behavioral responses, depending on the regions of space in which they are executed. We found that in rhesus monkeys, the premotor cortex neurons activated by both the execution and the observation of motor acts (mirror neurons) are differentially modulated by the location in space of the observed motor acts relative to the monkey, with about half of them preferring either the monkey's peripersonal or extrapersonal space. A portion of these spatially selective mirror neurons encode space according to a metric representation, whereas other neurons encode space in operational terms, changing their properties according to the possibility that the monkey will interact with the object. These results suggest that a set of mirror neurons encodes the observed motor acts not only for action understanding, but also to analyze such acts in terms of features that are relevant to generating appropriate behaviors.

In the monkey premotor area set of neurons, first described in the monkey premotor area F5, that respond both when the monkey performs an active goal-directed motor act and when he observes the same motor act performed by others (1, 2). The most accepted interpretation of the function of mirror neurons is that they are involved in action understanding. Here, we investigated whether mirror neurons, besides playing a role in this function, also encode aspects of the observed actions that are relevant to subse-

quent interacting behaviors. A way to test this hypothesis is to examine the effect of relative distance between observer and actor on mirror neuron responses. Although completely irrelevant for "understanding" what the actor is doing, a precise knowledge of the distance at which the observed action is performed is crucial for selecting the most appropriate behavioral reaction.

To investigate quantitatively the possible degree of spatial modulation of the visual responses of mirror neurons, we first isolated hand movement-related neurons in area F5 of two rhesus monkeys by measuring the neurons' discharge while each monkey was executing hand goal-directed motor acts. The visual properties of these neurons were then assessed by having the experimenter perform the same motor acts in the monkey's peripersonal and extrapersonal (3-7) space, respectively (Fig. 1, A and B). The position of the experimenter's body was the same in all conditions, and actions were performed in the middle sagittal plane of the monkey's body. The selectivity for one of the two regions of space was then assessed by means of quantitative statistical analysis of the response patterns of 105 mirror neurons recorded from two monkeys (8).

Figure 2A shows the visual responses of three mirror neurons to motor acts executed in the perior extrapersonal space of the monkey. All three neurons responded during active movements of the monkey. However, their visual responses exhibited different types of tuning depending on whether the observed actions were executed in the monkey's peri- or extrapersonal space. Of all F5 mirror neurons tested, 26% (n = 27) exhibited a

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