Poverty Impedes Cognitive Function

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The poor often behave in less capable ways, which can further perpetuate poverty. We hypothesize that poverty directly impedes cognitive function and present two studies that test this hypothesis. First, we experimentally induced thoughts about finances and found that this reduces cognitive performance among poor but not in well-off participants. Second, we examined the cognitive function of farmers over the planting cycle. We found that the same farmer showed diminished cognitive performance before harvest, when poor, as compared with after harvest, when rich. This cannot be explained by differences in time available, nutrition, or work effort. Nor can it be explained with stress: Although farmers do show more stress before harvest, that does not account for diminished cognitive performance. Instead, it appears that poverty itself reduces cognitive capacity. We suggest that this is because poverty-related concerns consume mental resources, leaving less for other tasks. These data provide a previously unexamined perspective and help explain a spectrum of behaviors among the poor. We discuss some implications for poverty policy.

A variety of studies point to a correlation between poverty and counterproductive behavior. The poor use less preventive health care (1), fail to adhere to drug regimens (2), are tardier and less likely to keep appointments (3, 4), are less productive workers (5), less attentive parents (6), and worse managers of their finances (7–9). These behaviors are troubling in their own right, but they are particularly troubling because they can further deepen poverty. Some explanations of this correlation focus on the environmental conditions of poverty. Predatory lenders in poor areas, for example, may create high-interest-rate borrowing, and unreliable transportation can cause tardiness and absenteeism. More generally, poverty may leave less room for error so that the “same” mistake can lead to worse outcomes (10, 11). Other explanations focus on the characteristics of the poor themselves. Lower levels of formal education, for example, may create misunderstandings about contract terms, and less parental attention may influence the next generation’s parenting style.

We propose a different kind of explanation, which focuses on the mental processes required by poverty. The poor must manage sporadic income, juggle expenses, and make difficult trade-offs. Even when not actually making a financial decision, these preoccupations can be present and distracting. The human cognitive system has limited capacity (12–15). Preoccupations with pressing budgetary concerns leave fewer cognitive resources available to guide choice and action. Just as an air traffic controller focusing on a potential collision course is prone to neglect other planes in the air, the poor, when attending to monetary concerns, lose their capacity to give other problems their full consideration.

This suggests a causal, not merely correlational, relationship between poverty and mental function. We tested this using two very different but complementary designs (16, 17). The first is a laboratory study: We induced richer and poorer participants to think about everyday financial demands. We hypothesized that for the rich, these run-of-the-mill financial snags are of little consequence. For the poor, however, these demands can trigger persistent and distracting concerns (18, 19). The laboratory study is designed to show that similarly sized financial challenges can have different cognitive impacts on the poor and the rich. But, the study cannot fully capture our hypothesis that in the world, the poor face more challenging demands. In principle, the cognitive impact in situ may be different given that the scale of the problems can vary between the rich and the poor. Perhaps the rich in the world face larger monetary problems that also cause greater load. Perhaps the poor manage to restructure their lives so that they do not face as many cognitively challenging problems. Put simply, the laboratory study, although illustrating the mechanism, does not show its relevance in natural settings.

Our second study takes a different approach and allows us to assess what happens when income varies naturally. We conducted a field study that used quasi-experimental variation in actual wealth. Indian sugarcane farmers receive income annually at harvest time and find it hard to smooth their consumption (20). As a result, they experience cycles of poverty—poor before harvest and richer after. This allows us to compare cognitive capacity for the same farmer when poor (pre-harvest) versus richer (post-harvest). Because harvest dates are distributed arbitrarily across farmers, we can further control for calendar effects. In this study, we did not experimentally induce financial concerns; we relied on whatever concerns occurred naturally. We were careful to control for other possible changes, such as nutrition and work effort. Additionally, we accounted for the impact of stress. Any effect on cognitive performance then observed would illustrate a causal relationship between actual income and cognitive function in situ. As such, the two studies are highly complementary. The laboratory study has a great deal of internal validity and illustrates our proposed mechanism, whereas the field study boosts the external validity of the laboratory study.

We note two observations about these studies. First, they sidestep the discussion on whether poverty is best defined in absolute or relative terms (21). Because our hypothesis is about how monetary concerns tax the cognitive system, we define poverty broadly as the gap between one’s needs and the resources available to fulfill them. Because this is based on subjective needs, it encompasses low-income individuals both in the developing and the developed world as well as those experiencing sharp transitory income shocks, such

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Fig. 1. Accuracy on the Raven’s matrices and the cognitive control tasks in the hard and easy conditions for the poor and the rich participants in experiment 1. (Left) Performance on the Raven’s Matrices task. (Right) Performance on the cognitive control task. Error bars reflect ±1 SEM. Top horizontal bars show two-way interaction (poor versus rich × hard versus easy). *P < 0.05, **P < 0.01, ***P < 0.001.
as the unemployed. Second, existing theory and data suggest a possibly cumulative long-term impact of poverty on cognition (22, 23): Childhood poverty may hinder brain development and eventually reduce adult cognitive capacity (24). Our hypothesis and tests focus on an immediate impact of poverty on cognition: Budgetary preoccupations can in real time impede cognitive function. Our proposed mechanism does not operate through brain development at early childhood but through an immediate cognitive load caused by financial concerns. Whether this mechanism also contributes to the long-term impacts is an open question.

The Laboratory Studies

The first study consisted of four experiments, with shoppers at a New Jersey mall who participated for pay (details are available in the supplementary materials). This sample encompasses a diverse income range, with the median household income at roughly $70,000 and a lower bound of roughly $20,000. This, broadly speaking, provides a cross-section of the United States, with the poor in our sample roughly corresponding to those in the lower quartile or third of the U.S. income distribution. We computed effective income by dividing household income by the square root of household size (25) and defined “rich” and “poor” through a median split on this variable (26).

In experiment 1, participants (n = 101) were presented with four hypothetical scenarios a few minutes apart. Each scenario described a financial problem the participants might experience. For example: “Your car is having some trouble and requires $X to be fixed. You can pay in full, take a loan, or take a chance and forego the service at the moment... How would you go about making this decision?” These scenarios, by touching on monetary issues, are meant to trigger thoughts of the participant’s own finances. They are intended to bring to the forefront any nascent, easy to activate, financial concerns.

After viewing each scenario, and while thinking about how they might go about solving the problem, participants performed two computer-based tasks used to measure cognitive function: Raven’s Progressive Matrices and a spatial compatibility task. The Raven’s test involves a sequence of shapes with one shape missing (27). Participants must choose which of several alternatives best fits in the missing space. Raven’s test is a common component in IQ tests and is used to measure “fluid intelligence,” the capacity to think logically and solve problems in novel situations, independent of acquired knowledge (28, 29). The spatial incompatibility task requires participants to respond quickly and often contrary to their initial impulse. Presented with figures on the screen, they must press the same side in response to some stimuli but press the opposite side in response to others. The speed and accuracy of response measures cognitive control (30), the ability to guide thought and action in accordance with internal goals (31). Both are nonverbal tasks, intended to minimize the potential impact of literacy skills.

Upon completion of these tasks, participants responded to the original scenario by typing their answers on the computer or speaking to a tape recorder and then moved on to the next scenario (an analysis of participants’ responses to the scenarios is available in table S1). We also collected participants’ income information at the end of the experiment.

Participants were randomly assigned either to a “hard” condition, in which the scenarios involved costs that were relatively high (for example, the car would require $1500 to fix); or to an “easy” condition, where costs were lower (for example, the car would require $150 to fix). Because the sums in the easy condition are small, we expected this condition to evoke few of one’s own monetary concerns, for either poor or rich participants. In contrast, the large sums in the hard condition, we hypothesized, would evoke monetary concerns in the poor but not in the rich participants.

Cognitive performance in experiment 1 is plotted in Fig. 1. For the financially “easy” scenarios, designed to generate relatively trivial concerns, the poor and rich performed similarly [Raven’s: t(50) = 0.13, P = 0.90; cognitive control: t(50) = 1.55, P = 0.13]. In contrast, in the context of the financially “hard” condition, the poor performed significantly worse than did the rich on both Raven’s [t(47) = 3.21, P < 0.01] and on cognitive control [t(47) = 5.22, P < 0.001]. A two-way analysis of variance revealed a robust interaction between income and condition [Raven’s: F(1,97) = 5.12, P = 0.03; cognitive control: F(1,97) = 7.86, P < 0.01]. In both tasks, the rich were uninfluenced by condition [Raven’s: t(48) = 0.56, P = .58; cognitive control: t(48) = 1.04, P = 0.30], whereas the poor performed significantly worse in the hard condition [Raven’s: t(49) = 2.63, P = 0.01; cognitive control: t(49) = 3.98, P < 0.001]. As a result, the poor performed reliably worse than the rich performed overall [Raven’s: F(1,97) = 5.61, P = 0.02; cognitive control: F(1,97) = 23.24, P < 0.001]. The magnitudes of the effect here are substantial, with Cohen’s d in this and ensuing replications ranging between 0.88 and 0.94.
To rule out the effect of “math anxiety,” experiment 2 used the same set of numbers as in experiment 1 but with nonfinancial scenarios. This recreates a mathematical problem but without evoking financial concerns. There was no interaction between the difficulty of the scenario and participants’ income (further details are available in supplementary materials, experiment 2). Thus, the reduced cognitive performance in the poor participants in experiment 1 was not due to anxiety with large numbers.

Experiment 3 added incentives to experiment 1: In addition to the standard participation fee, participants earned $0.25 for every correct response on both tasks. Performance in experiment 3 (n = 100 participants) is summarized in Fig. 2. As before, the poor performed similarly to the rich in the easy condition [Raven’s: t(46) = 0.26, P = 0.79; cognitive control: t(46) = 1.02, P = 0.31] and worse in the hard condition [Raven’s: t(50) = 3.34, P < 0.01; cognitive control: t(50) = 3.54, P < 0.001]. The rich performed equally well in the easy and hard conditions [Raven’s: t(45) = 0.07, P = 0.94; cognitive control: t(45) = 1.42, P = 0.16], whereas the poor performed significantly worse in the hard condition [Raven’s: t(51) = 3.75, P < 0.001; cognitive control: t(51) = 3.67, P < 0.001], yielding a robust interaction between income and scenario [Raven’s: F(1,96) = 4.34, P = 0.04; cognitive control: F(1,96) = 4.31, P = 0.04]. Despite the incentives, and the fact that they presumably needed the money more, the poor performed worse overall [Raven’s: F(1,96) = 6.55, P = 0.01; cognitive control: F(1,96) = 11.88, P < 0.001] and earned 18% ($0.71) less than the rich earned.

The hypothetical scenarios are intended to trigger participants’ financial concerns. Yet in experiments 1 to 3, the cognitive tests themselves may have created additional load because they were performed while the participant was contemplating the scenarios. To rule this out, experiment 4 (n = 96 participants) replicated experiment 1, except that participants finished responding to each scenario before proceeding to the Raven’s and cognitive control tasks. That is, participants viewed each scenario as in experiment 1, responded to the scenario, and only then completed the Raven’s and cognitive control tasks. Because there were no intervening tasks between scenario presentation and response, we added a few scenario-relevant questions in order to equate the time spent with that of experiment 1. Performance is summarized in Fig. 3.

The results match those in experiments 1 and 3. As before, there was a robust interaction between income and condition [Raven’s: F(1,92) = 4.04, P = 0.04; cognitive control: F(1,92) = 6.66, P = 0.01]; the rich and poor performed similarly in the easy condition [Raven’s: t(48) = 0.41, P = 0.69; cognitive control: t(48) = 0.43, P = 0.67], and the poor performed significantly worse than the rich performed in the hard condition [Raven’s: t(44) = 3.55, P < 0.001; cognitive control: t(44) = 3.34, p = .002]. Condition was insignificant for the rich [Raven’s: t(47) = 0.08, P = 0.93; cognitive control: t(47) = 0.72, P = 0.47], but significant for the poor [Raven’s: t(45) = 3.26, P = 0.002; cognitive control: t(59) = 3.94, P < 0.001]. Again, the poor performed worse than the rich performed overall [Raven’s: F(1,92) = 6.42, P = 0.01; cognitive control: F(1,92) = 8.74, P = 0.004].

Although remarkably consistent, these findings have limitations. The causal attribution made possible by laboratory studies comes at the expense of some external validity. For example, in experiment 4 the hypothetical scenarios themselves—even after answers were given—may still have weighed on people’s minds. More generally, in all the experiments we explicitly primed monetary concerns. Such explicit priming may not mirror naturally occurring circumstances. It is possible that environments in which one is richer bring to mind other concerns (such as bigger purchases), creating load comparable with that experienced by the poor. It is also possible—that less plausible—that the poor structure their lives to avoid these.

### Table 1. Changes in financial situation and cognitive capacity around harvest.

This table presents changes in farmers’ financial situation (panel A) and their cognitive capacity (panel B) before and after harvest. Each coefficient reported here is the result of an ordinary least-squares regression for the dependent variable in the row heading. For instance, row 1 in column 1 shows that on average, a farmer is 56.6% less likely to have pawned his belongings in the 15-day interval before the post-harvest survey than in the same time interval before the pre-harvest survey. These coefficients also account for any differences that may be attributed to the specific months in which tests were taken. Column 1 reports results for the entire sample; column 2 reports results for farmers who had already completed the harvesting process, but had not yet been paid for the harvest, at the time of the first-round survey. Each cell is the coefficient γ from a separate regression of the type γ = α + β1 + γPostHarvest, where the dependent variable varies in each row. Here, i denotes individuals, t denotes time, y denotes various outcome variables, and PostHarvest is a dummy for whether the observation occurs after harvest. The variables α and β reflect a set of individual and time fixed effects, respectively, controlling for all fixed differences between time periods (months) and individuals. Robust standard errors are in square brackets. *Significant at 10%; **significant at 5%; ***significant at 1%. Main independent variable = 1 for the post-harvest period and 0 pre-harvest.

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Full sample: Household + time fixed effects</th>
<th>Subsample: Farmers who completed harvest, but had not received payment</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Column 1</td>
<td>Column 2</td>
</tr>
<tr>
<td>Belongings pawned</td>
<td></td>
<td></td>
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<td>(last 15 days: 0 = no, 1 = yes)</td>
<td>-0.566***</td>
<td>-0.598</td>
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<tr>
<td>Observations</td>
<td>924</td>
<td>630</td>
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<tr>
<td>Mean: 0.41 (0.78 pre-harvest, 0.04 post-harvest)</td>
<td>-0.885***</td>
<td>-0.899</td>
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<tr>
<td>Loans outstanding</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(0 = no, 1 = yes)</td>
<td>0.033</td>
<td>0.032</td>
</tr>
<tr>
<td>Observations</td>
<td>922</td>
<td>626</td>
</tr>
<tr>
<td>Mean: 0.56 (0.99 pre-harvest, 0.13 post-harvest)</td>
<td>-1.979***</td>
<td>-2.033***</td>
</tr>
<tr>
<td>Number of loans outstanding</td>
<td>0.111***</td>
<td>0.109***</td>
</tr>
<tr>
<td>Observations</td>
<td>924</td>
<td>630</td>
</tr>
<tr>
<td>Mean: 1.69 (1.62 pre-harvest, 1.76 post-harvest)</td>
<td>1.367***</td>
<td>1.321***</td>
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<td>Raven’s accuracy</td>
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<td>(Min = 0; max = 10)</td>
<td>0.256</td>
<td>0.274</td>
</tr>
<tr>
<td>Observations</td>
<td>920</td>
<td>624</td>
</tr>
<tr>
<td>Mean: 4.9 (4.35 pre-harvest, 5.45 post-harvest)</td>
<td>-30.582***</td>
<td>-32.319***</td>
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<tr>
<td>Stroop-time taken</td>
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<td></td>
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<tr>
<td>(in seconds)</td>
<td>5.923</td>
<td>6.208</td>
</tr>
<tr>
<td>Observations</td>
<td>904</td>
<td>618</td>
</tr>
<tr>
<td>Mean: 138.94 (146.05 pre, 131.83 post-harvest)</td>
<td>-1.818***</td>
<td>-1.937***</td>
</tr>
<tr>
<td>Stroop-number of errors</td>
<td>0.566</td>
<td>0.588</td>
</tr>
<tr>
<td>Observations</td>
<td>906</td>
<td>620</td>
</tr>
<tr>
<td>Mean: 5.55 (5.93 pre, 5.16 post-harvest)</td>
<td></td>
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</tbody>
</table>
concerns. To address these issues, we conducted the field study.

The Field Studies

Our second study examined 464 sugarcane farmers living in 54 villages in the sugarcane-growing areas around the districts of Villupuram and Tiruvannamalai in Tamil Nadu, India. These were a random sample of small farmers (with land plots of between 1.5 and 3 acres) who earned at least 60% of their income from sugarcane and were interviewed twice—before and after harvest—over a 4-month period in 2010. There were occasional nonresponses, but all of our pre-post comparisons include only farmers we surveyed twice.

A challenge with pre-post comparisons is calendar effects: Differences between months (such as a festival or the weather) can create a spurious correlation. We overcame this through a particular feature of this context: Farmers’ harvest (and planting) dates are staggered over a 3- to 5-month period being set by sugar mills with processing capacity constraints. One farmer may harvest, for example, in June, whereas another harvests in August. The same month then is pre-harvest for some farmers and post-harvest for others. This feature allows us to control for calendar effects.

Our data show that farmers indeed faced greater financial pressures pre- as compared with post-harvest: They pawned items at a higher rate (78 versus 44%, P < 0.001, n = 462 participants) and were more likely to have loans (99 versus 13%, P < 0.001, n = 461 participants). On average, farmers had 1.97 more loans before harvest than they did after it. They were also more likely to answer “Yes” to the question, “Did you have trouble coping with ordinary bills in the last fifteen days?” before harvest than after (1.62 and 1.76, respectively, on a 3-point scale, where 1 corresponded to low ability and 3 to high ability to cope; P < 0.001, n = 462 participants). (Regressions adjusted to take out farmer and month fixed effects are shown in Table 1, panel A.)

We again used Raven’s to gauge fluid intelligence. For cognitive control, we could not administer the spatial incompatibility task in the field. Instead, we used a numeric version of the traditional Stroop task, which is appropriate for participants with low literacy rates. In a typical trial, participants would see “5 5 5” and have to quickly respond “3,” which is the number of 5s in the sequence, rather than “5” that comes to mind most naturally. Both response speed and error rates were recorded. Each participant performed 75 trials on the numerical Stroop.

Pre- and post-harvest differences on both tests were pronounced and are illustrated in Fig. 4. On Raven’s, the farmers scored an average of 5.45 items correct pre-harvest but only 4.35 items correct pre-harvest (P < 0.001, n = 460 participants). On Stroop, they took an average of 131 s to respond to all items post-harvest, as compared with 146 s pre-harvest (P < .001, n = 452). In addition, the average number of errors the farmers committed was higher before harvest than after (5.93 versus 5.16 errors; P < .001, n = 453).

We also report results of regressions that control for farmer and month fixed effects (Table 1, panel B). Each cell in Table 1 is a distinct regression. Table 1, column 1 shows that even after regression adjustment, strong pre-post harvest differences remain for both Raven’s and Stroop performance. In addition to these pre-post differences, we found that farmers’ perceived intensity of how financially constrained they are—as captured by how they rate their ability to cope with ordinary bills in the preceding 15-day period—correlates negatively with performance on Raven’s and time taken on Stroop tests (table S2).

Other factors besides income that vary pre- and post-harvest could drive these effects. One major candidate is physical exertion; preparing the land for harvest might involve increased physical labor. Another candidate is anxiety over crop yield; farmers might be preoccupied not with making ends meet but with how much they will earn. In practice, neither is likely to be true in the case of sugarcane farming. Farmers typically use external labor on their lands, and sugarcane crop size can be readily estimated months before harvest. Still, to address this further we observe that there is a several-week delay between physical harvest and the actual receipt of payment. Financial burdens are only relieved at the time of payment, but labor and anxiety over crop size are fully resolved at the time of harvest. For 316 farmers in our sample, the “pre-harvest” survey was actually post–physical harvest but pre-payment. We reestimated our equation on this subsample as shown in Table 1, column 2, and found highly similar results, which suggests that neither physical exertion nor anxiety pre-harvest drives our results.

Training effects present another potential confound; post-harvest farmers may do better simply because they are taking the test a second time. To address this, we held back 100 randomly selected farmers at the time of initial sampling. These farmers were surveyed for the first time post-harvest, and their scores were compared with the post-harvest scores of the original sample. If our results were due to learning, we would expect these novice farmers to do worse. Instead, we found that they performed similarly on Raven’s accuracy and Stroop reaction time (table S3), suggesting no training effect. There is some evidence for training effects on Stroop error rates (table S3), but the overall pattern cannot be attributed to simple test familiarity. Taken together, the two sets of studies—in the New Jersey mall and the Indian fields—illustrate how challenging financial conditions, which are endemic to poverty, can result in diminished cognitive capacity.

We have argued that the attentional demands created by poverty are a plausible mechanism (29). But there could be other mediating factors. Nutrition is one candidate—in the harvest findings, if not in the mall study; farmers may eat less when poor. In 2009, we ran a pilot study with the same design in the districts of Thanjavur, Thiruvur, Perambalur, and Pudukottai in Tamil Nadu, in which we surveyed 188 farmers and also asked about food consumption. We found similar effects on Stroop (1.47 errors post-harvest versus 2.12 errors pre-harvest; P = 0.006 via t test, n = 111 participants). Pre-harvest farmers were not eating less; they spent 2663 rupees a month on food pre-harvest and 2592 rupees post-harvest (roughly $53 and $52, respectively, not accounting for purchasing power parity). Additionally, the Stroop results persist even in regressions in which food consumption is included as a control variable.

A potential explanation of these findings is stress. Financial concerns could reasonably induce stress in pre-harvest farmers. Indeed, we examined biological stress. In the 2009 study, we collected two biomarkers of stress: heart rate and blood pressure. Both measures showed that the farmers were more stressed before the harvest; heart rate was higher pre-harvest than post-harvest (78.42 versus 76.38, P = 0.088 via t test, n = 188 participants), and so were diastolic blood pressure (74.70 versus 74.26, P < 0.001 via t test, n = 188) and systolic blood pressure (128.64 versus 121.56, P < 0.001 via t test, n = 188).

However, these differences in stress do not explain our findings. When we reestimated the impact of harvest on Stroop performance, controlling

Fig. 4. Accuracy on the Raven’s matrices and the cognitive control tasks for pre-harvest and post-harvest farmers in the field study. (Left) Performance on Raven’s matrices task. (Middle and Right) Stroop task (measuring cognitive control) response times (RT) and error rates, respectively; error bars reflect ±1 SEM. Top horizontal bars show test for main effect of pre- versus post-harvest (***P < 0.001).
for all three stress measures, the findings remained significant. In fact, the coefficient on post-harvest did not change [for Stroop, we continued to find a coefficient of \(-1.46 (0.52)\) on the post-harvest dummy, with \(t = -2.80\) and \(P < 0.006; n = 222\) participants]. This suggests that although the pre-harvest farmers did experience stress, stress cannot fully explain the impairment in cognitive function. Our suggested mechanism—that poverty captures attention, triggers intrusive thoughts, and reduces cognitive resources—could itself be described colloquially as “stress”; persistent mental engagement induced by some trigger. The 2009 data, however, suggest that the biological view of stress—as proxied by these biomarkers of stress—is not sufficient to account for our findings. This is consistent with the existing literature on the effects of stress on cognitive function, in which both facilitation and impairment have been found (32). For example, there is evidence that stress can increase working memory capacity (33).

We find additional capture to be the most compelling explanatory mechanism. It matches findings on the effects of scarcity on borrowing (34) and is consistent with demand and distraction observed in domains of scarcity other than poverty—from insufficient time to limited calorie budgets (35). But surely, other mechanisms might be operating. For example, poverty might influence cognitive load by changing people’s affective state (36, 37). We hope future work will test other mechanisms for explaining these findings.

New Perspectives on Policy
The data reported here suggest a different perspective on poverty: Being poor means coping with the existing literature on the effects of stress proxied by these biomarkers of stress: persistent mental engagement imposed by some trigger. The 2009 data, however, suggest that the biological view of stress—as proxied by these biomarkers of stress—is not sufficient to account for our findings. This is consistent with the existing literature on the effects of stress on cognitive function, in which both facilitation and impairment have been found (32). For example, there is evidence that stress can increase working memory capacity (33).

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References and Notes
18. This design resembles “stereotype threat” studies, in which identity-relevant primes diminish cognitive performance (19).
26. Alternative measures, such as dividing household income by number of people in the household, yield similar findings.
29. E. Hunt, Human Intelligence (Cambridge Univ. Press, New York, 2010).
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Acknowledgments: Authors’ names are listed alphabetically; the authors contributed equally to this work. The authors gratefully acknowledge support from the National Science Foundation (award SES-0933497), the John Simon Guggenheim Memorial Foundation, the International Finance Corporation, and the Institute for Financial Management and Research Trust. S. Krishnan, D. Mackenzie, and especially D. Bulla provided able research assistance. The authors declare no conflict of interest.

Supplementary Materials
www.sciencemag.org/cgi/content/full/341/6149/976/DC1 Materials and Methods. Figs. 51 and 52 Tables 51 to 53 References and Notes
19 March 2013; accepted 23 July 2013 10.1126/science.1238041