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we searched within the extended promoter regions of *Prox* and *Dist* groups for the presence of 232 additional functional DNA elements (26) (fig. S8E), only the GAGA element, residing ~80 base pairs (bp) upstream of the TSS (3, 15), showed strong associations with *Prox* genes (Fig. 3B), as did the level of GAGA-factor binding (27). Thus, core promoter elements and GAGA factor appear to play an important role in the mechanism of pausing.

Pausing positions could be determined through direct tethering of elongating Pol II to promoter elements. Alternatively, in a “complex interaction” model, pausing could be mediated through protein complexes that function best when cognate elements are located at specific positions in the core promoter. Thus, if we examine the association of the positions of the DNA elements and the pausing sites in this model, we expect a V-shaped plot of association rather than a simple linear correlation. Displacement of the element from the optimal position will weaken the interactions within the core complex, resulting in downstream scattering and a reduced level of pausing (Fig. 3C). To test this, we examined genes in which a particular promoter DNA element occurs only once, and divided genes into three subsets: the optimal consensus position, upstream, and downstream. Genes with the DNA elements nearest to the consensus positions showed more proximal pausing. Genes with TATA near -30 had more proximal pausing than genes with TATA at positions of -40 or more, showing a V-shaped association (Fig. 3D). This V pattern was observed in both the upstream elements TATA and Inr (fig. S9A) and the downstream elements PB (Fig. 3D) and MTE (fig. S9B). Also, pausing tended to be stronger in genes with the elements at the optimal positions (fig. S9D). Furthermore, the extent of pausing showed strong dependency on the match of the DNA elements to their consensus sequence and consensus positions (Fig. 3E). Together, these patterns of association between core promoter elements and pausing support the complex interaction model and explain the strong and focused pausing on *Prox* promoters.

The complex interaction model depends on both the presence and the correct positioning of core promoter elements. We disrupted the positional relationship of core elements in the well-studied *Drosophila* gene *Hsp70* (*I*). Transgenic fly lines were generated that carry mutant *Hsp70* promoters with spacers inserted at the +15 position between the upstream and downstream promoter elements (Fig. 4A) and were analyzed by PRO-seq (fig. S10). The initiation sites remained constant in these mutant promoters, as indicated by the 5' ends of the PRO-seq reads (Fig. 4B). The transgenic *Hsp70* without spacers showed a strong pause peak mainly at position +31 (Fig. 4D). When a 5-bp spacer was inserted, the pause peak was shifted 5 to 7 bp downstream from the original site. Because additional bases were transcribed before pausing, the position of pausing is not predetermined by elongation distance. When

a 10-bp spacer was inserted, pausing sites became scattered between positions +20 and +60 (Fig. 4D) and had fewer reads (Fig. 4C). Collectively, these results support the core interaction model and suggest that the interaction complex can accommodate a small change (5 bp) in the positional context of the DNA sequences, whereas a larger change (10 bp) results in reduced and dispersed pausing.

The advances in resolution provided by PRO-seq enable the precise and genome-wide assessment of the relationship between promoter-proximal pausing and the core promoter structure. For the strong and tightly clustered pausing of the *Prox* genes, our results provide support for a complex interaction model involving the promoter initiation complex, which can extend up to 30 bp from the TSS (28), physically contacting and tethering the pausing complexes. This may share a kinship with bacterial initiation factor σ , which is retained within the early elongation complex and interacts with promoter proximal DNA during transcription pausing in *Escherichia coli* (29). It is noteworthy that the *Prox* genes are expressed on average at a lower level but show a broader range of expression (fig. S6D), and that the *Dist* genes are enriched in constitutively active genes (table S5). These results suggest that the mechanistic distinctions have regulatory consequences. A well-structured core promoter may strongly recruit Pol II; however, it can also effectively retain Pol II in a paused configuration close to the TSS, until activation signals allow its escape into productive elongation.

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Acknowledgments: Supported by NIH grants GM25232 and HG004845 (J.T.L.) and a Howard Hughes Medical Institute fellowship (H.K.). Sequence data are in the Gene Expression Omnibus (GEO) database under accession number GSE42117. Part of this work is included in a broader U.S. patent application (12/554,472, “Genome-wide Method for Mapping of Engaged RNA Polymerases Quantitatively and at High Resolution”), which refers to variants of the method that we use here.

Supplementary Materials

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Materials and Methods

Supplementary Text

Figs. S1 to S10

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Source Codes for Analysis Scripts

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27 August 2012; accepted 21 December 2012

10.1126/science.1229386

Little Emperors: Behavioral Impacts of China's One-Child Policy

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We document that China's One-Child Policy (OCP), one of the most radical approaches to limiting population growth, has produced significantly less trusting, less trustworthy, more risk-averse, less competitive, more pessimistic, and less conscientious individuals. Our data were collected from economics experiments conducted with 421 individuals born just before and just after the OCP's introduction in 1979. Surveys to elicit personality traits were also used. We used the exogenous imposition of the OCP to identify the causal impact of being an only child, net of family background effects. The OCP thus has significant ramifications for Chinese society.

China's One-Child Policy (OCP) restricts the number of children that urban couples can have to one, with exceptions for those from ethnic minorities or with a severely disabled child. The policy has given rise to a land of “little emperors,” whose parents dote on them exclu-

sively. This has led to widespread concern within China about the social skills of this generation and the observation that these children tend to be more self-centered and less cooperative (1–3). This can be seen in developments such as employers including phrases like “no single children”

in job advertisements (4). In March 2007, 30 delegates at the Chinese People's Political Consultative Conference called on the government to abolish the policy (5). Their concerns centered on "social problems and personality disorders in young people."

The question about the behavioral consequences of not having siblings has been of interest in developmental psychology for many decades. China's OCP provides us with a natural experiment that allows us to identify the causal impact of being a single child. Prosocial development is believed to be shaped by parents as well as by social interactions with peers, including siblings (6). Different relationships with parents and lack of interaction with siblings have thus been identified in the psychology literature as two reasons why only children may develop differently from their counterparts with siblings (7). For example, parents of only children may be more responsive to their needs, which may produce a greater sense of security, confidence, and intellectual competence (8, 9). Parents of only children may also be more able to interact with their children in ways that promote desirable development (10). More attention from parents can, however, come with downsides in terms of higher expectations and pressure to succeed in life (11). Only children are often viewed as disadvantaged as a result of "sibling deprivation," which may lead to their being self-centered, less cooperative, and less likely to get along with peers (12).

In this paper, we describe how we used techniques from experimental economics to measure behavioral differences between the pre- and post-OCP generations. Behavior in economic games has been widely shown to be correlated with actions outside the experimental setting (13–18). We investigated the impact of the OCP on altruism, trust, trustworthiness, attitudes toward risk, and competitiveness. The OCP can be thought of as a natural experiment that enables us to separate out the effect of being an only child from the effects of family background. In addition to our experimental results, personality survey questions revealed that the OCP cohorts are also substantially more pessimistic, less conscientious, and possibly more neurotic.

We conducted experiments with participants recruited from the general population of Beijing, where the policy is strictly enforced (19). The OCP was introduced in 1979. We required participants to be born in either 1975 or 1978 (our pre-OCP cohorts) or in 1980 or 1983 (our post-OCP cohorts). Participants were also required to have both parents with urban residency status

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(hukou) at the time of the participant's birth. This sampling ensured that those in the post-OCP cohorts were subject to the strictly enforced policy and that all the cohorts were similar with respect to their parental hukou status. The final sample consisted of 421 participants spread evenly across the birth cohorts 1975, 1978, 1980, and 1983, with gender balance within these cohorts.

A postexperiment participant survey collected demographic and socioeconomic information. We tested the representativeness of our sample by comparing it with the Beijing subsample of the National Bureau of Statistics 2009 Urban Household Survey data. Our sample was better educated than the general population but otherwise similar (table S1). We carefully controlled for education in the empirical specifications below.

Table 1 shows the proportion of only children in each birth cohort. This increased from 27% in the 1975 cohort to 91% for the cohort born in 1983. The average number of siblings decreased from 0.97 to 0.12 over the same period (20). The proportion of single children had increased before the 1979 introduction of the policy as a result of other noncompulsory population growth policies that were precursors to the OCP (fig. S1) (21). In this paper, we thus identify the behavioral impact of the OCP relative to the noncompulsory fertility policies implemented before the OCP.

Although in later years the policy undoubtedly reduced the size of extended families, extended family size differed only slightly between the pre- and post-OCP cohorts we studied. The number of cousins declined slightly from an average of 7.4 to 7.0 cousins (Table 1). We are thus identifying the impact of growing up as an only child, not the impact of having a smaller extended family.

The experiments we conducted are standard games from the economics literature. The dictator game (22) is designed to elicit the extent of altruism among participants. The trust game elicits the extent to which participants are able to trust one another and the extent of their trustworthiness (23). These games are explained in the supplementary materials.

In the risk game (24), each participant is given 100 yuan (which is approximately U.S. \$15) and the choice to put any amount between 0 and 100 yuan into an "investment," which yields triple the amount invested with 50% probability and 0 with 50% probability. More risk-averse participants will invest less in the risky option. The outcome of the investment is decided by the flip of a coin at the completion of the session.

In the competition game, participants are asked to add up as many sets of five two-digit numbers as possible in 5 min (25). The numbers are randomly generated and presented in rows. Participants write the total in a blank box provided at the end of the row. Calculators cannot be used, but scrap paper is provided for handwritten calculations.

Participants are asked to choose between two different payment schemes. Option 1 is a piece rate which pays 5 yuan for every sum correctly completed. In option 2, payments are determined in a competitive way. Each participant is randomly and anonymously paired with someone else in the room. S/he is paid 10 yuan for every sum correctly completed if s/he completes more sums correctly than the person with whom s/he is paired, 5 yuan if both participants complete the same amount of correct sums, and 0 yuan if s/he loses the competition.

Figure 1 presents the unconditional differences in behavior between participants born before and after the OCP, for each of the games. The underlying data are presented in table S2 in the supplementary materials. Those born under the OCP shared slightly less of the endowment in the dictator game with the other player (40.1% of the endowment on average as compared to 43.4% sent by those born before the policy's introduction). The *t* test of difference in means is statistically insignificant ($P = 0.11$). OCP participants on average were less trusting, sending less to the other player (46.1 versus 50.6%) and returning less than those not born under the policy (30.4 versus 35.4%). Both of these differences are statistically significant.

OCP participants invested significantly less in the riskier investment (58.1 versus 66.4%). In the competition game, fewer OCP participants

Table 1. Demographic composition by cohort. We present means of variables by birth cohort and pre- and post-OCP. Column two reports means for those born in 1978 but excludes those born in 1978 who report they are an only child as a result of the policy.

	1975	1978 ^a	1978	1980	1983	Pre-OCP	Post-OCP
% Only children	27.0	23.7	60.9	81.8	90.7	45.1	86.4
% With one sibling	56.0	62.7	32.2	17.2	5.6	43.3	11.2
% With two siblings	10.0	8.5	4.4	1.0	1.9	7.0	1.5
% With three sibling	4.0	3.4	1.7	0.0	0.9	2.8	0.5
% With four siblings	2.0	1.7	0.9	0.0	0.0	1.4	0
Average no. of siblings	0.97	0.97	0.50	0.19	0.12	0.72	0.16
% Being the first born	52.0	35.6	67.0	85.9	93.5	60.0	89.8
Average no. of cousins	6.93	7.95	7.78	7.14	6.90	7.4	7.0
Average no. of aunts and uncles	5.15	5.42	5.81	5.91	6.27	5.5	6.1
Age (years)	34.7	31.8	31.7	29.7	26.7	33.1	28.2
<i>N</i>	100	59	115	99	107	215	206

chose to compete than those born before the policy (44.2 versus 51.8%). This difference is substantial but not statistically significant ($P = 0.12$).

Differences in competitiveness may reflect beliefs in one's ability. Participants were asked in which performance quintile they expected themselves to be relative to others in the room. There is no significant difference in this self-reported ranking between the pre- and post-OCP cohorts, although participants born under the OCP completed significantly more sums correctly than their counterparts (table S2). This is consistent with the findings in the literature that only children perform better academically (26).

The effects discussed above are simple mean differences. These could be due to differences in the demographic backgrounds of the pre- and post-OCP samples. To examine the OCP effects net of these observable characteristics, we estimated an econometric model in which we controlled for participants' gender and education, maternal education, and whether the individual was born in Beijing; in addition to the main variable of interest, whether the participant was born under the OCP. The summary statistics for the control variables are presented in table S3. Table 2 reports the estimation results. We find that even when the demographic and family background variables were controlled for, the unconditional effects we observed in Fig. 1 above persisted in terms of signs, magnitudes, and significance levels. The only difference from the unconditional estimates is that the regression results indicate that the lesser propensity for those who were born after the OCP to choose to compete becomes statistically significant once one controls for demographic characteristics.

The OCP indicator is defined according to birth cohort and hence is highly correlated with

age. There is no evidence that age has a strong systematic effect on behavior in experiments of the type we conducted, particularly over the relatively small age range in our sample (24, 27–32). Age was not a determinant of behavior within the pre- and post-OCP cohorts (table S8). Our results are also largely unaffected when we limit the potential for age effects by focusing on just the 1978 and 1980 cohorts (table S9). We thus conclude that age effects were not driving our results. Consistent with this result, marital status, being a parent, the age of parents, and people potentially becoming more capitalistic over time do not seem to explain our results either (tables S10 and S11).

Although the main effect of the OCP is to produce single children, the coefficients we estimate in Table 2 are not estimates of the effect of being a single child, because being a single child is not a unique characteristic of the after-OCP cohort. Many before-cohort individuals were also single children, and some children born after the policy were not single children (Table 1). The coefficient on the OCP indicator is thus the average behavioral effect of the OCP across the population.

If being a single child were exogenous, then the effect of growing up without siblings would be estimated consistently from

$$Y_i = \alpha + \beta X_i + \varphi Single_i + v_i \quad (1)$$

where Y_i is the behavior of interest; $Single_i$ is an indicator for being an only child; α , β , and φ are coefficients to be estimated; and v_i is a random error term. The coefficient of interest would be φ . Being a single child in the pre-policy cohort was, however, largely a choice of parents. Thus, the coefficient on $Single_i$ in Eq. 1 would pick up not only the effect of being a single child but also the effect of any omitted family background

variables that influenced the probability of being an only child. This is a problem if the unobserved parental characteristics that make parents choose to have one child also affect individuals' behavioral outcomes via genetic or nurture channels, which is likely. The variable $Single_i$ is thus endogenous.

We can, however, exploit the exogeneity of the imposition of the OCP and use the indicator of whether one was born under the policy, D_i , to instrument for the endogenous variable $Single_i$. We can thus identify the causal effect of growing up without siblings as a result of the OCP. That is, we estimate the equations below using an instrumental variables (IV) approach. Equation 2b is the first-stage regression.

$$Y_i = \alpha + \beta X_i + \varphi Single_i + v_i \quad (2a)$$

$$Single_i = \eta + \delta X_i + \kappa D_i + u_i \quad (2b)$$

where η , δ , and κ are coefficients to be estimated; u_i is a random error term; and the other terms are defined as above. Provided that the instrument satisfies a few assumptions (see section 2.1 in the supplementary materials), the IV estimate of φ can be interpreted as the Local Average Treatment Effect (LATE) of growing up as only children because of the OCP (33).

The IV results are reported in Table 3. In every case where we identified a difference in behavior between the pre- and post-OCP cohorts, being an only child as a result of the OCP was also shown to have a significant causal impact on behavior. The coefficients on being an only child are over double the coefficients on the indicator of whether one was born under the OCP reported in Table 2. Individuals who were only children as a result of the policy sent on average 16 percentage points less of the endowment to the other

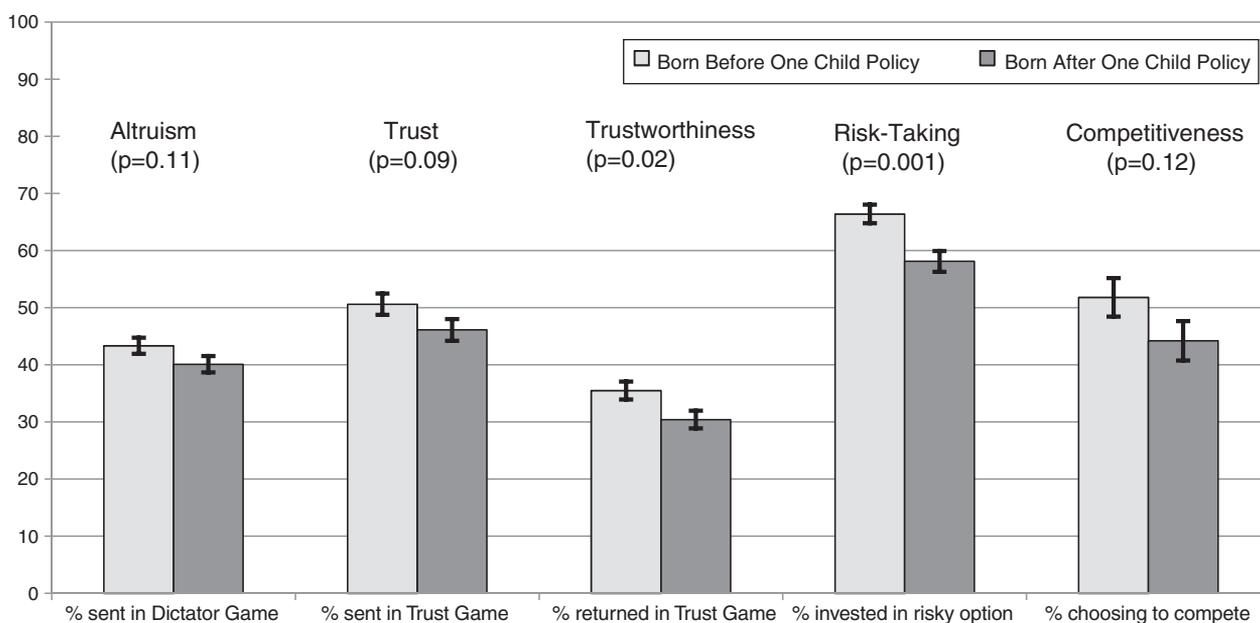


Fig. 1. Behavioral consequences of the OCP. Mean differences in behavior between participants born before and after the OCP are shown. The P values reported in parentheses are from t tests of differences in means. Error bars are mean \pm SEM.

player and returned 11 percentage points less of what they received in the trust game, invested 20 percentage points less of the endowment in the risky option in the risk game, and were 20% less likely to choose the competitive option in the competition game. In terms of standard deviations (SD) of the dependent variable, being a single child is associated with a decrease of 0.58 SD of the

percentage sent in the trust game, 0.44 SD of the percentage returned in the trust game, 0.75 SD of the percentage invested in the risky option, and 0.41 SD of the probability of competing. These are thus sizeable effects.

In the post-experiment survey, participants were asked a number of questions that sought to assess their personality type and outlook on life.

Table 2. Estimation results. We estimated $Y_i = \alpha + \beta X_i + \gamma D_i + \varepsilon_i$, where Y_i is a behavioral outcome observed in the experiments, and X_i is a vector of control variables, which includes participants' gender and education, maternal education, and whether the individual was born in Beijing. The main variable of interest is D_i , which equals 1 if an individual is born after the introduction of the OCP and 0 otherwise. The coefficient γ identifies any differences between those born before and after the policy and is our estimate of the behavioral impact of the OCP. Columns one to four report coefficients from Tobit estimation with lower censoring at 0 and upper censoring at 100. Column five presents marginal effects from a Probit estimation on whether to compete or not. Robust standard errors are shown in square brackets. *, **, *** indicate statistical significance at the 10, 5, and 1% levels, respectively.

	Trust and				
	Altruism	trustworthiness		Risk-taking	Competitiveness
	Dictator game	Trust game	Risk game	Competition game	
	% Sent	% Sent	% Returned	% Invested	Chose to compete
OCP	-2.834 [2.275]	-6.980** [3.116]	-5.024* [2.728]	-7.987** [3.213]	-0.090* [0.050]
Male	-0.646 [2.299]	10.73*** [3.120]	0.694 [2.687]	3.086 [3.152]	0.072 [0.049]
University or above	-14.37*** [5.484]	1.496 [6.407]	-15.34** [6.314]	-14.030* [8.111]	0.149 [0.115]
3-year college	-13.28** [5.538]	-3.989 [6.429]	-15.53** [6.290]	-5.323 [8.143]	0.12 [0.118]
Born in Beijing	-5.319* [2.977]	-11.02** [4.656]	4.788 [4.485]	5.391 [4.096]	0.082 [0.075]
Mother with 3-year college	0.518 [3.784]	8.887* [4.669]	4.594 [4.253]	8.123* [4.220]	-0.009 [0.067]
Mother with university or above	-4.363 [5.320]	6.983 [5.998]	-2.612 [5.439]	5.004 [5.406]	0.091 [0.100]
Observations	410	408	398	416	419

Participants were asked, "What do you think are the chances that it will be sunny tomorrow? Please write a number from 0 to 100, where 0 means 'absolutely no chance' and 100 means 'absolutely certain.'" Responses to this question are widely used as an indicator of optimism (34). We found that those born under the OCP and those who grew up as single children as a result of the OCP were significantly less optimistic than others (table S15).

The post-experiment survey also implemented the Big Five Inventory, which contains 44 questions designed to categorize people in terms of openness (inventive/curious versus consistent/cautious), conscientiousness, extraversion, agreeableness, and neuroticism (sensitive/nervous versus secure/confident). These five broad factors together encompass most known personality traits, and the 44 questions are used to construct scores for each of these traits (35). We examined to what extent these traits were determined by the OCP and single-child status. Being born under the OCP and growing up as a single child as a result of the OCP are associated with a higher neuroticism score and a lower conscientiousness score (table S15).

These effects are not small: 0.69 SD of our optimism indicator, 0.52 SD of the conscientiousness score, and 0.71 SD of the neuroticism score. The result for neuroticism is consistent with the finding that positive sibling relationships moderate the relationship between stressful life events and internalizing behaviors (36). The finding that conscientiousness is lower is counter to the argument in the empirical literature in psychology that single children have a greater motivation to achieve, but it is consistent with Chinese parents' views of their only children (37).

Like the experimental results, our results for conscientiousness and optimism are qualitatively similar when estimated using just the 1978 and

Table 3. Causal impact of being an only child. We present results from IV estimation. We used an indicator of being born under the OCP as an instrument for being an only child. Columns one to four present the results of IV

Tobit estimation. Column five presents marginal effects from IV Probit estimation. Robust standard errors are shown in square brackets. *, **, *** indicate statistical significance at the 10, 5, and 1% levels, respectively.

Dependent variables	Altruism	Trust	Trustworthiness	Risk-taking	Competitiveness
	(Dictator game; % sent)	(Trust game; % sent)	(Trust game; % returned)	(Risk game; % invested)	(Competition game; competing)
Only-child	-6.743 [5.454]	-15.998** [7.219]	-11.34* [6.199]	-19.002** [7.920]	-0.203* [0.108]
Male	-0.829 [2.307]	10.604*** [3.153]	0.584 [2.693]	2.641 [3.280]	0.067 [0.049]
University or above	-13.742** [5.657]	3.064 [6.593]	-14.19** [6.680]	-11.998 [8.788]	0.166 [0.114]
3-year college	-12.573** [5.692]	-2.323 [6.571]	-14.49** [6.657]	-2.93 [8.807]	0.138 [0.118]
Born in Beijing	-3.054 [3.486]	-5.914 [4.981]	8.442* [4.606]	11.528** [4.797]	0.142* [0.075]
Mother with 3-year college	1.238 [3.837]	10.396** [4.721]	5.642 [4.251]	10.045** [4.605]	0.011 [0.069]
Mother with university or above	-3.418 [5.440]	8.522 [6.038]	-1.571 [5.554]	7.361 [5.456]	0.109 [0.099]
Observations	410	408	398	416	419

1980 cohorts, and age is not a significant determinant within pre- and post-OCP periods. The results for neuroticism are less robust to checks for age effects (table S16).

Previous research has shown that noncognitive attributes such as conscientiousness, neuroticism, and optimism are important determinants of educational attainment, labor market outcomes, health, and marriage and divorce (38–40). Prosocial behavior is consistently seen to be an important determinant of social capital and plays a role in institutional development (41). A willingness to take risks is an important component of entrepreneurship (17). Our data show that being an only child as a result of the OCP is associated with taking less risk in the labor market (table S19).

Although our findings were obtained from a comparison of cohorts in Beijing born directly around the time of the policy's introduction, our results are generalizable to other urban areas of China where the OCP was strictly implemented. Previous work suggests that differences between only children and others in Beijing are similar to those in other urban areas (26). The effect of the policy on the behavior of people born long after the policy's introduction may, however, differ from what we found here, because later cohorts will have grown up with very limited extended family and in a society dominated by only children. Under such circumstances, we would expect that the policy's effect would, if anything, be magnified.

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Acknowledgments: We gratefully acknowledge funding from the Australian Research Council. We thank Simon Gaechter, Elaine Liu, and participants of various conferences and seminars for their useful comments on previous drafts. The data used in this paper will be made available from the ICPSR data depository, number 33353. The Rumici data are available at rse.anu.edu.au/rumici. All authors contributed equally to this paper.

Supplementary Materials

www.sciencemag.org/cgi/content/full/science.1230221/DC1
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14 September 2012; accepted 18 December 2012
Published online 10 January 2013;
10.1126/science.1230221

Highly Recurrent *TERT* Promoter Mutations in Human Melanoma

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Systematic sequencing of human cancer genomes has identified many recurrent mutations in the protein-coding regions of genes but rarely in gene regulatory regions. Here, we describe two independent mutations within the core promoter of *telomerase reverse transcriptase* (*TERT*), the gene coding for the catalytic subunit of telomerase, which collectively occur in 50 of 70 (71%) melanomas examined. These mutations generate de novo consensus binding motifs for E-twenty-six (ETS) transcription factors, and in reporter assays, the mutations increased transcriptional activity from the *TERT* promoter by two- to fourfold. Examination of 150 cancer cell lines derived from diverse tumor types revealed the same mutations in 24 cases (16%), with preliminary evidence of elevated frequency in bladder and hepatocellular cancer cells. Thus, somatic mutations in regulatory regions of the genome may represent an important tumorigenic mechanism.

Systematic characterization of human cancer genomes has led to the discovery of a wide range of mutated genes that contribute

to tumor development and progression. Most of the somatic mutations in tumors reside within the protein-coding regions of genes or at splice junc-

tions. To determine whether tumor genomes harbor recurrent mutations outside of protein-coding regions, we systematically queried noncoding somatic mutations using published whole-genome sequencing data.

Analysis of whole-genome sequencing data from malignant melanomas (1, 2) revealed two somatic *telomerase reverse transcriptase* (*TERT*) gene promoter mutations in 17 of 19 (89%) cases examined. The average sequence coverage at the *TERT* promoter locus was 30-fold in normal samples and 60-fold in tumor samples (fig. S1A).

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