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The dynamics of Machiavellian intelligence

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The ''Machiavellian intelligence'' hypothesis (or the ''social brain'' hypothesis) posits that large brains and distinctive cognitive abilities of humans have evolved via intense social competition in which social competitors developed increasingly sophisticated ''Machiavellian'' strategies as a means to achieve higher social and reproductive success. Here we build a mathematical model aiming to explore this hypothesis. In the model, genes control brains which invent and learn strategies (memes) which are used by males to gain advantage in competition for mates. We show that the dynamics of intelligence has three distinct phases. During the dormant phase only newly invented memes are present in the population. During the cognitive explosion phase the population's meme count and the learning ability, cerebral capacity (controlling the number of different memes that the brain can learn and use), and Machiavellian fitness of individuals increase in a runaway fashion. During the saturation phase natural selection resulting from the costs of having large brains checks further increases in cognitive abilities. Overall, our results suggest that the mechanisms underlying the ''Machiavellian intelligence'' hypothesis can indeed result in the evolution of significant cognitive abilities on the time scale of 10 to 20 thousand generations. We show that cerebral capacity evolves faster and to a larger degree than learning ability. Our model suggests that there may be a tendency toward a reduction in cognitive abilities (driven by the costs of having a large brain) as the reproductive advantage of having a large brain decreases and the exposure to memes increases in modern societies.

There are many features that make us a "uniquely unique species" but the most crucial of them are related to the size and complexity of our brain (1–3). The brain size in *Homo sapiens* increased in a runaway fashion over a period of a couple hundred thousand years, but then stabilized or even slightly declined in the last 35–50 thousand years (1, 2, 4). In humans, the brain is very expensive metabolically: it represents ≈2% of the body's weight but utilizes ≈20% of total body metabolism at rest (5). The two burning questions are what factors drove the evolution of brain size and why our ancestors 50,000 years ago needed the brains they had. A number of potential answers have been hotly debated focusing on the effects of climatic (6), ecological (7), and social factors. One controversial set of ideas (1–3, 8–14) coming under the rubric of the "Machiavellian intelligence" or "social brain" hypothesis identifies selective forces resulting from social competitive interactions as the most important factor in the evolution of hominids, who at some point in the past became an ecologically dominant species (10, 14). These forces selected for more and more effective strategies of achieving social success (including deception, manipulation, alliance formation, exploitation of the expertise of others, etc.) and for ability to learn and use them. The social success translated into reproductive success (15–17) selecting for larger and more complex brains. Once a tool for inventing, learning, and using these strategies (i.e., a complex brain) is in place, it can be used for a variety of other purposes including coping with environmental, ecological, technological, linguistic, and other challenges.

Although these ideas are by now well appreciated by many, and some components of the general scenario are supported by data (18–21), verbal arguments and generalization from limited data alone are not enough to establish their general plausibility and predict the relevant time scales and expected dynamic patterns. Here we attempt to shed some light on these questions using a stochastic individual-based explicit–genetic model.

Model

We consider a sexual diploid population, and focus on socially learned strategies (memes) used by males to gain advantage in competition for mates. As a first step, we neglect analogous processes in females (both for simplicity and because sexual selection in females is expected to be much less intense than in males). Genes control the learning ability a and cerebral capacity c of the brain, which in turn control how easily a brain learns new strategies (memes) and how many memes a brain can host, respectively. Both a and c are treated as additive quantitative characters. That is, each trait value is found by summing up the contributions of the corresponding alleles and then normalizing the result. Learning ability a is normalized to be between 0 and 1, and cerebral capacity c is normalized to be between 0 and a positive integer $c_{\max}$. The loci controlling the two traits are independent, unlinked, diallelic, and have equal effects. Both traits are viewed to be directly related to brain size and complexity and are assumed to be under direct viability selection toward 0. This selection reflects costs (e.g., energetic or due to increased death at childbirth) of having large brains. Note that setting the optimum values at 0 does not mean that having no brain at all is optimum but rather reflects a scale chosen. Individuals surviving to adulthood experience density-dependent mortality maintaining the population size close to a carrying capacity K.

Memes are invented and forgotten by individuals at small constant rates. Each meme is characterized by its Machiavellian fitness μ and complexity π ($0 < \mu, \pi < 1$). The former contributes to a male's fitness in between-male competitive interactions, whereas the latter defines how easily the meme can be learned. The correlation ρ between μ and π in newly invented memes is positive reflecting the idea that more advantageous memes are, generally, more complex and more difficult to learn. The rate of learning a meme is directly proportional to learning ability a, inversely proportional to the meme's complexity π, and declines with the ratio n/c where n is the number of memes already learned by the brain.

The Machiavellian fitness m of a male is given by the sum of Machiavellian fitnesses of the memes he has learned; this implies that fitness increases with the number of memes learned. The probability that a contest between two males is won by a specific male is given by an S-shaped function of the corresponding difference in their Machiavellian fitnesses. The male's mating rate increases with the average proportion of contests won. The strength of sexual selection in males is characterized by a parameter $f_{\max}$ measuring the number of

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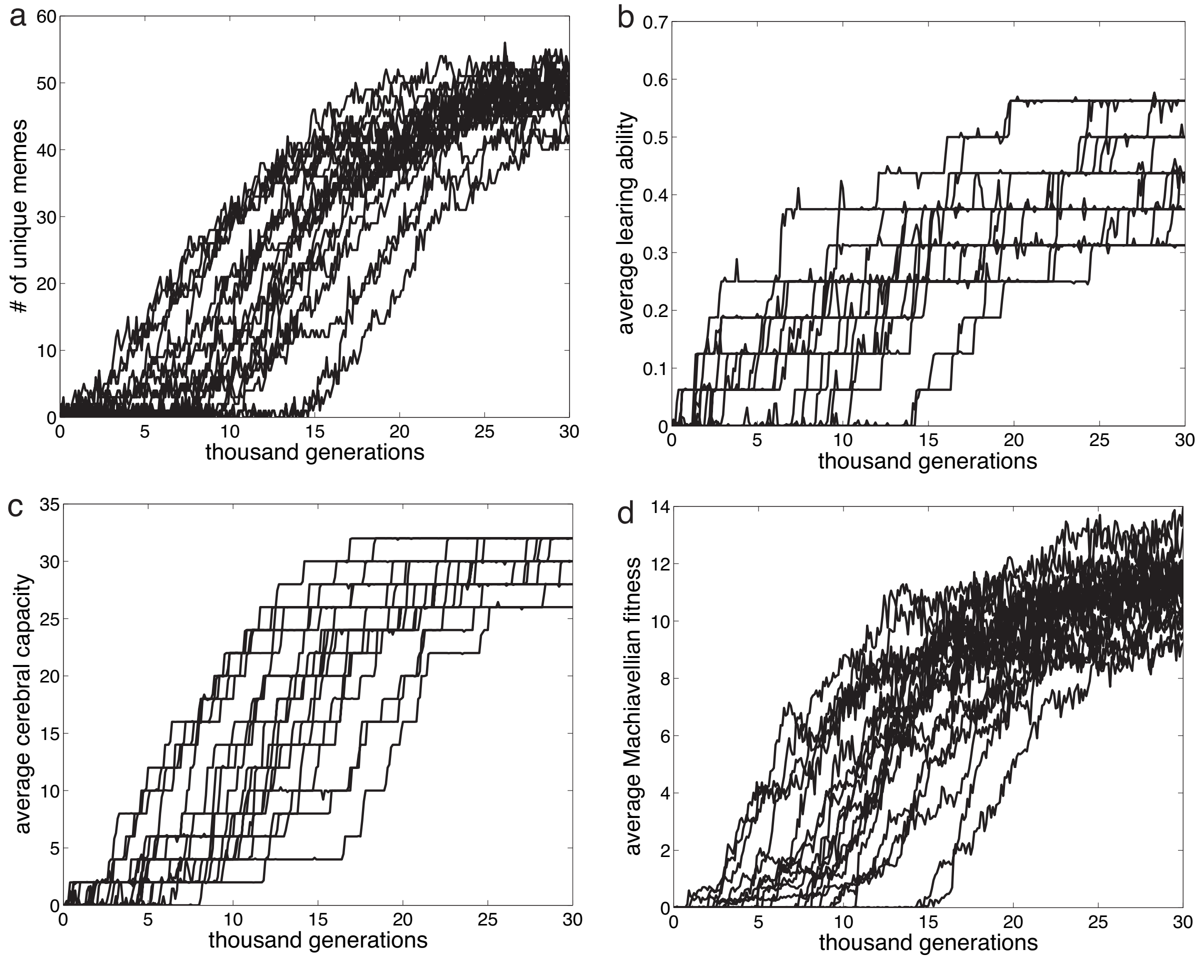

Fig. 1. The dynamics of the number of unique memes (*a*), the average learning ability (*b*), the average cerebral capacity (*c*), and the average Machiavellian fitness (*d*) in 20 runs with a default set of parameter values ($L = 16$, $K = 100$, $c_{max} = 32$, $f_{max} = 10$, $\rho = 0.5$).

females fertilized by a male who wins all contests. The importance of competition for mating success among males in the model captures another unique feature of hominids: that mating is possible at most times and that the possibility of continual sexual provocation and competition between males is very high (22). Offspring are produced with account of recombination, segregation, and mutation.

In our model, there are two types of selection: among memes and among genes. Although interrelated, they operate at different time scales: fast for memes and slow for genes. To adequately capture this important feature of gene–culture coevolution, we use an event-driven modeling framework in which time is treated as continuous (see *Methods*). Our simulations start with a population of individuals having zero learning ability and cerebral capacity. The population size varied between 50 and 150 individuals, which is compatible with social group sizes in hominids (13).

Numerical Results and Biological Interpretations

Fig. 1 shows the dynamics of the number of unique memes, the average learning ability, the average cerebral capacity, and the average Machiavellian fitness of males in 20 runs with a default set of parameter values. Each of these characteristics stays close to zero for several thousand generations during the "dormant phase" and then suddenly starts rapidly increasing in a process that we will refer to as "cognitive explosion." Cognitive explosion ends when natural selection stops further increase in cognitive abilities due to the costs of having large brains, and the system enters the "saturation phase." During the whole process, the population stays genetically monomorphic except during relatively short periods of "selective sweeps" when mutant alleles go to fixation (data not shown).

The dynamics before and at the onset of the cognitive explosion can be understood as follows. Nonzero learning ability a and cerebral capacity c are advantageous only if the individual has both of them simultaneously and, during his life time, learns a meme (or memes) from other individuals. Otherwise, individuals with $a > 0$ and/or $c > 0$ have reduced fitness due to decreased viability. The resulting fitness landscape resembles that in models of compensatory mutations (23, 24) where a deleterious mutation in one locus can be compensated later on by an advantagenous mutation in a different locus. During the dormant phase, one of the traits (i.e., learning ability or cerebral capacity) can sporadically deviate away from zero by mutation and random genetic drift despite this deviation causing a reduction in fitness. Cognitive explosion takes place when individuals with nonzero values of one trait are maintained in the population sufficiently long for mutations changing the value of the other trait in their offspring to occur and when both sets of new genes are maintained in the population long enough for the individuals to learn new memes and start enjoying a fitness advantage.

The onset of cognitive explosion depends on parameter values and varies from run to run. Fig. 2 illustrates the dependence of the median time T to cognitive explosion on the population

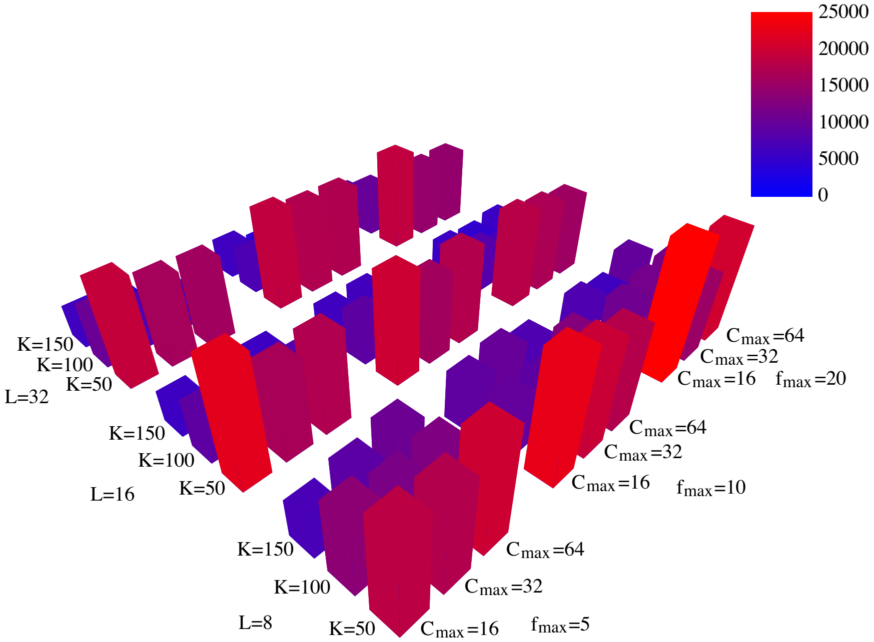

Fig. 2. The median time to cognitive explosion with $\rho = 0.5$.

carrying capacity K, the number of loci L underlying each trait, the maximum cerebral capacity $c_{\max}$, and the maximum mating group size $f_{\max}$ when the correlation ρ between meme fitness and complexity is 0.5. Fig. 2, as well as a statistical analysis based on the Cox proportional-hazard regression (25) (data not shown), show that T decreases with increasing K, L, $c_{\max}$, $f_{\max}$, and decreasing ρ. The effects of K and L are the most pronounced, which is compatible with the idea that the process of fixation of compensatory mutations is mostly limited by the availability of new genetic variation (23, 24). With realistic parameter values, the waiting time until the onset of cognitive explosion is on the order of 5–25 thousand generations.

After the onset of the cognitive explosion, further increases in a and c by mutation are advantageous because they allow individuals to learn more memes and, thus, achieve higher Machiavellian fitness and mating rate. A unique feature of our framework is an explicit consideration of the dynamics of cerebral capacity c, which we defined as a measure of the number of memes that the brain can host. In previous models, c was implicitly assumed to be fixed at one (26, 27) or infinity (28). During the cognitive explosion phase, cerebral capacity c typically evolves faster and achieves higher values than learning ability a (see Fig. 3). This observation suggests that higher values of cerebral capacity are more important than high learning ability and that there is more potential for improving the latter than the former. Evolution of cognitive abilities results in a significant reduction in individual viability (Fig. 3), thus creating conditions for the evolution of mechanisms that would reduce costs of having large brains such as postponing much of the brain growth to after birth (1) and reduction of the guts (29). In our model, more complex memes provide more fitness benefit to individuals. However, the complexity of memes present in the population does not increase but, on the contrary, decreases in time (data not shown). This happens as a result of intense competition among memes: whereas complex memes give advantage to individuals on a longer (biological) time scale, they lose competition to simpler memes on a shorter (social) time scale.

In our simulations, the cognitive explosion phase lasts until the cerebral capacity reaches a maximum possible level, whereas the learning ability appears to equilibrate at an intermediate level determined by a balance of reduced viability and increased mating success of individuals having big brains. Fig. 4 illustrates the state of the population reached in 8,000 generations after the cognitive explosion. Fig. 4 and an analysis of variance (data not shown) shows that the average learning ability, cerebral capacity, Machiavellian fitness, and the number of memes per individual all increase with $c_{\max}$, $f_{\max}$, and K and decrease with ρ and L. The negative effect of the number of loci L on the characteristics of cognitive abilities is explained by the fact that more loci means weaker selection on each individual locus and, thus, weaker evolutionary response. Both the average Machiavellian fitness (Fig. 4*c*) and the average number of memes per individual (Fig. 4*d*) correlate almost perfectly with the average cerebral capacity

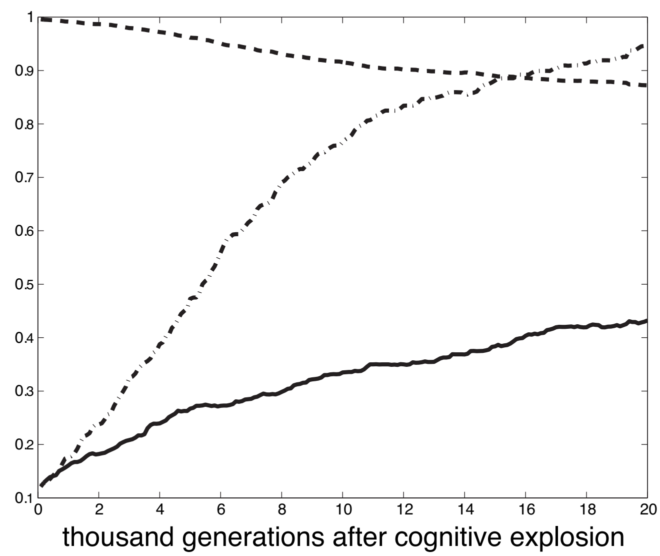

Fig. 3. The dynamics of the learning ability a (solid line), normalized cerebral capacity $c/c_{\max}$ (dashed-dot line), and viability v (dashed line) averaged over 20 runs shown in Fig. 1.

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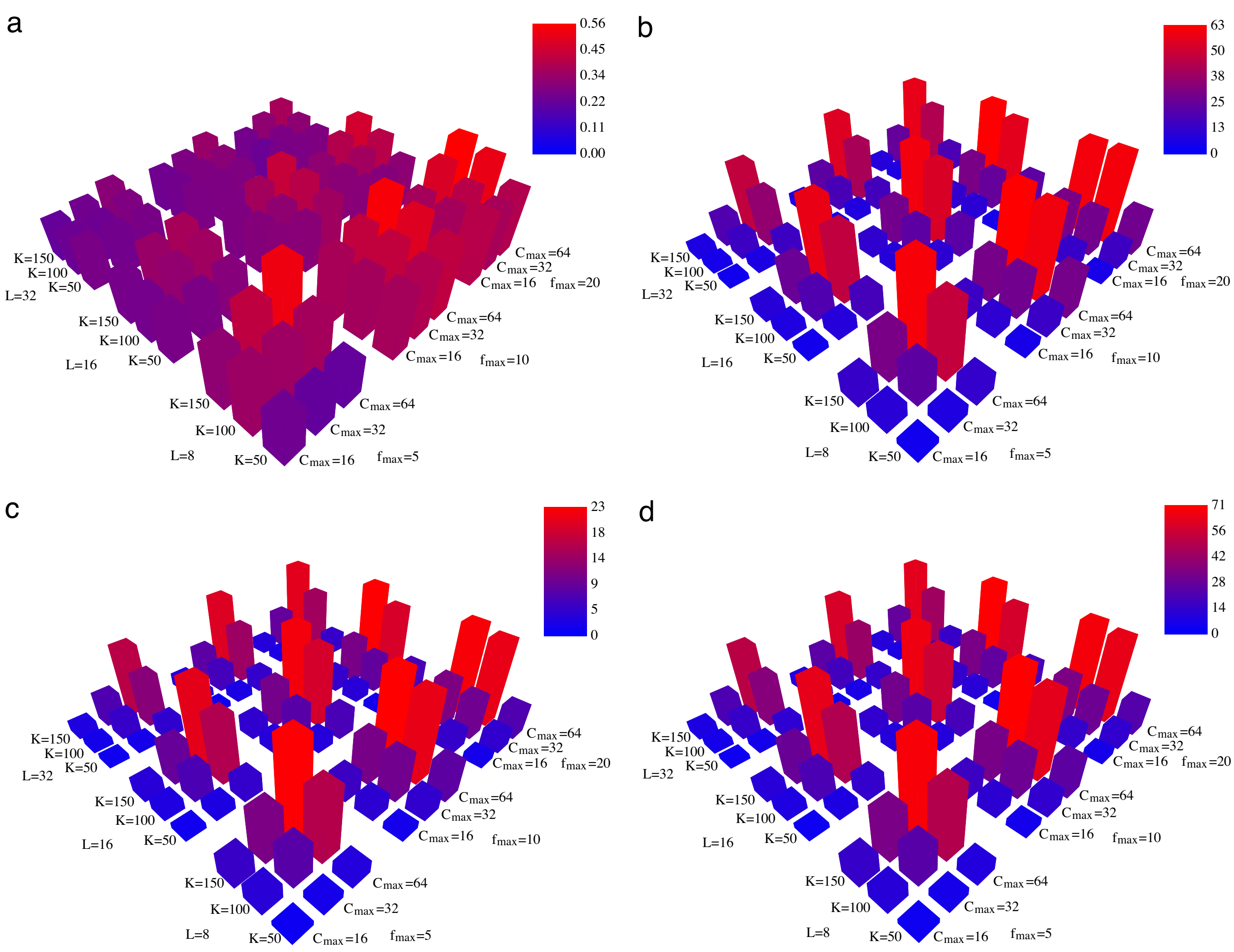

Fig. 4. The characteristics of the population 8,000 generations after the cognitive explosion. (*a*) The average learning ability. (*b*) The average cerebral capacity. (*c*) The average Machiavellian fitness. (*d*) The average number of memes per individual. $\rho = 0.5$.

(Fig. 4*b*), with the corresponding coefficients of correlation being 0.995. Overall, the simulations show that significant values of c and a can be achieved within 5–10 thousand generations after the onset of cognitive explosion.

It has been argued that, throughout most of human history, success in social competition translated into reproductive success with the most powerful men enjoying a disproportionate share of women and offspring (15–17). In our model, this effect is characterized by parameter $f_{\max}$ measuring the mating group size of a male who wins all between-male contests. This parameter strongly affects the levels of learning ability and cerebral capacity achieved in the population. For example, with $L = 32$, $c_{\max} = 64$, $K = 150$, and $\rho = 0.5$ as $f_{\max}$ decreases from 20 to 10 to 5, the average learning ability decreases from 0.36 to 0.33 to 0.30 (Fig. 4*a*), whereas the average cerebral capacity decreases from 57.0 to 54.5 to 47.5 (Fig. 4*b*). This finding suggests that, as the extent to which social success translates into reproductive success declines in modern societies, cognitive abilities are expected to be significantly reduced by natural selection. We also expect that as the number of memes in the population dramatically increases, learning ability will decrease further (because given a sufficiently large exposure to memes, they will be learned even by individuals with relatively low learning abilities).

Discussion

Here, we have built an explicit–genetic, individual-based, stochastic mathematical model of the coevolution of genes and memes aiming to explore the hypothesis of "Machiavellian intelligence." In the model, genes control the learning ability and cerebral capacity of brains, which invent and learn strategies (memes), which are used by males to gain advantage in competition for mates. Overall, our results suggest that the mechanisms underlying this hypothesis can indeed result in a significant increase in the brain size and in the evolution of significant cognitive abilities on the time scale of 10–20 thousand generations.

We show that, in our model, the dynamics of intelligence has three distinct phases. During the dormant phase, only newly invented memes are present in the population. These memes are not learned by other individuals. During the cognitive explosion phase, the population's meme count and the learning ability, cerebral capacity, and Machiavellian fitness of individuals rapidly increase in a runaway fashion. During the saturation phase, natural selection resulting from the costs of having large brains checks further increases in cognitive abilities. Both the learning ability and cerebral capacity are subject to negative natural selection due to costs of having large brains, but having nonzero values of both traits is necessary for learning and using different memes. The process of transition from the dormant phase to the cognitive explosion phase is somewhat similar to that of the fixation of a compensatory mutation when higher fitness is achieved by fixing two mutations each of which is deleterious by itself. As in the case of compensatory mutations, the transition from the dormant phase to the cognitive explosion phase is mostly limited by the availability of new genetic variation. The levels of cognitive abilities achieved during the cognitive explosion phase increase with the intensity of competition for mates among males and decrease with the number of loci controlling the brain size. The latter effect is explained by the fact that a larger number of loci implies weaker selection on each individual locus. In our model, evolutionary processes occur at two different time scales: fast for memes and slow for genes. More complex memes provide more fitness benefit to individuals. However, during the cognitive explosion phase the complexity of memes present in the population does not increase but, on the contrary, decreases in time. This happens as a result of intense competition among memes: whereas complex memes give advantage to individuals on a slow (biological) time scale, they lose competition to simpler memes on a fast (social) time scale because they are more difficult to learn. The increase in brain size results in a significant reduction in viability thus creating conditions that favor rapid evolution of the mechanisms reducing the costs of having large brains. One such mechanism is postponing much of the brain growth to after birth (1), whereas another is reduction of the guts (29). Our model suggests that there may be a tendency toward a reduction in cognitive abilities (driven by the costs of having a large brain) as the reproductive advantage of having a large brain decreases and the exposure to memes increases in modern societies.

The model studied here is based on a notion of "cerebral capacity" as a measure of the number of different memes/ideas/strategies that the brain can learn socially and use. This measure is analogous to "carrying capacity" used in ecology to characterize the number of individuals that can survive in a given ecological niche. During the cognitive explosion phase, the cerebral capacity evolves faster and to a larger degree than learning ability. Both the average Machiavellian fitness and the average number of memes per individual achieved during the cognitive explosion phase are largely controlled by the average cerebral capacity. The importance of cerebral capacity in our model suggests that incorporation of this notion into theoretical and empirical studies of cognitive processes can potentially be very beneficial.

The model studied here aims to describe only some aspects of the early stages of the evolution of intelligence. The model should not be applied directly to actual human history and society. Our model does not aim to explain why a cognitive explosion has occurred only in the lineage leading to modern *Homo sapiens*. Rather, it tests whether a particular set of explanations advanced and discussed in detail by many (1–3, 8–14), which places special emphasis on the achievement of "ecological dominance" and on competition in regard to social competencies, is plausible from the population genetics perspective. Alternative explanations do exist (e.g., refs. 6, 7, and 30), and much more work remains necessary to better understand the origins of human uniqueness. As with most other mathematical models used in evolutionary biology (e.g., refs. 24 and 31–36), the goal of our model is not to prove that a particular phemomena arises as a result of particular factors. Rather, we wished to explore the logic and plausibility of the arguments used to explain the phenomenon, to identify important factors, parameters, and time scales, and to check the robustness of conclusions to variation in assumptions.

Our model has a number of limitations. Here we discuss some potential consequences of their violation. We concentrated on a single population of small size. Allowing for more populations connected by migration should accelerate the onset of cognitive explosion by increasing the amount of new genetic variation. Once the cognitive explosion is initiated in a local population, emigrants (males or females) will quickly spread their genes across the whole system. We allowed only for positive Machiavellian fitness μ of memes. If memes with both positive and negative values of μ are possible, the process of cognitive explosion is expected to be delayed as deleterious memes will occasionally spread through the population like an epidemic reducing the fitness advantage of having high cognitive abilities. We assumed that memes are copied with no regard to the fitness or status of individuals they are learned from. Selective imitation when memes are more likely to be learned from high fitness/status individuals, should accelerate the evolution of brain size. This expectation is supported by the fact that a behavior analogous to cognitive explosion was observed in a much simpler and less realistic model of selective imitation (28) formalizing an integrant of Blackmore's "big brain" hypothesis (37). We did not allow for errors in meme copying. If such errors can only decrease the Machiavellian fitness of memes, then the process of cognitive explosion will be slowed down. However, if copying errors resulting in meme improvement are possible, we expect higher Machiavellian fitnesses to be achieved that potentially can accelerate the process. We conclude that, overall, from the theoretical perspective, the phenomenon of cognitive explosion, its patterns, and time scales identified here appear to be robust.

Finally, we note that the modeling framework we have developed can potentially be used to study the evolution of languages (38) and the coevolution of genes and culture in general (26, 27).

Methods

Here we provide some additional details on the model and simulations.

Constant Viability Selection. Viability (i.e., the probability to survive to the age of reproduction) of a child with trait values a and c is

$$v = \exp\left\{-0.5\left[\left(\frac{a}{\sigma_a}\right)^2 + \left(\frac{c/c_{\max}}{\sigma_c}\right)^2\right]\right\},$$

where σ_a and σ_c are parameters measuring the strength of viability selection.

Frequency-dependent selection for mating success in males. The probability that a contest between males i and j with Machiavellian fitnesses $m(i)$ and $m(i)$ is won by male i is

$$p(i,j) = \frac{\exp\{\alpha[m(i) - m(j)]\}}{1 + \exp\{\alpha[m(i) - m(j)]\}},$$

where α is a scaling parameter measuring how effectively an advantage in m is translated into larger value of p. With this parameterization $p(j,i) = 1 - p(i,j)$ and the effects of memes known to both contestants cancel out. The expected proportion of contests won by male i is $p_e(i) = \Sigma_{j,j\neq i}\, p(i,j)/(N_m - 1)$, where N_m is the number of males in the population. The male's mating rate is a function of $p_e(i)$ to be specified below.

Events. There are five types of events: birth and death of individuals and invention, loss, and replication of memes. We say that an event occurs at rate x if the probability of this event during a short time interval dt is xdt.

Each female gives birth at a constant rate b. Male i is chosen to be the father with a probability proportional to his mating group size

$$f(i) = f_{\min} + (f_{\max} - f_{\min})p_e(i)^{\lambda},$$

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where $f_{\min}$, $f_{\max}$, and λ are parameters. Note that if $p_e(i) = 1$ (i.e., the male wins all contests), $f(i) = f_{\max}$, and if $p_e(i) = 0$ (i.e., the male looses all contests), $f(i) = f_{\min}$. If one defines a parameter f_0 as the mating group size at $p_e(i) = 1/2$ (which is the case when everybody has the same Machiavellian fitness), then

$$\lambda = \ln\left(\frac{f_{\max} - f_{\min}}{f_0 - f_{\min}}\right) \Big/ \ln 2.$$

Parameters $f_{\min}$, f_0, and $f_{\max}$ can be thought of as the effective number of females available to a male in the corresponding category. One can set $f_0 = 1$ with $f_{\min} < 1 < f_{\max}$. If a birth is to take place, a single offspring is produced with account of recombination, segregation, and mutation. The sex is assigned randomly. Then viability selection follows and surviving offspring instantaneously become adults.

Adults die at rate $d = N/K$, where N is the overall population size and K is the population carrying capacity.

Males invent new memes at a constant rate ν. The values of Machiavellian fitness μ and complexity π to be assigned to a new meme are drawn randomly from a truncated bivariate normal distribution with constant means $\mu = 0.5$, $\pi = 0.5$, standard deviations σ_μ and σ_π, and positive correlation ρ. Only the values satisfying the conditions $0 < \mu < 1$, $\pi_{\min} < \pi < 1$, where $\pi_{\min}$ is a minimum meme complexity, are allowed.

Each meme is forgotten at a constant rate δ. Consider a meme with complexity π present in the population in M copies. Consider also a male with learning ability a and cerebral capacity c who has already learned n other memes. The rate at which the male aquires the new meme is $\eta a/\pi \exp[-\beta(n/c)^\gamma]\, M$, where η, β, and γ are positive scaling parameters. The exponential term describes the brain's saturation with memes. Note that if γ is large, then this term is either close to 1 (if $n < c$) or close to zero (if $n > c$).

Simulations. The model dynamics are simulated by using Gillespie's direct method (39). That is, the next event to happen is chosen according to the corresponding rates. The time interval until the next event is drawn from an exponential distribution with a parameter equal to the sum of the rates of all possible events. All rates are recomputed after each event.

Initial Conditions and Parameters. Initially, all individuals are identical homozygotes with $a = c = 0$ and no memes. We varied the number of loci per trait ($L = 8, 16, 32$), the population carrying capacity ($K = 50, 100, 150$), the maximum cerebral capacity ($c_{\max} = 16, 32, 64$), the maximum mating group size ($f_{\max} = 5, 10, 20$), and the correlation between meme Machiavellian fitness and complexity ($\rho = 0.25, 0.5, 0.75$). The following parameters did not change: mutation probability per locus 10^{-5}, $\sigma_a = \sigma_c = 2$, $\alpha = 0.5$, $\beta = 1$, $\gamma = 10$, $b = 2.2$, $f_{\min} = 0$, $\nu = 0.01$, $\delta = 0.02$, $\eta = 0.05$, $\sigma_\mu = \sigma_\pi = 0.25$, $\pi_{\min} = 0.05$. Forty runs were done for each of 243 parameter combinations. Simulations ran for 30,000 time units (roughly corresponding to 30,000 generations)

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