

Does self-replication imply evolvability?

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Abstract

The most prominent property of life on Earth is its ability to evolve. It is often taken for granted that self-replication—the characteristic that makes life possible—implies evolvability, but many examples such as the lack of evolvability in computer viruses seem to challenge this view. Is evolvability itself a property that needs to evolve, or is it automatically present within any chemistry that supports sequences that can evolve in principle? Here, we study evolvability in the digital life system Avida, where self-replicating sequences written by hand are used to seed evolutionary experiments. We use 170 self-replicators that we found in a search through 3 billion randomly generated sequences (at three different sequence lengths) to study the evolvability of *generic* rather than hand-designed self-replicators. We find that most can evolve but some are evolutionarily sterile. From this limited data set we are led to conclude that evolvability is a likely—but not a guaranteed—property of random replicators in a digital chemistry.

Introduction

For life of the type as we experience it on Earth to emerge from an initially abiotic state requires two seemingly independent things to happen. First, a self-replicator has to emerge (or else, to arrive on Earth from extraterrestrial sources (Arrhenius, 1908; Hoyle and Wickramasinghe, 1981; Wickramasinghe, 2011)). Secondly, this self-replicator must be able to evolve and thus diversify into the complexity we see today. In general we think of self-replicators as extremely rare (von Neumann, 1966). But in order to jump-start the process of evolution, these rare self-replicators now also must be endowed with another property—evolvability (Wagner and Altenberg, 1996; Kirschner and Gerhart, 1998; Wagner, 2005). By evolvability here we mean the ability to produce variants or mutants (produced by a faulty self replication process or else by external noise) that can also self-replicate. Without evolvability the self-replicator would just multiply but not adapt. While it is safe to assume that one of the first self-replicators on Earth was evolvable ($n = 1$), it is not at all clear whether evolvability is a general property of self-replicators, or else is an additional constraint that renders the emergence of

life even more improbable. Here we use the computational evolution system Avida (Adami and Brown, 1994; Adami, 1998; Ofria et al., 2009) to investigate whether random self-replicators, that is, randomly generated sequences of code written in the avidian instruction set that happen to be able to self-replicate, also are automatically endowed with the capacity to evolve. Even though evolvability appears to be inherent to avidians, we cannot rule out a priori whether the observed evolvability of avidians is a consequence of the evolvability of the hand-written ancestor or is instead a germane property of all self-replicators that can exist within this digital chemistry. To resolve this question, we searched for self-replicating sequences that we generated randomly, within the three size classes $L = 8$, $L = 15$ (the size of the standard avidian self-replicator), and $L = 30$. We found 170 such sequences after generating 3 billion random sequences, and report their evolvability below.

Self-replicators in Avida

In Avida, small self-replicating computer programs (“avidians”) compete for limited memory space and limited CPU resources needed to successfully self-replicate (see Ofria et al. 2009 for a complete description of the Avida system). This ability to self-replicate is contained within an individual avidian’s genome of instructions (see Fig. 1). Because this genome is then passed on to an avidian’s descendants, the ability to self-replicate is heritable. Selection in Avida is implicit, since faster replicators have a higher chance of making offspring. During the process of self-replication, mutations may be introduced, resulting in error-prone replication and variation within the population. Thus, Avida is an *instance* of evolution by natural selection (Pennock, 2007), because it contains inheritance, variation, and differential fitness among individuals. Avida has been used to explore a diverse set of topics in evolutionary biology such as the evolution of genomic complexity (Lenski et al., 1999), the “survival of the flattest” effect at high mutation rates (Wilke et al., 2001), the evolution of complex features (Lenski et al., 2003), the evolution of reproductive division of labor (Goldsby et al., 2014), and the role of co-

evolution in the origin of complexity (Zaman et al., 2014).

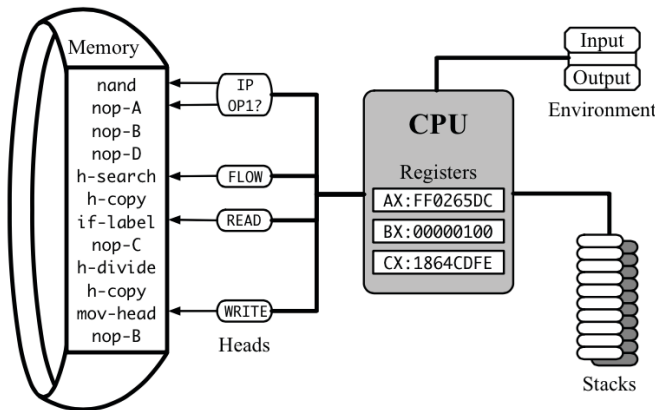


Figure 1: The avidian CPU in the process of executing a segment of code. The CPU uses three registers (AX,BX,CX) as well as an instruction pointer (IP) that reads the program into the CPU. A read-head, a write-head, and a flow-head are used to specify positions in the CPU’s memory. The ‘copy’ command reads from the read-head and writes to the write-head, while ‘jump’-type statements move the instruction pointer to the flow-head. The CPU uses two stacks to simulate an “infinite Turing tape”, while input/output buffers serve to communicate between the CPU and its environment (reproduced from Ofria et al. (2009), with permission).

Avidian genomes are composed of usually 26 different instructions, typically rendered as a string of lowercase letters, where each letter corresponds to one command (see Table 1). These instructions can be considered analogous to the 20 amino acids common to all biological organisms.

A self-replicator in Avida must have a set of instructions in the right order to: first allocate memory, then copy itself into this newly allocated memory, and finally it has to split the new memory from the old one in order to create a new organism. These instructions and their interactions are complex and in general it is not possible to predict if an organism will replicate just by examining the sequence. As a consequence, the ability to self-replicate has to be tested directly by allowing the instructions to execute (we surmise that this problem of predicting the ability to self-replicate is similar to the Halting Problem (Turing, 1936), where it is necessary to run the algorithm to find out if it halts or not).

In the majority of all Avida experiments a default hand-designed “start” organism is used to seed a population. This choice is to some extent historical: the designers assumed that self-replicators were too rare to be found by a random process (Adami, 1998). Indeed, any particular sequence of

length $L=15$ for example (the length of one of the standard hand-written ancestors) has a likelihood of $p = 26^{-15} \approx 6 \times 10^{-22}$. If a million of such sequences could be checked per second, on one thousand CPUs running in parallel, it would take about 50,000 years to find it. As a remedy, the designers wrote one instead (most of the common ancestors in Avida were written by Charles Ofria). However, it is clear that the density of self-replicators in the space of all sequences depends on the chemistry (here, the instruction set) used. Since the inception of Avida in 1993, the standard instruction set has changed, and it appears that using the current set (that is, the current “chemistry”) self-replicators can be found among randomly generated sequences (as reported here) because the information content of the sequences is significantly smaller than 15.

No self-replicator in nature (or within Avida) replicates without error, because noise in the system is inevitable and will always affect replication by increasing variation. Variation in Avida can have two different causes. First, it is possible that the sequence of commands performs in such ways that the resulting copy is modified. This typically leads to repeated commands, insertions, or deletions. Such changes are inherent to the self-replicator (they are genetically encoded and thus deterministic) and referred to as “implicit” mutations. A second mechanism is less deterministic, and occurs during the processes of division and reproduction, processes that are inherently made to be error-prone to a degree that can be specified by the user. These copy-errors, as well as the probabilistic insertion and deletion of instructions or code snippets reflect the noisiness of the system and are not under control of the organism itself. Note that even the most sophisticated polymerases that also have proof reading abilities cannot create perfect replicates every time, while this is in principle possible for avidians without implicit mutations by turning the mutation rate to zero. While biochemical-based life does not have a mutational mechanism similar to the implicit mutations seen in avidians, it is not unreasonable to assume that early replicators also underwent large mutations due to a lack of error-correction during replication.

Evolvability in Avida

Evolvability describes the ability of an organism to undergo evolutionary adaptation (Wagner and Altenberg, 1996; Kirschner and Gerhart, 1998; Wagner, 2005). There are two main pathways to adaptation in Avida. The first is *optimization*, where organisms with a minimal replication time out-compete others in the population (akin to *r*-selection (Pianka, 1970)). The second is *innovation*, where avidians can evolve new phenotypic traits that enable a fitness increase (the *K*-selection mode). These phenotypic traits are the ability to perform certain Boolean logic operations; these logic operations allow an individual to execute a greater proportion of its genome than other avidians that do not perform such logic operations. This indirectly allows them to self-

Instruction	Description	Symbol
nop-A	no operation (type A)	a
nop-B	no operation (type B)	b
nop-C	no operation (type C)	c
if-n-eq	Execute next instruction only-if ?BX? does not equal complement	d
if-less	Execute next instruction only if ?BX? is less than its complement	e
if-label	Execute next instruction only if template complement was just copied	f
mov-head	Move instruction pointer to same position as flow-head	g
jmp-head	Move instruction pointer by fixed amount found in register CX	h
get-head	Write position of instruction pointer into register CX	i
set-flow	Move the flow-head to the memory position specified by ?CX?	j
shift-r	Shift all the bits in ?BX? one to the right	k
shift-l	Shift all the bits in ?BX? one to the left	l
inc	Increment ?BX?	m
dec	Decrement ?BX?	n
push	Copy value of ?BX? onto top of current stack	o
pop	Remove number from current stack and place in ?BX?	p
swap-stk	Toggle the active stack	q
swap	Swap the contents of ?BX? with its complement	r
add	Calculate sum of BX and CX; put result in ?BX?	s
sub	Calculate BX minus CX; put result in ?BX?	t
nand	Perform bitwise NAND on BX and CX; put result in ?BX?	u
h-copy	Copy instruction from read-head to write-head and advance both	v
h-alloc	Allocate memory for offspring	w
h-divide	Divide off an offspring located between read-head and write-head	x
IO	Output value ?BX? and replace with new input	y
h-search	Find complement template and place flow-head after it	z

Table 1: Instruction set of the avidian programming language used in this study. The notation ?BX? implies that the command operates on a register specified by the subsequent nop instruction (for example, nop-A specifies the AX register, and so forth). If no nop instruction follows, use the register BX as a default. More details about this instruction set can be found in Ofria et al. (2009).

replicate at a greater rate (see, for example, Adami 1998, 2006). These different modes of survival can be thought of as different niches that avidians can inhabit (White and Adami, 2004).

It is possible in general that an organism (digital or otherwise) carries such a specific sequence of nucleotides or (as in Avida) commands that every possible mutation prevents self-replication. From a fitness landscape point of view, such replicators would represent an isolated fitness peak where self replication is only possible at the top, and where each mutation is lethal. Such self-replicators, born at the top of the fitness peak, so to speak, would be unevolvable. A self-replicator that can evolve, on the other hand, would never emerge at peak in the landscape, but rather on a lower level and subsequently find positive and or neutral mutations that ultimately lead to higher fitness levels in the landscape. We know that the hand-written replicators in Avida are evolvable, but it is not clear how likely evolvability is among randomly generated replicators.

Methods

All experiments are performed using Avida version 2.14, which can be downloaded from <https://github.com/devosoft/avida>. We first randomly generated Avida sequences to discover individuals that could self-replicate, using a uniform random distribution for each command at each site, which ensures that each sequence has the same likelihood to be generated, given by

$$p = \frac{1}{D^L}, \quad (1)$$

where D is the size of the alphabet ($D=26$ here) and L is the length of the sequence generated (Adami and LaBar, 2015). To decide whether a sequence could successfully self-replicate, it must pass two tests. First, we tested whether the organism could successfully divide within its lifespan. Here, we used standard Avida parameters for an organism's lifespan: it must divide before it executes $20 \times L$ instructions. This test indicates that an avidian can successfully reproduce, it does not imply that its descendants also can reproduce. In our search we discovered many viable avidians that were able to successfully divide into two non-viable organisms. Therefore, we only counted sequences that could replicate and produce offspring that could also replicate as true self-replicators (in other words, they are "colony-forming"). This does not imply that every self-replicator produces a perfect copy of itself in the absence of mutation. Indeed, most of these replicators undergo implicit mutations solely due to their genome sequence, and their offspring differ in length from the parent. In analyzing a genome's ability to self-replicate, we used the default Avida settings, described for example in (Ofria et al., 2009). For our study of evolvability, we also included the default length 15 hand-written ancestor in our set of self-replicators.

In order to test whether these self-replicators could optimize their fitness, we evolved them in an environment where *only* decreased self-replication speed was under positive selection (the r -selection niche). We evolved these replicators for 10^3 generations at a population size of 3,600 individuals (10 replicates). Instruction mutations occurred at a genomic rate of 0.1 at division (meaning the likelihood to incur an error is length-independent), and both insertions and deletions occurred at a genomic rate of 0.005 per division. We measured an organism's evolvability as its gain in relative fitness at the end of the experiment.

Finally, we tested the self-replicators' ability to evolve greater complexity by evolving new phenotypic traits (that is, in the K -selection mode). The traits that are rewarded are logical functions that an avidian can solve by stringing together code involving the `nand` function (given by the letter `u`, see Table 1). In this setting, nine different logic tasks may be rewarded, denoted as the bit-wise NOT, NAND, AND, OR-NOT, OR, AND-NOT, NOR, XOR, and EQU. We evolved the self-replicators of length 15 in an environment where nine Boolean logic operations, and hence nine phenotypic traits, are under positive selection; this is often referred to as the logic-9 environment (Lenski et al., 2003). For this experiment, we evolved these replicators for 10^4 generations at a population size of 10^4 individual (ten replicates). Increased population size and experiment time was used to allow time for trait evolution. The mutation rates were the same as in the optimization experiments. We quantified an organism's evolvability in these experiments by measuring the number of evolved phenotypic traits.

Results

Of the 10^9 randomly-generated Avidian genomes in each length class, we found 6 self-replicators of length 8, 58 self-replicators of length 15, and 106 self-replicators of length 30 (see Table for their sequences). However, it is unlikely that each self-replicator needs every instruction in its genome in order to self-replicate (Adami, 2015). Many of these self-replicators could be unstable and would generate implicit mutations upon replication. Therefore, we tested the replication fidelity of each self-replicator (Fig. 2). All replicators of length 8 were able to undergo error-free replication without external noise (mutation rate set to zero). This is likely due to the fact that avidian genomes cannot be shorter than length 8; however, that does not prevent the occurrence of genomes that replicate to a length larger than 8, which we did not see among this set. Self-replicators of length 15 and 30 could not replicate error-free, even without external noise, and most of their genome sequences decreased upon successful replication.

Next, we tested the evolvability of these replicators in the sense of how well they could optimize their genomes as a way to increase replication speed, and thus their fitness. We found that the majority of these spontaneous self-replicators

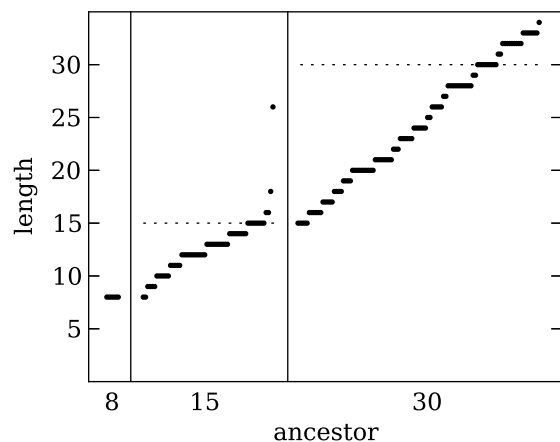


Figure 2: Change in length after the first round of replication for all self replicators we found of length 8, 15, and 30. The self-replicators are ordered by length increase within their individual groups. The dashed lines indicate the start organism's length.

of length 8, 15, and 30 possess the ability to optimize their replication algorithm (see Figure 3). While the increase in fitness across the different self-replicators varied due to differing ancestral fitness, most increased in fitness by more than two-fold over the course of 10^3 generations of evolution. However, we found a few replicators (3%) that were evolutionary sterile (defined as a relative fitness < 2), demonstrating that not all self-replicators can easily undergo significant adaptation.

Because the ability to optimize replication speed does not automatically imply the ability to evolve greater complexity, we also tested at the ability of the length 15 replicators to evolve new phenotypic traits (see Methods for a description of those traits). All 58 self-replicators were able to evolve at least one phenotypic trait in one replicate, although the likelihood of the emergence of phenotypic traits varied greatly across the different replicators and within the replicates for each specific replicator (see Fig. 4). Moreover, most self-replicators were able to evolve multiple traits. The hand-written Avida ancestor of length 15 displayed the *least* evolvability in regards to trait evolution compared to the 58 randomly-generated self-replicators. Only one out of ten replicates evolved any phenotypic traits in the allotted time, although that replicate did manage the evolution of two traits.

Discussion

Here, we asked if spontaneous self-replicators in Avida would all possess the additional ability to change in such a way that they could initiate evolution. We showed that the majority of self-replicators are robust enough to tolerate

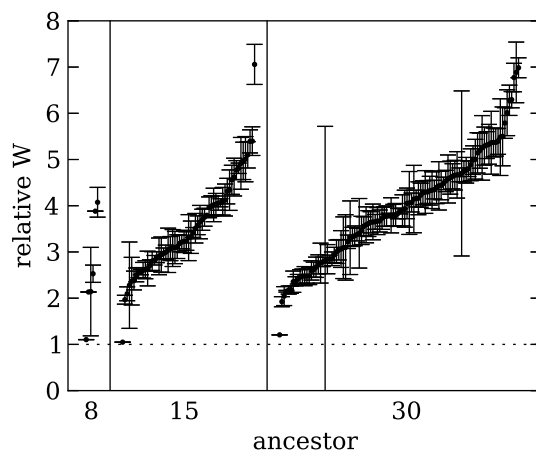


Figure 3: Relative fitness after 1,000 generations of evolution for all replicators we found of length 8, 15, and 30. The replicators are ordered by relative fitness increase within their groups of similar length. The fitness of all start organisms is normalized to 1, indicated by the dashed line. The error bars indicate the standard deviation over 10 replicate evolution trials with the same ancestor.

mutations as well as changes to their genome size. This suggests that self-replicators in this digital chemistry are robust and thus will most likely be able to jump-start evolution. Further, this result holds both when we looked at the ability of self-replicators to increase fitness through optimization or through the evolution of new phenotypes. In addition, many spontaneous self-replicators made faulty copies of themselves in the absence of external noise, which further supports the idea that variability is an inherent property of spontaneous self-replication.

These results confirm that not every spontaneous self-replicator necessarily is evolvable. On the other hand, we also find that the majority of spontaneous self-replicators deterministically do not make exact copies even in the absence of mutation, questioning the term “self-replicator” for these genotypes. Indeed, while these spontaneously generated sequences are “colony-forming” (in the sense that they produce sequences that can also replicate themselves), these are not self-replicators in the strictest sense of the definition. Instead, these replicators mutate themselves to become a self-replicator: we call these individuals “proto-self-replicators” or “proto-replicators”. This means that the number of potential sequences that can start evolution is increased by existence of these proto-replicators. In natural chemistries, this phenomenon has been discussed widely (Bernal, 1949; Miller et al., 1953; Eigen, 1971; Miller and Orgel, 1974; Eschenmoser and Loewenthal, 1992), suggesting that the first self-replicator might have needed either self organisation or some other forms of catalysis or autocatalysis in order to

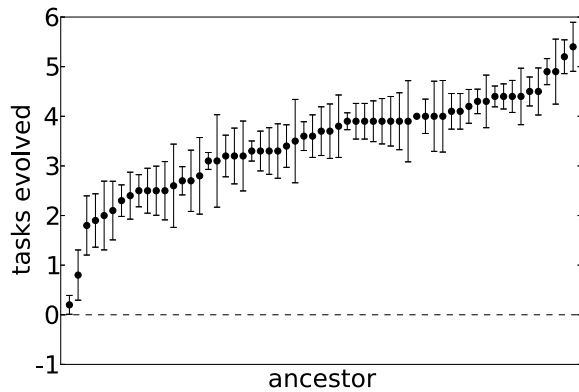


Figure 4: The number of logic tasks that spontaneous replicators of length 15 were able to perform after 10,000 generations of evolution in the Avida logic-9 environment. Replicators are ordered by number of tasks achieved. Error bars indicate the standard error of the mean for 10 replicates per ancestral organism.

create the right chemistry to start polymerization in the first place. Figure 5 gives an illustration of this concept.

Leo Tolstoy famously begun his “Anna Karenina” by remarking that “*Happy families are all alike; every unhappy family is unhappy in its own way.*”. In the same manner we asked here whether, with respect to evolvability, all self-replicators are alike (while of course all non-replicators are non-replicating in their own way). Our results show that not every self-replicator is suitable as the ancestor for evolution. But we also find that, with respect to the capacity to evolve functional complexity, random replicators are better than even those designed by thinking humans.

Our results further suggest that life, if possibly found elsewhere, does not necessarily experience evolution. We might at some point in the future find self-replicators that maintained their ancestral form due to their inability to tolerate enough variation to evolve. Similarly, it seems possible that, if such a mutationally-fragile self-replicator exists, it might be outcompeted by other self replicators that can take advantage of mutations, and thus attain higher fitness and ultimately outcompete those mutationally-fragile self-replicators. Thus, as long as evolvability is evolvable, complexity should ensue even when sparked by the most humble and awkward replicators.

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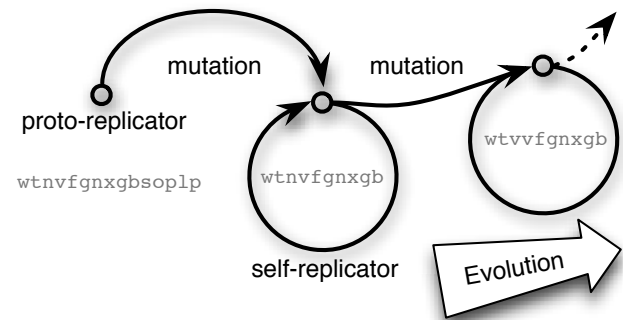


Figure 5: Illustration how an Avida proto-replicator (left) “copies” itself into a self-replicator (middle). This replicator can now experience external mutations, which leads to a new self replicator. The repetition of such process is what jump-starts evolution (right). The text string is a program example from Avida.

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Appendix: Sequences of replicators

Table 2: Sequences of 8-mer replicators and 15-mer replicators. The sequence denoted (1) is the hand-written $L=15$ ancestor. The 106 proto- and self-replicators of length $L=30$ can be downloaded from <http://dx.doi.org/10.6084/m9.figshare.1416247>

$L = 8$			
qxrchcwv	vxfgwjgb	wxvxfgg	vfhgxwgb
wxrchcvz	wvfgjxgb		
$L = 15$			
wtnvfgnxgbsoplp	mwtepvfgskvrxb	wxvxfagbchcmwse	nvlvfgqnsxwgbzf
wlmvmfgowxdogbf	wvfgmwxgbjgpylp	voovvnfgxlrjbjn	prvfgemsxwepgbo
vfgxqhmwmfjphgb	vtwfgxgbyhdnahk	vlfgvuiofxwgbpc	dywqvphfguxqdg
wvufguuxltsgbwd	vmfifgwpowxgbt	wzvfqxrpojgjn	jivfgzkwjxogbtw
wvfgnxwhgbaplye	vwowfgqxqwxgbo	vfgwxqwdfoghq	wvfgofeoxgbrmg
wvfguzxqjgbiokn	vkhwfgyfrxwgbtr	vfgwvtljvrwxgbl	vfglqwxljgbwdsf
lwvfgxoetfdgbhp	lsvrwfgxmmwgbwg	vnfgudsftwxwhgb	vlfvgmhwuxwlgbq
rrowvmfgxjgbuyx	drvfgwioxrmgbjx	inoidjwvfglxgbd	iwlkvfgxgbssez
vfgwpxpbyxxddi	nvqwqfgfnoxpgbm	vfgkqldxidwgbxt	vnwdfgxgbyeavg
vmfgqwrmdkyxuhc	qvufgxwdgbojyom	vhfgtxlwgbfbryb	wrvvnfgxmgbctol
vwqfmgxgbeixsh	vqvfqvqxwygbwn	vyhfgxwkyppgbyny	yvdwfgxgbvwrfgp
wvfghtzoxjirgb	irwovfgxjgbwhbr	wvfgxdmoprllwgb	liwvlfgxgbnhsn
vfgfyxnwmgbtmk	vfgxqdrkswgbpgz	vfgwpmmxhqqbkmc	svkfgxlujlmgbx
vwt srlfgxhgbi je	vpdtwfgkfkxgbkp	zvyfgsdwxjgbzdn	kvdsovfwgxgbyhf
vmnfgmxxwigbcc	qwvqfgfwxxfegbg	wzcagczvfcaxgab ⁽¹⁾	