Question Marks about the Period of Punctuation

Aviv Bergman[ab*],

and

Marcus W. Feldman[ab]

[a]Interval Research Corporation,

1801 Page Mill Rd. Bldg. C,

Palo Alto, CA 94304

[b]Department of Biological Sciences,

Stanford University,

Stanford, CA 94305

*Corresponding author

May 1995

Newman et al. (1985) also demonstrated that long periods of stasis with occasional rapid unidirectional jumps between fitness peaks of a morphological character may be triggered by random effects such as genetic drift. They also suggest that this pattern of punctuation is unlikely to be observed in highly structured or very large populations. Such punctuations were also demonstrated by Kirkpatrick (1982) when the environmental variance was altered in a two-peak model of Gaussian stabilizing selection, or when the mutation rate changed.

Charlesworth et al. (loc. cit.) stress the importance of what population genetics can tell us about patterns of morphological change over time. They point out that a more detailed understanding of the relevant population genetic theory is desirable before neo-Darwinian theory is discarded as an explanation of paleontological observation.

In this study, we return to our previous NK diploid model and, instead of averaging over a set of fitness landscapes specified by a fixed K, we investigate the time trajectory of the mean fitness for a given realization of K. We shall see that a remarkable pattern of stasis and punctuation emerges. We then make a very simple mapping from genotype to phenotype and see that the dynamics of this phenotype exhibits a pattern of stasis and punctuation. This pattern may or may not parallel that for the mean fitness. Finally, we compare these patterns with trajectories for the multilocus system subject only to drift and see that stasis and punctuation are also frequent outcomes in the latter case. Examination of the trajectories of haplotype frequencies allows us to offer plausible explanation for these observations.

step mutation neighbors have a lower fitness value. The number of mutation steps separating such local optima seems to decrease as an approximately linear function of K (Kauffman, 1993), suggesting that these surfaces become more rugged in a regular way as K increases.

2.2 Population structure.

Our simulation method follows that of Bergman et al. (1995). A population of n individuals is arranged as a one-dimensional array of cells, each cell housing one individual. Goldstein and Holsinger (1992) showed that there was little qualitative difference between one and two dimensions; only the scale on which genetic differentiation occurs is different (see also Kimura and Weiss, 1964). We chose the one-dimensional array to reduce computation time and population sizes of 100, 200, and 500 diploid individuals.

An offspring generation is constructed from the parental generation as follows. For each cell in the array, two parents are chosen at random from the set of locations that lie within $\pm d$ of that cell's position, where d is called the maximal dispersal distance. The parents undergo Mendelian segregation with recombination. We simulate recombination by choosing a fixed probability r that a crossover event occurs in each 10-locus parent and then selecting the location of the crossover uniformly across the 10 loci. Two values, $r = 0.01$ and $r = 0.5$ were examined. Multiple crossovers are not allowed. Mutation is symmetric: if we designate the two alleles at each locus by 1 and 0, then 1 mutates to 0 and 0 mutates to 1 each at 10^{-4} per locus per generation. Once the genotype of the offspring is chosen in this way, the probability that it survives is calculated using the NK scheme. If it survives, it occupies the originally chosen cell; if it does not survive, the process is repeated

During the course of the simulation we tracked the mean fitness, $\bar{w}$, in the population (except in the case without selection). We also assigned to each genotype a phenotype simply by counting the number of 1's (this is additive phenotypic determination), and tracked the evolution of the mean phenotype, denoted by $\bar{\pi}$, over time in all cases. At crucial stages in this process, we examined the distribution of haplotype frequencies in the form of a histogram. Table 2 reports the complete set of parameters investigated in the simulations. Table 3 lists the variables followed during the iteration.

3 The Detection and Measurement of Punctuation.

Figures 1–3 provide a sample from among the thousands of trajectories we have seen. There is clearly considerable noise, as would be expected with a population of size 100. Our interest was in measuring the degree of punctuation if and when it occurred. To this end, we chose to pre-process the trajectories using a smoothing operation in the form of a median filter to locate apparent punctuation events

This is a conservative approach and, looking particularly at Figure 1, might seem unecessary. In a number of cases, however, the occurrence of punctuation was not as clear to the eye as in Figure 1. After identifying an event from the filtered data, we return to the original data and measure the ratio of the average change (in $\bar{w}$ or $\bar{\pi}$) during the punctuation event to the average change during the periods of apparent stasis that precede and follow each punctuation. In observation is in accord with the result of Lande (1985) who found that the expected duration of the transition between two adaptive peaks under Gaussian stabilizing selection increases approximately logarithmically with the population size.

Figure 3 shows the effect of the number of loci, N, on the existence and nature of punctuation. Here $K = 0$ and $d = 1$. Figure 3a shows a typical evolutionary trajectory of a 5-locus diploid population of size 100. A clear punctuation event can be observed. Note the increase in the phenotypic standard deviation during the punctuation period relative to the stasis period. Figure 3b illustrates a typical trajectory for a 10-locus diploid population of size 100. There is no obvious punctuation in this trajectory, a typical observation for this parameter setting.

The effect of epistasis among the loci on the nature of punctuation events is shown in Figure 4, where we set $N = 10$ and $d = 50$. $K = 0$ in Figure 4a which exhibits punctuation, although this is not a typical trajectory with these parameters; even when punctuation is observed, it may not be a true punctuation given the high phenotypic standard deviation throughout the evolutionary trajectory. Figure 4b, on the other hand, shows a typical trajectory for $K = 3$ with all other parameters as in Figure 4a. Punctuation is clearly exhibited and the phenotypic standard deviation is low throughout the trajectory with a slight increase during the duration of punctuation.

Figure 5 demonstrates the effect of dispersal. Dispersal distance here incorporates effects of both migration and sub-population size. When dispersal distance is small, migration rate is low so that effective sub-population size is low. In Figure 5, we show an evolutionary trajectory with dispersal distances $d = 1, 3$ and 50, the last representing a panmictic population. Note first that the phenotypic standard deviation is highest for the lowest dispersal distance $d = 1$ (i.e., phenotypic polymorphism is maintained at a higher level throughout the evolutionary trajectory, lations move from near-fixation in one haplotype to near fixation in another during the punctuation events. We drew the haplotype histogram before and after the punctuation event, and in, Figure 9a, we show a closeup view of the genetic changes that occur here. Figure 9b shows the haplotype histogram just before the punctuation. From this histogram one can see that almost all haplotypes (195 out of 200) are of one type. Figure 9c shows the haplotype histogram just after punctuation. Again, almost all (198 out of 200) are of the same haplotype but different from that before punctuation occurs.

The above observation led us to investigate more closely the evolutionary trajectories of population of individuals with a single locus under no selection. The hypothesis is that a population will evolve toward a near-fixation state, stay at that state until a transition to near fixation in the other allele occurs. The transition period between the two near-fixation states should be significantly shorter than the time spent near the fixation states. Figure 10a shows a typical trajectory of a 1-locus population of size 100. Note the change in phenotypic standard deviation during the transition period. Figure 10b shows the histogram of an evolutionary trajectory over 10^6 generations of the same population. The "U" shape histogram resembles Wright's (1931) stationary probability distribution for a population evolving under the process of drift due to finite population size and bidirectional mutation.

Finally, we investigated the dynamics of a population under phenotypic stabilizing selection with 10-locus genetics. A simple mapping from genotype to phenotype can be made by adding the number of 1 alleles in the genotype. Individual fitness is proportional to

$$f(x) = e^{-\frac{(x-\mu)^2}{2\sigma^2}} \tag{4}$$

where x is the phenotype, μ is the optimal phenotype, and σ measures the strength of selection. To achieve stabilizing selection we set $\mu = 10$. When selection is strong,

Evolution. Proceedings of the Sixth Berkeley Symposium on Mathematics Statics and Probability, University of California Press.

[3] Charlsworth B. and R. Lande, 1982. A Neo-Darwinian commentary on macroevolution. Evolution 36: 474-498.

[4] Eldredge, N.; S.J. Gould, 1972. Punctuated equilibria: An alternative to phyletic gradualism. In T.J.M. Schopf (ed), Models in Paleobiology. Freeman, Cooper and Co. San Francisco.

[5] Gould, S.J. 1995. Speaking of Snails and Scales. Natural History, May 1995: 14-23

[6] Gould, S.J., N. Eldredge 1993. Punctuated equilibrium comes of age. Nature 366: 223-227.

[7] Gould, S.J., N. Eldredge 1977. Punctuated equilibria: the tempo and mode of evolution reconsidered. Paleobiology 3: 115-251.

[8] Kirkpatrick, M. 1981. Quantum evolution and punctuated equilibria in continous genetic characters. Amer. Natur. 119: 833-848.

[9] Lande, R. 1985. Expected time for random genetic drift of a population between stable phenotypic states. Proc. Natl. Acad. Sci. USA 82: 7641-7645.

[10] Lande, R. 1983. The response to selection on major and minor mutations affecting a metrical trait. Heredity 50: 47-65.

[11] Lande, R. 1978. Evolutionary mechanisms of limb loss in tetrapods. Evolution 32: 73-92.

[12] Lynch, M., W. G. Hill, 1986. Phenotypic evolution by neutral mutation. Evolution 40: 915-935.

Acknowledgment

The authors thank the Santa Fe Institute and the members of the Adaptive Computation Program at the Santa Fe Institute for many stimulating discussions.

Table 1.

The Diploid NK Model

Case of $N = 3$ and $K = 2$

A	B	C	w_A	w_B	w_C
0	0	0	a_0^{00}	b_0^{00}	c_0^{00}
0	0	1	a_0^{01}	b_0^{01}	c_1^{00}
0	0	2	a_0^{02}	b_0^{02}	c_2^{00}
0	1	0	a_0^{10}	b_1^{00}	c_0^{01}
0	1	1	a_0^{11}	b_1^{01}	c_1^{01}
0	1	2	a_0^{12}	b_1^{02}	c_2^{01}
$\vdots$	$\vdots$	$\vdots$	$\vdots$	$\vdots$	$\vdots$
1	2	0	a_1^{20}	b_2^{10}	c_0^{12}
1	2	1	a_1^{21}	b_2^{11}	c_1^{12}
1	2	2	a_1^{22}	b_2^{12}	c_2^{12}
2	0	0	a_2^{00}	b_0^{20}	c_0^{20}
$\vdots$	$\vdots$	$\vdots$	$\vdots$	$\vdots$	$\vdots$
2	2	0	a_2^{20}	b_2^{20}	c_0^{22}
2	2	1	a_2^{21}	b_2^{21}	c_1^{22}
2	2	2	a_2^{22}	b_2^{22}	c_2^{22}

where b_2^{10} is the contribution of the B locus when its genotype is 2, i.e, homozygous 1:1 and its genetic background is heterozygous 0:1 at the A locus and homozygous 0:0 at the C locus.

$w(g) = \frac{1}{N}\sum_{i=1}^{N} w_i$

$w(1,2,0) = \frac{1}{3}(a_1^{20} + b_2^{10} + c_0^{12})$

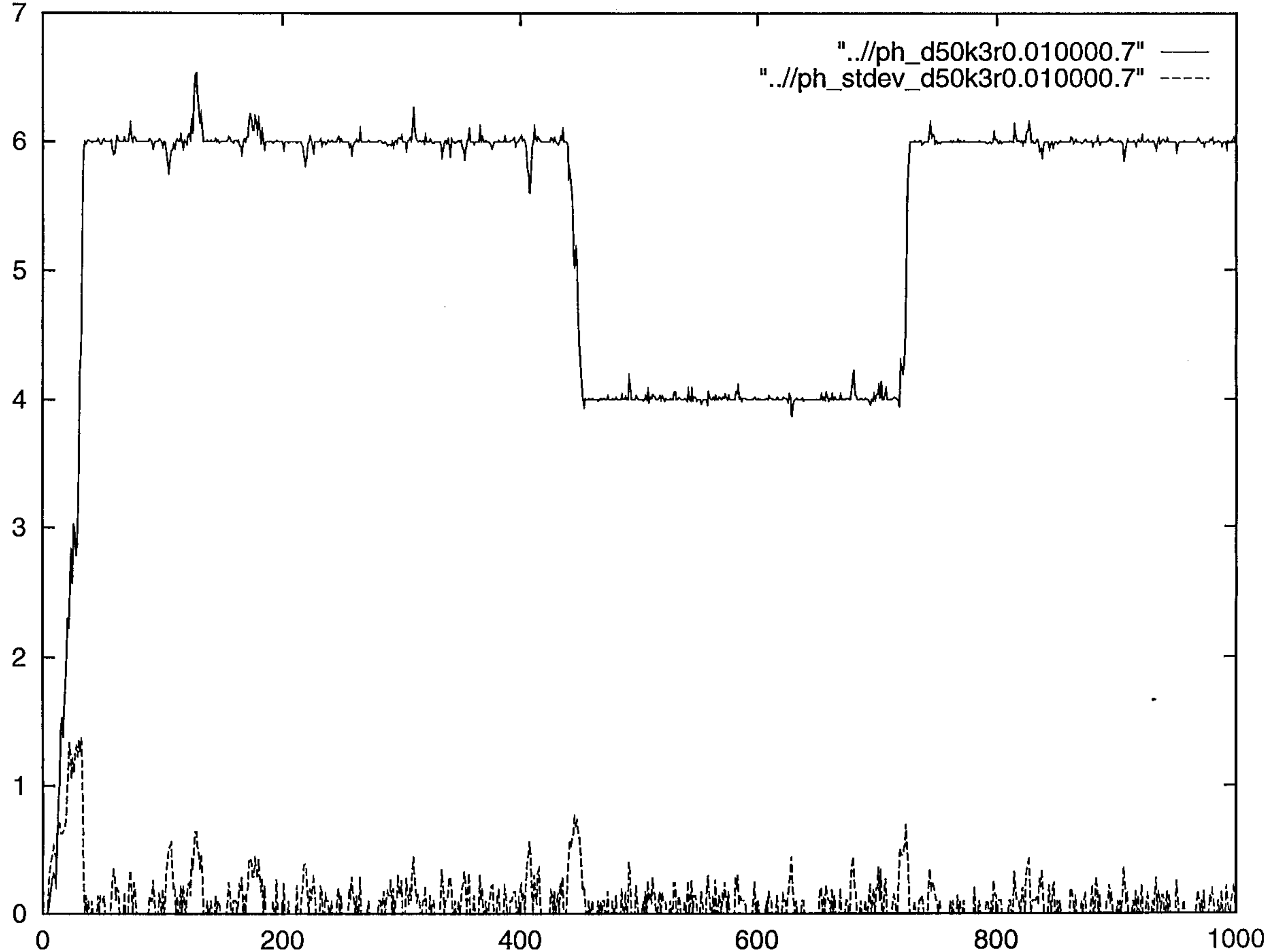

"..//ph_d50k3r0.010000.7"
"..//ph_stdev_d50k3r0.010000.7"
0
1
2
3
4
5
6
7
0
200
400
600
800
1000
Figure 1

Figure 2ap

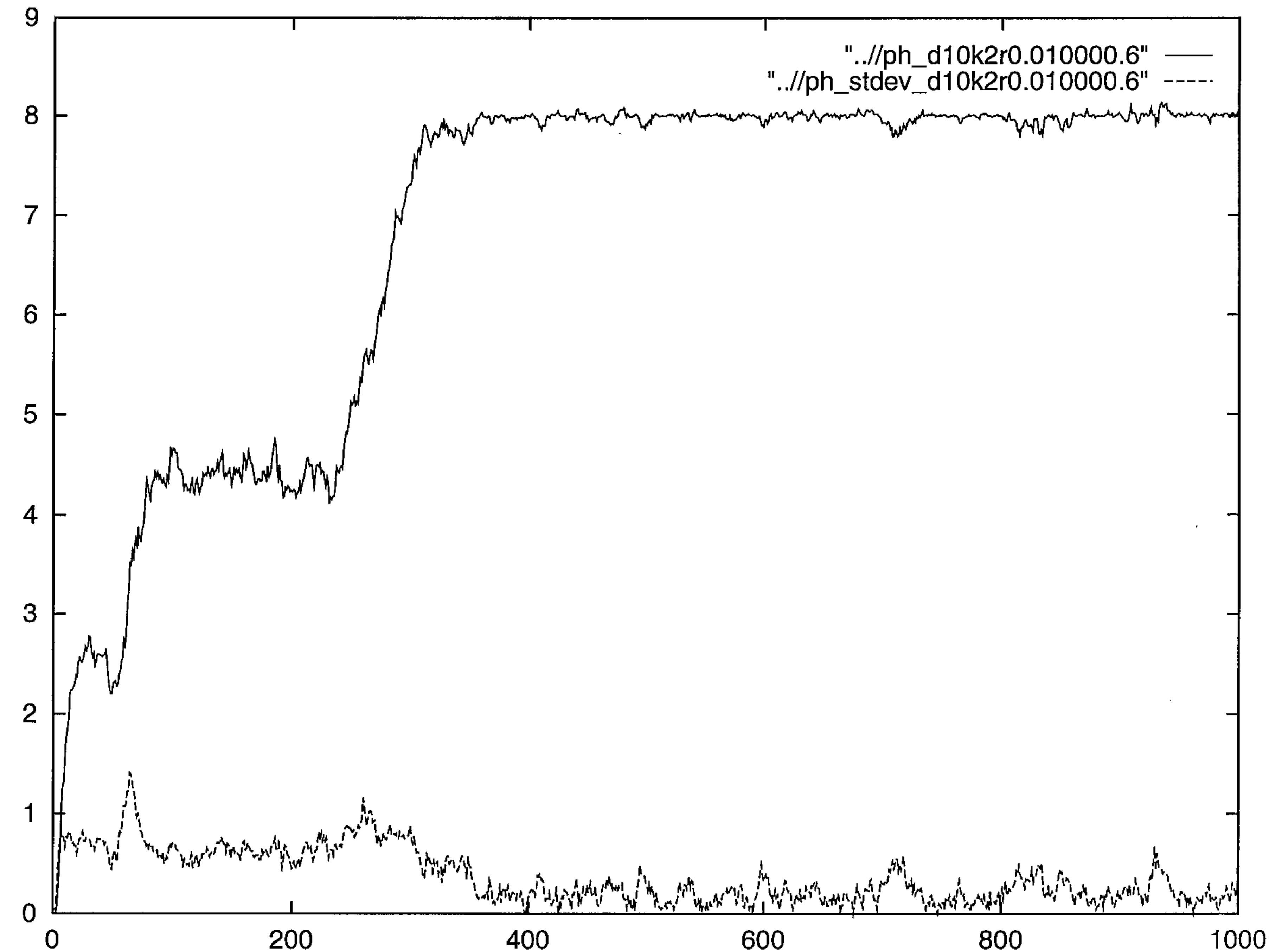


Figure 2ap

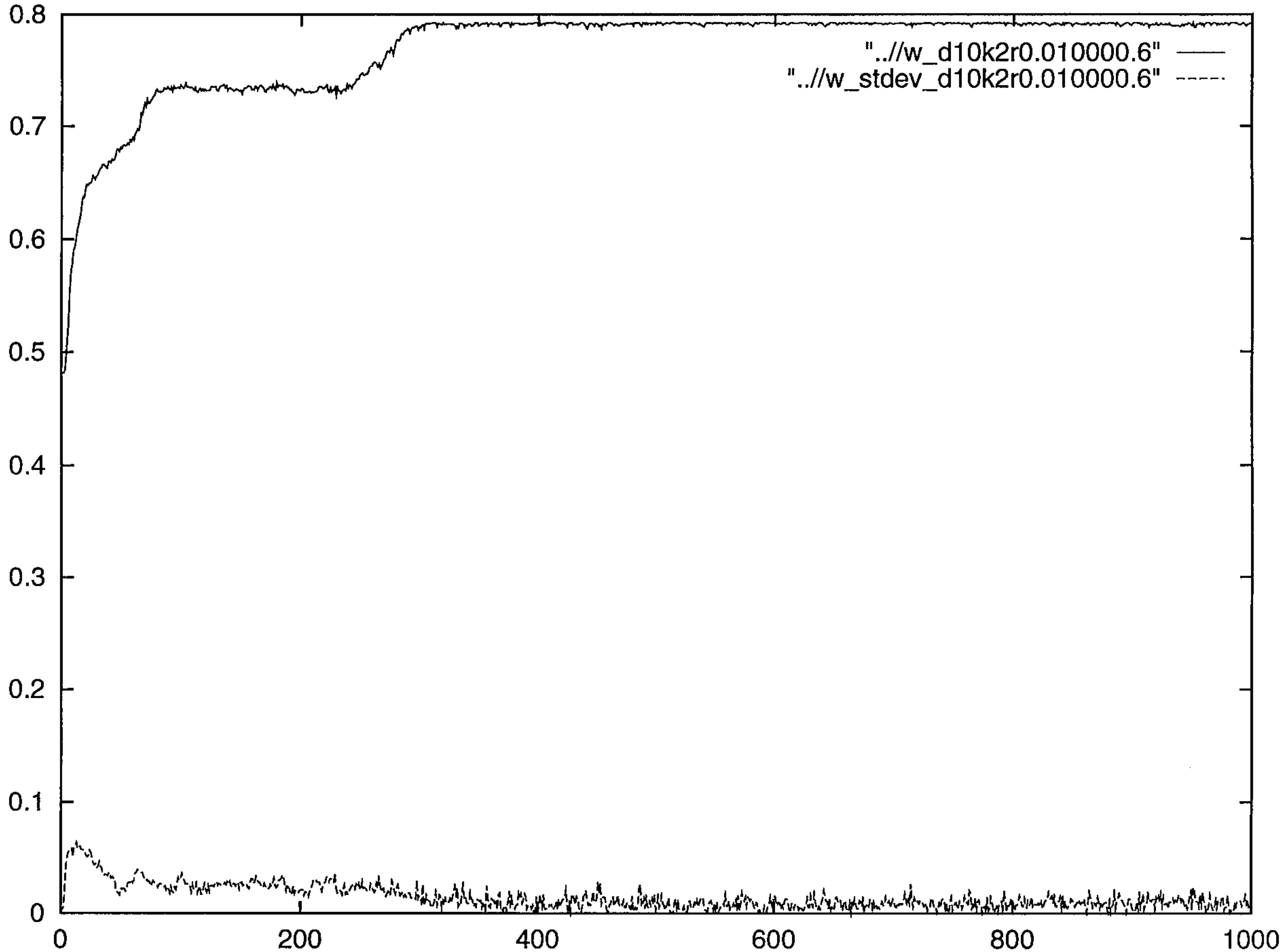

"..//w_d10k2r0.010000.6"
"..//w_stdev_d10k2r0.010000.6"
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
200
400
600
800
1000

Figure 2aw

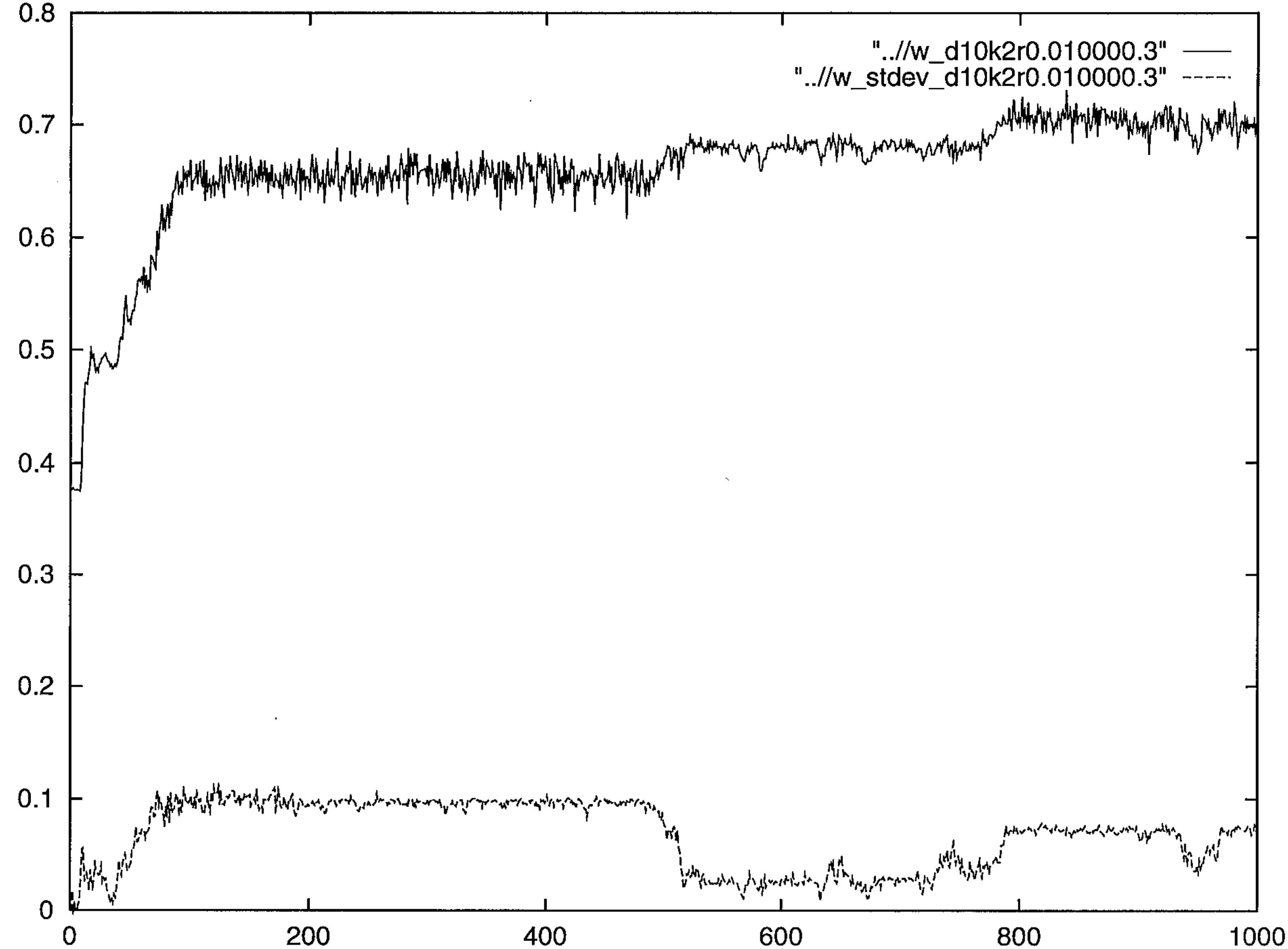

"..//w_d10k2r0.010000.3"
"..//w_stdev_d10k2r0.010000.3"
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
200
400
600
800
1000

Figure 2bw

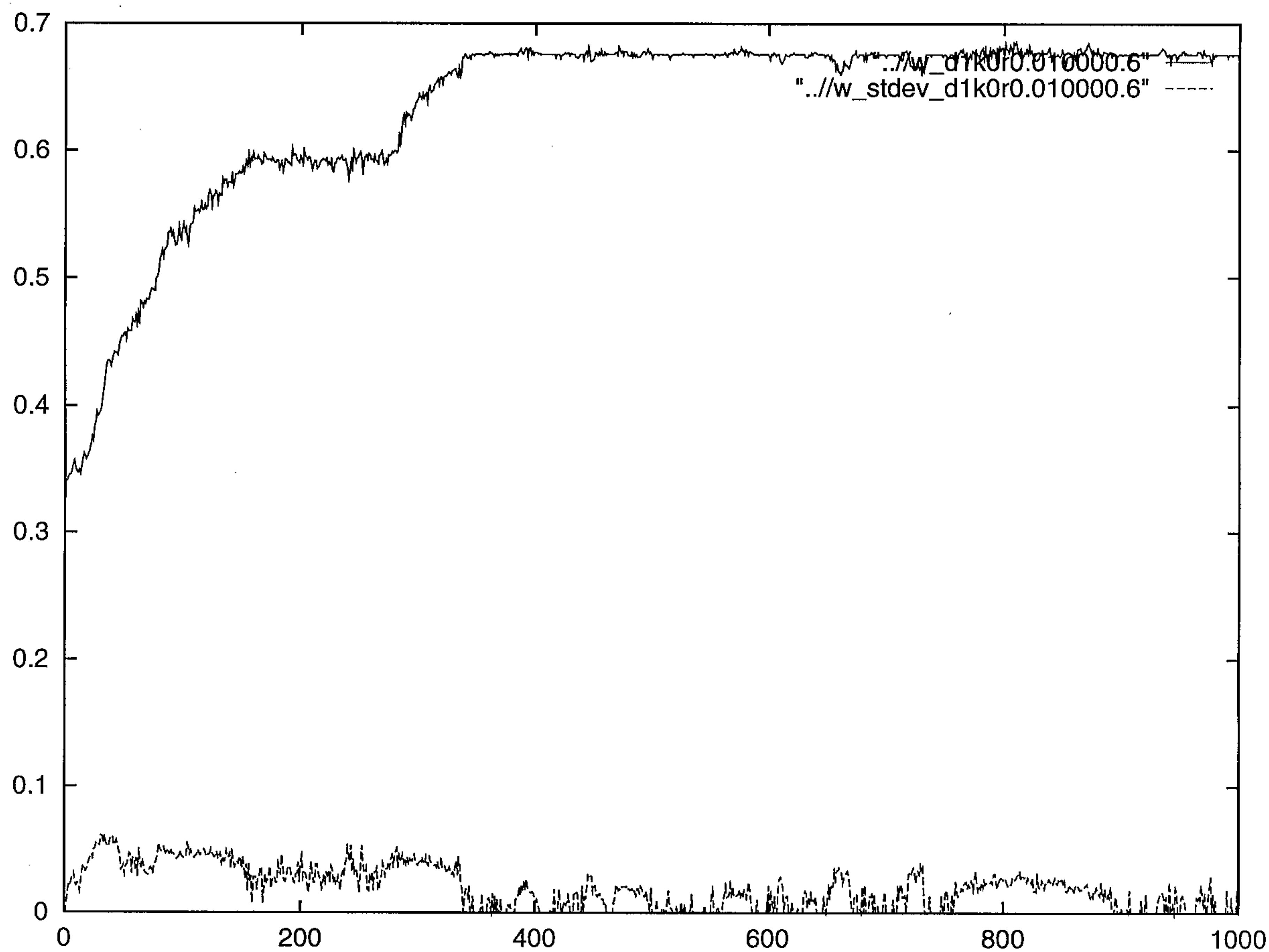
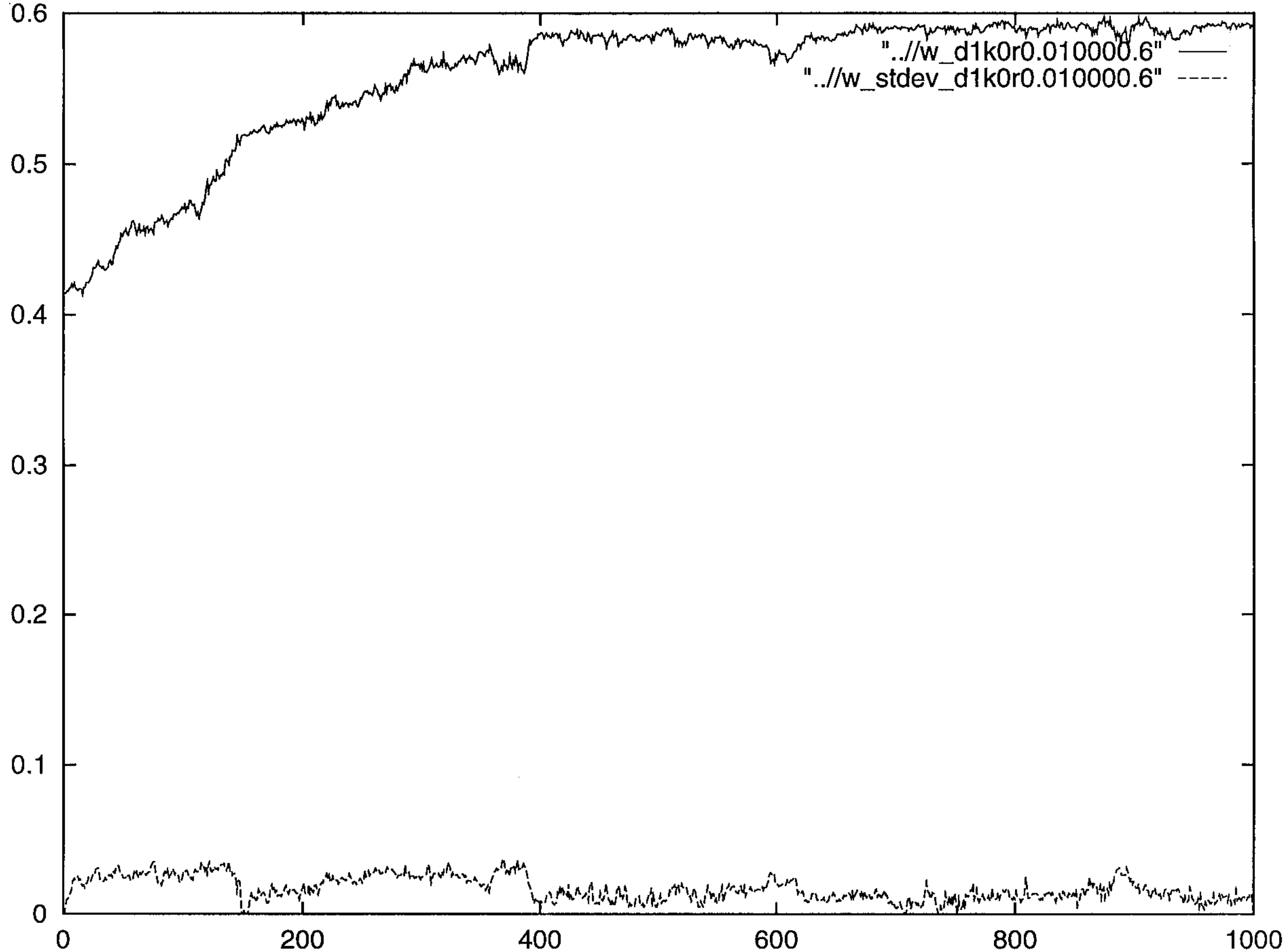
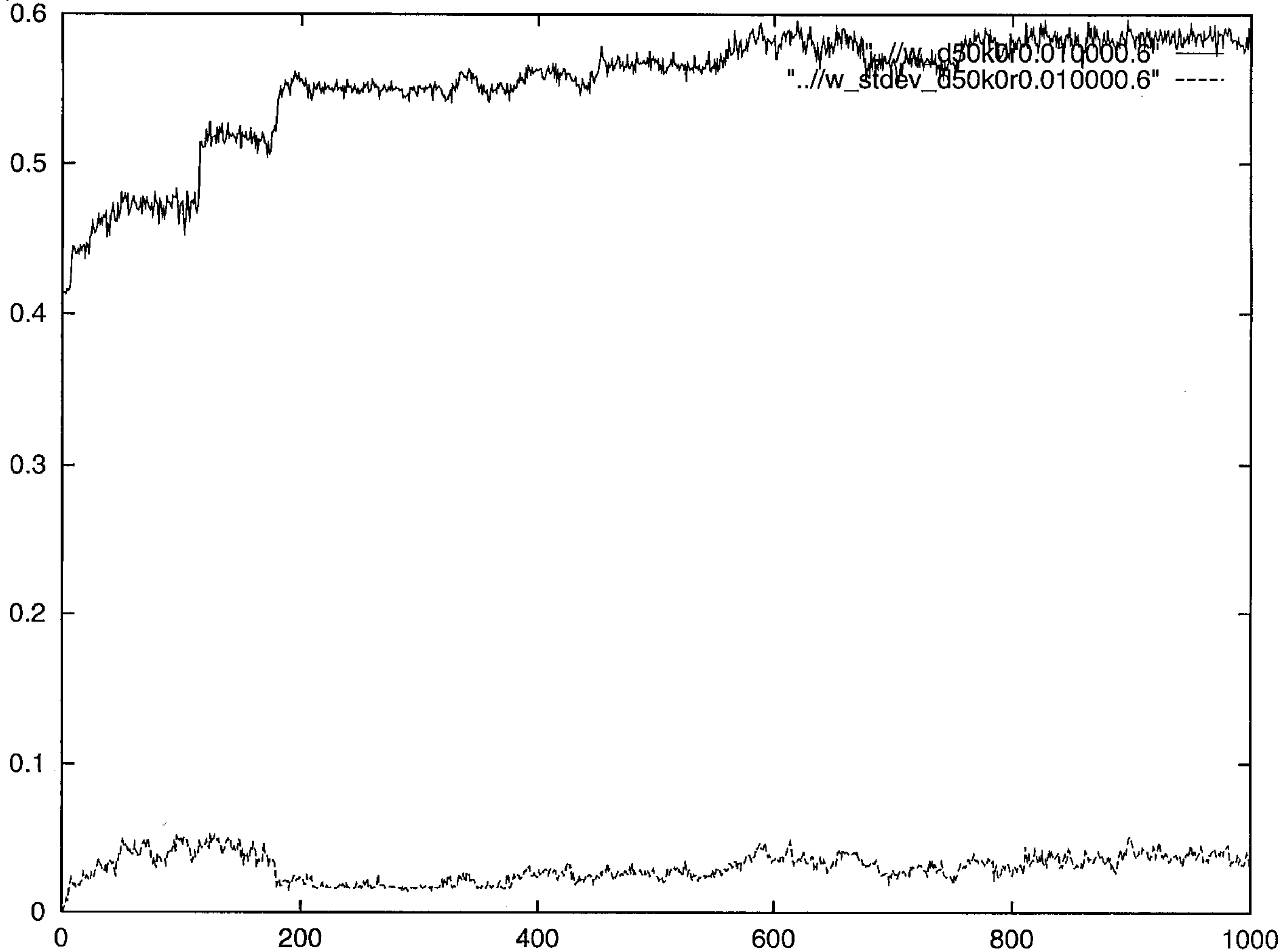

"..//w_d1k0r0.010000.6"
"..//w_stdev_d1k0r0.010000.6"
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
200
400
600
800
1000

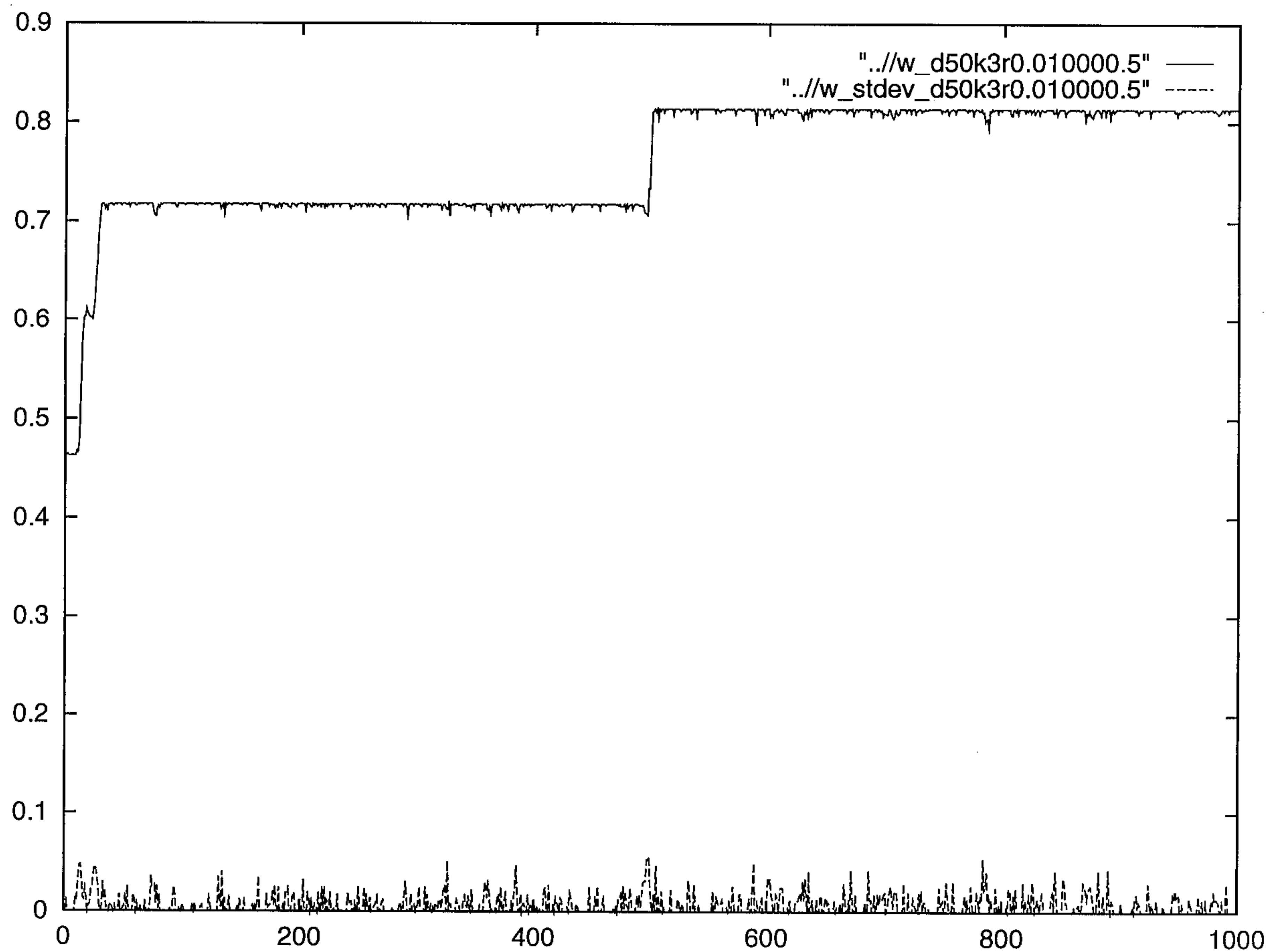
Figure 3aw


"..//w_d1k0r0.010000.6"
"..//w_stdev_d1k0r0.010000.6"
0.6
0.5
0.4
0.3
0.2
0.1
0
0
200
400
600
800
1000
Figure 3bw



0.6
0.5
0.4
0.3
0.2
0.1
0
0
200
400
600
800
1000
"..//w_d50k0r0.010000.6"
"..//w_stdev_d50k0r0.010000.6"

Figure 4aw



"..//w_d50k3r0.010000.5"
"..//w_stdev_d50k3r0.010000.5"
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
200
400
600
800
1000

Figure 4bw

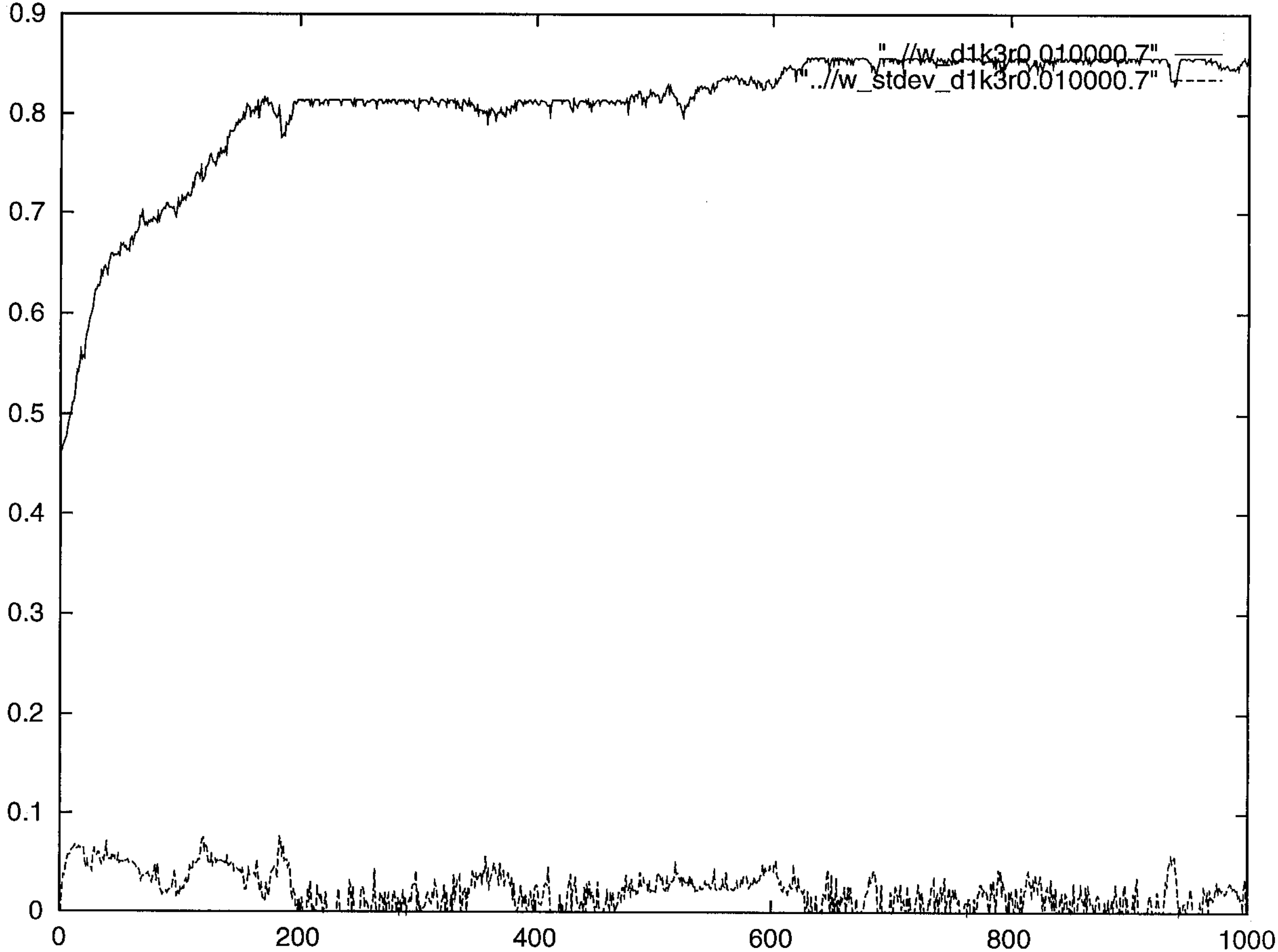
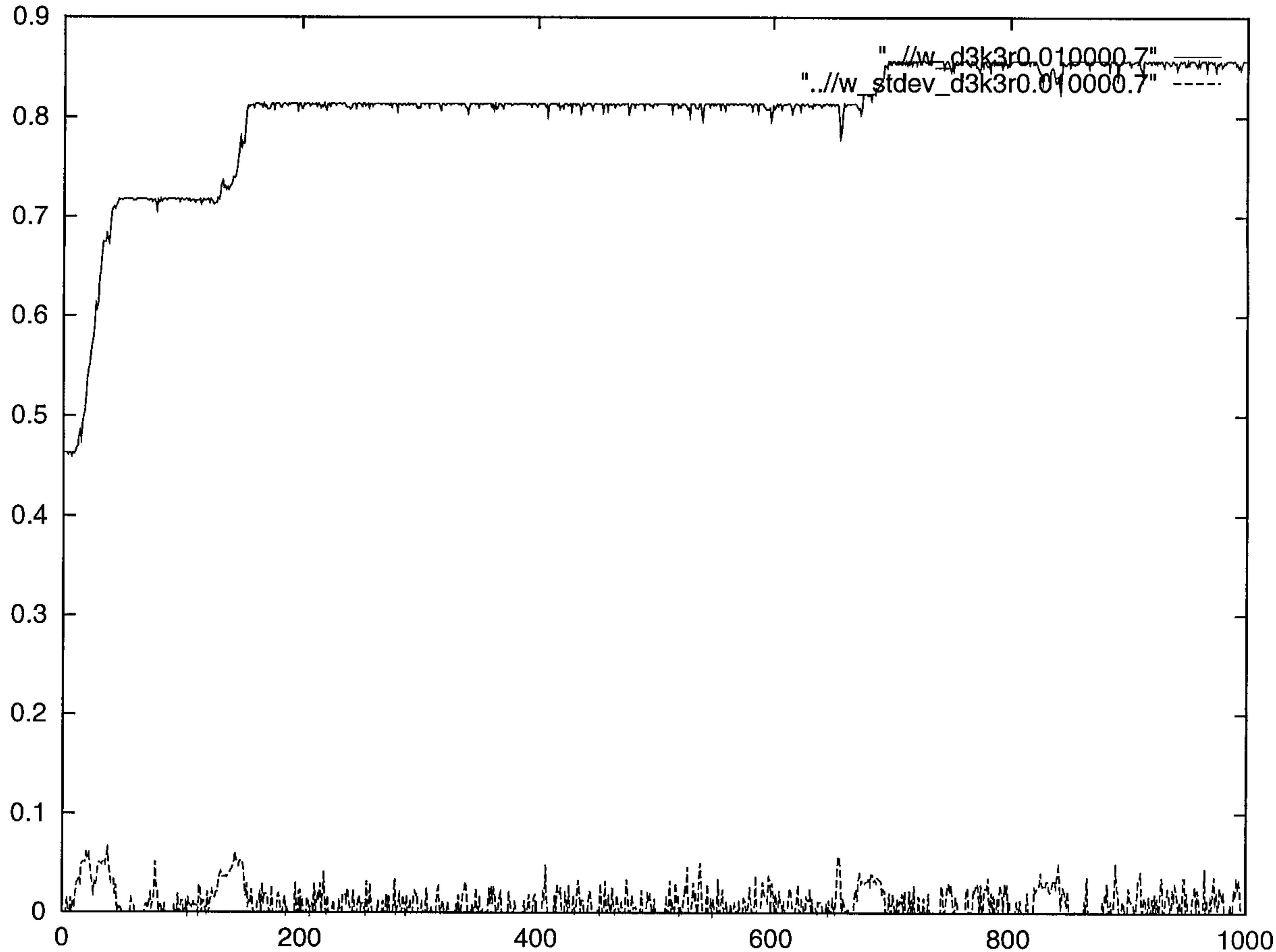

"../w_d1k3r0.010000.7"
"../w_stdev_d1k3r0.010000.7"
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
200
400
600
800
1000

Figure 5aw



"..//w_d3k3r0.010000.7"
"..//w_stdev_d3k3r0.010000.7"
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
200
400
600
800
1000

Figure 5bw

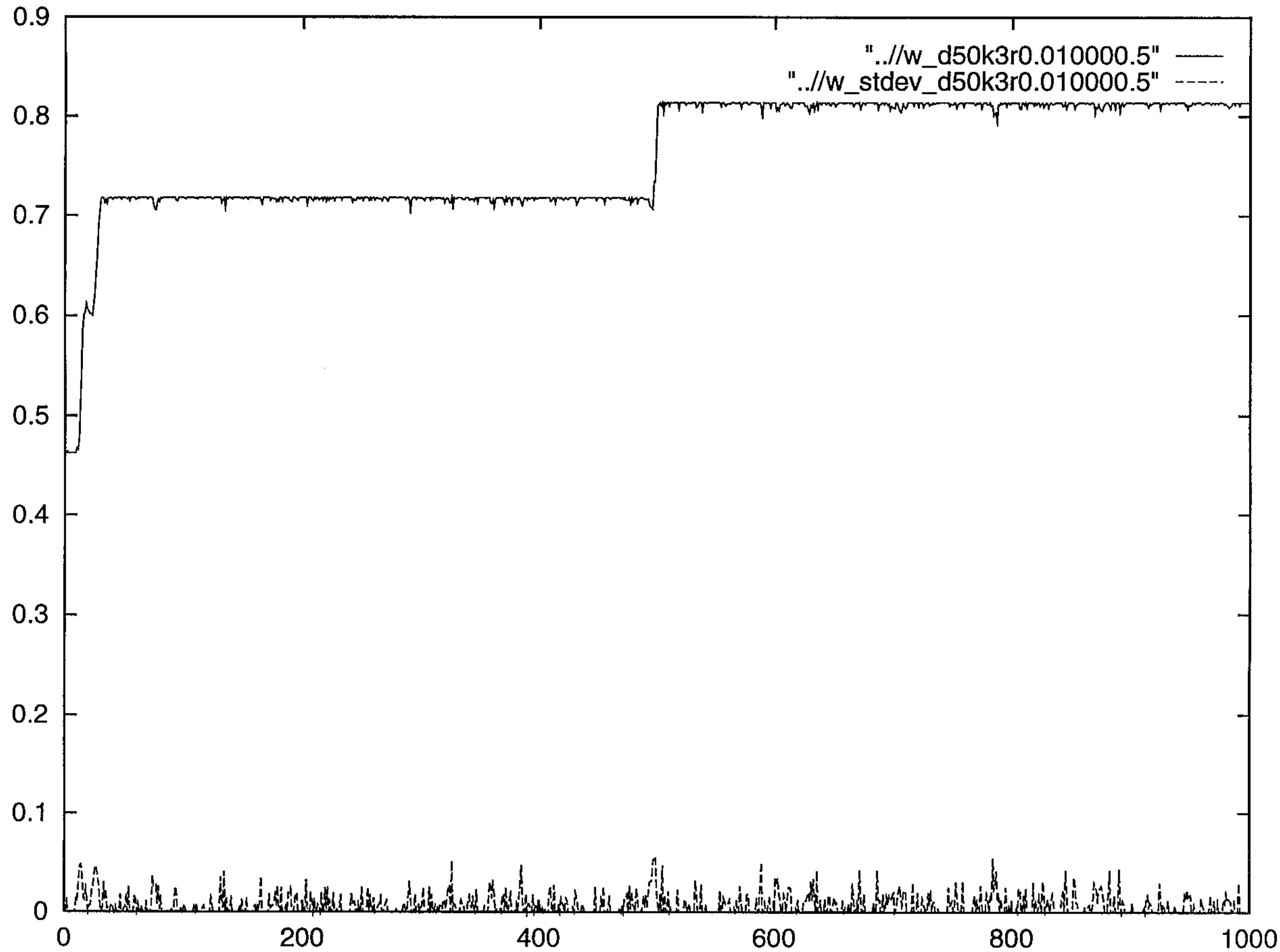
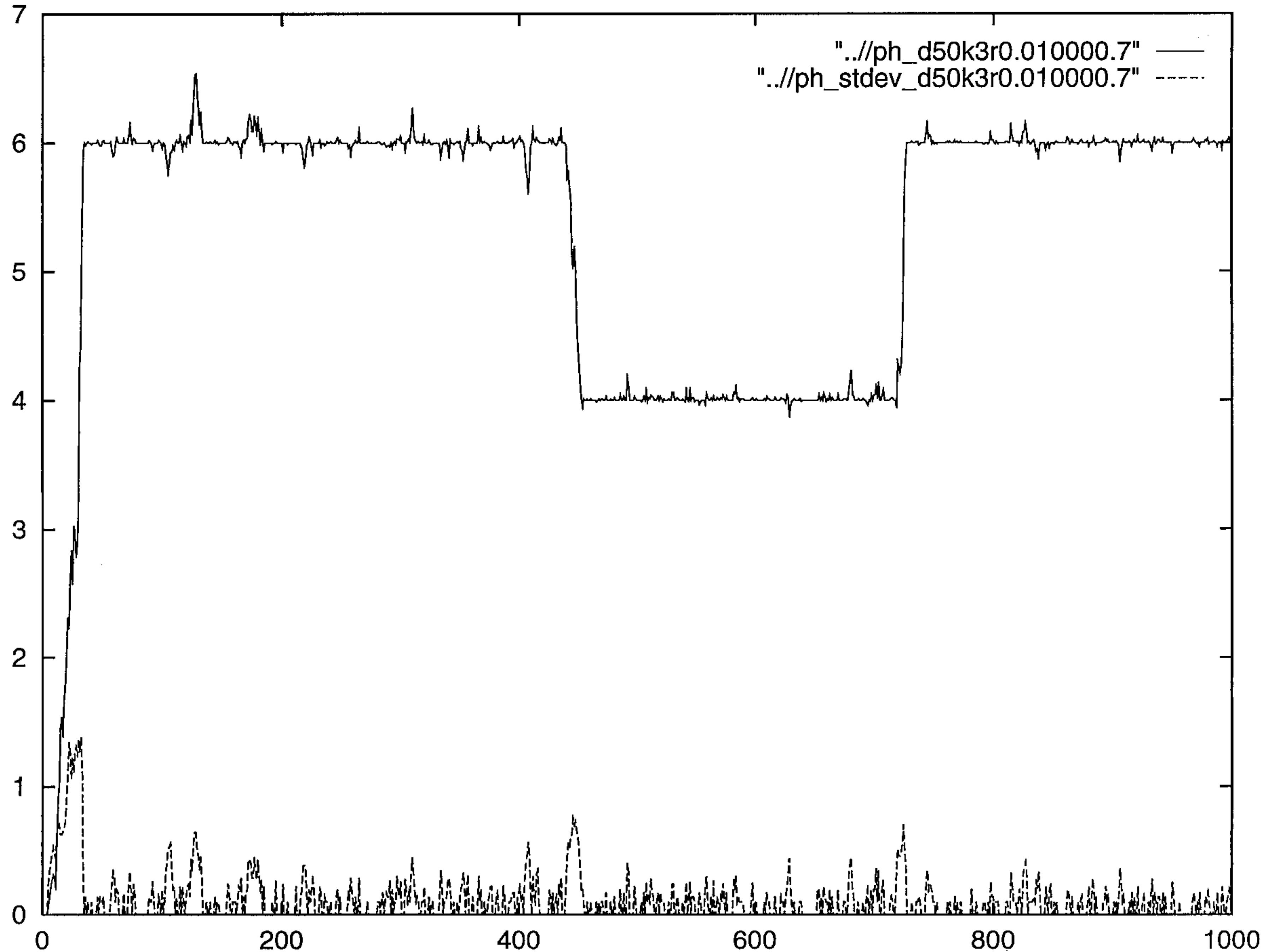

"..//w_d50k3r0.010000.5"
"..//w_stdev_d50k3r0.010000.5"
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
200
400
600
800
1000

Figure 5cw


"..//ph_d50k3r0.010000.7"
"..//ph_stdev_d50k3r0.010000.7"
7
6
5
4
3
2
1
0
0
200
400
600
800
1000
Figure 6bp

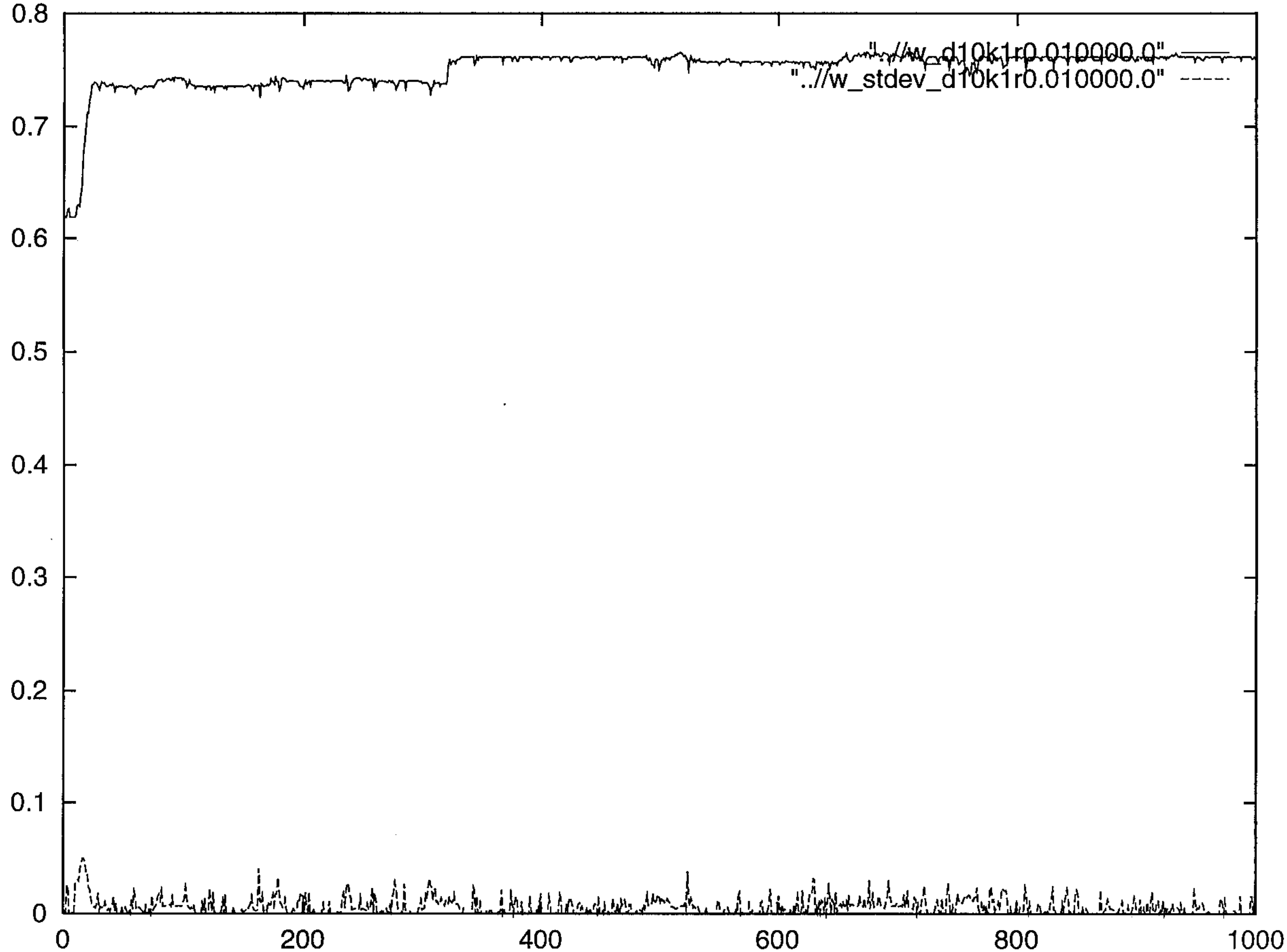

0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
200
400
600
800
1000
"..//w_d10k1r0.010000.0"
"..//w_stdev_d10k1r0.010000.0"

Figure 7bw

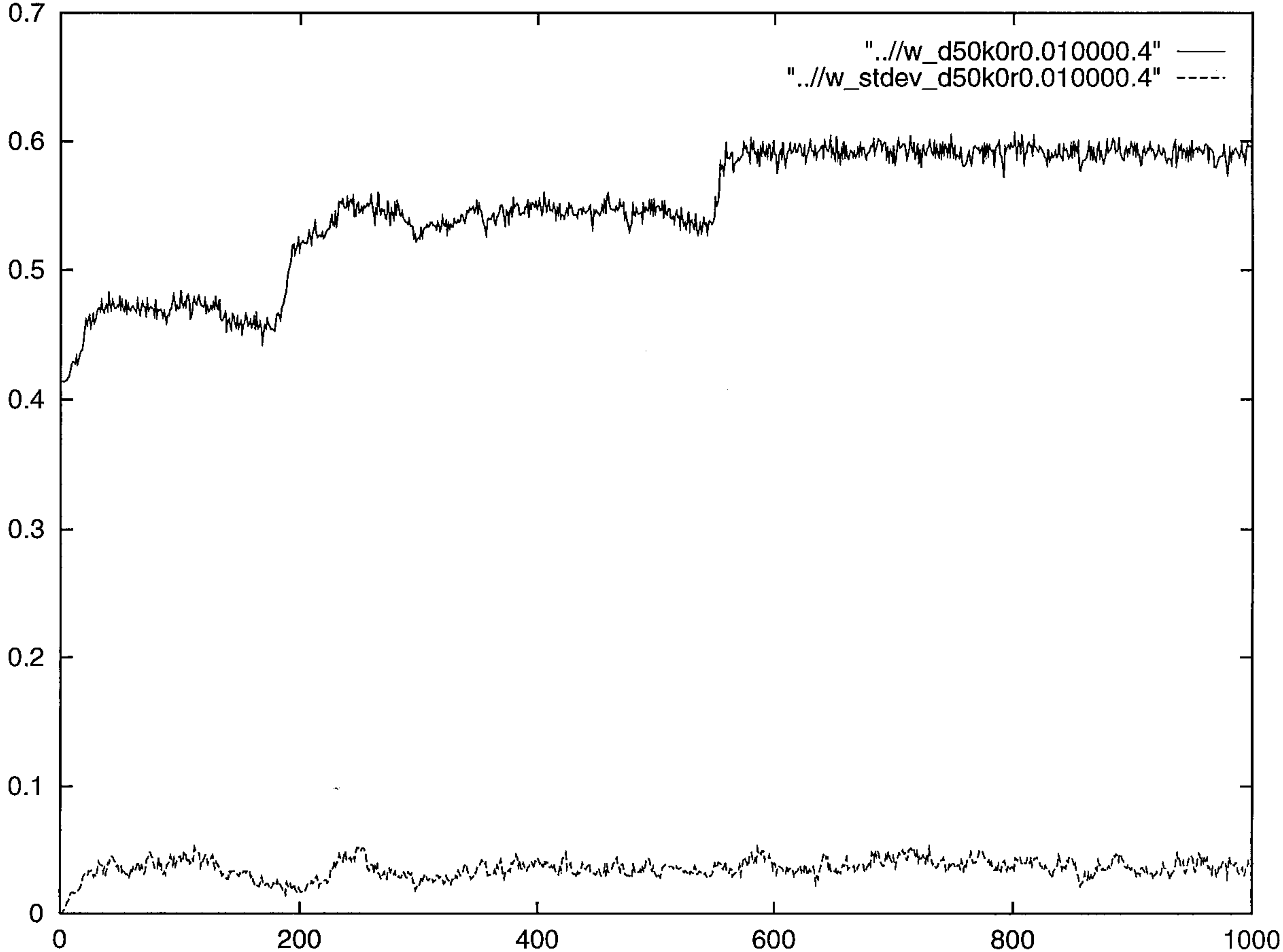

"..//w_d50k0r0.010000.4"
"..//w_stdev_d50k0r0.010000.4"
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
200
400
600
800
1000

Figure 7dw

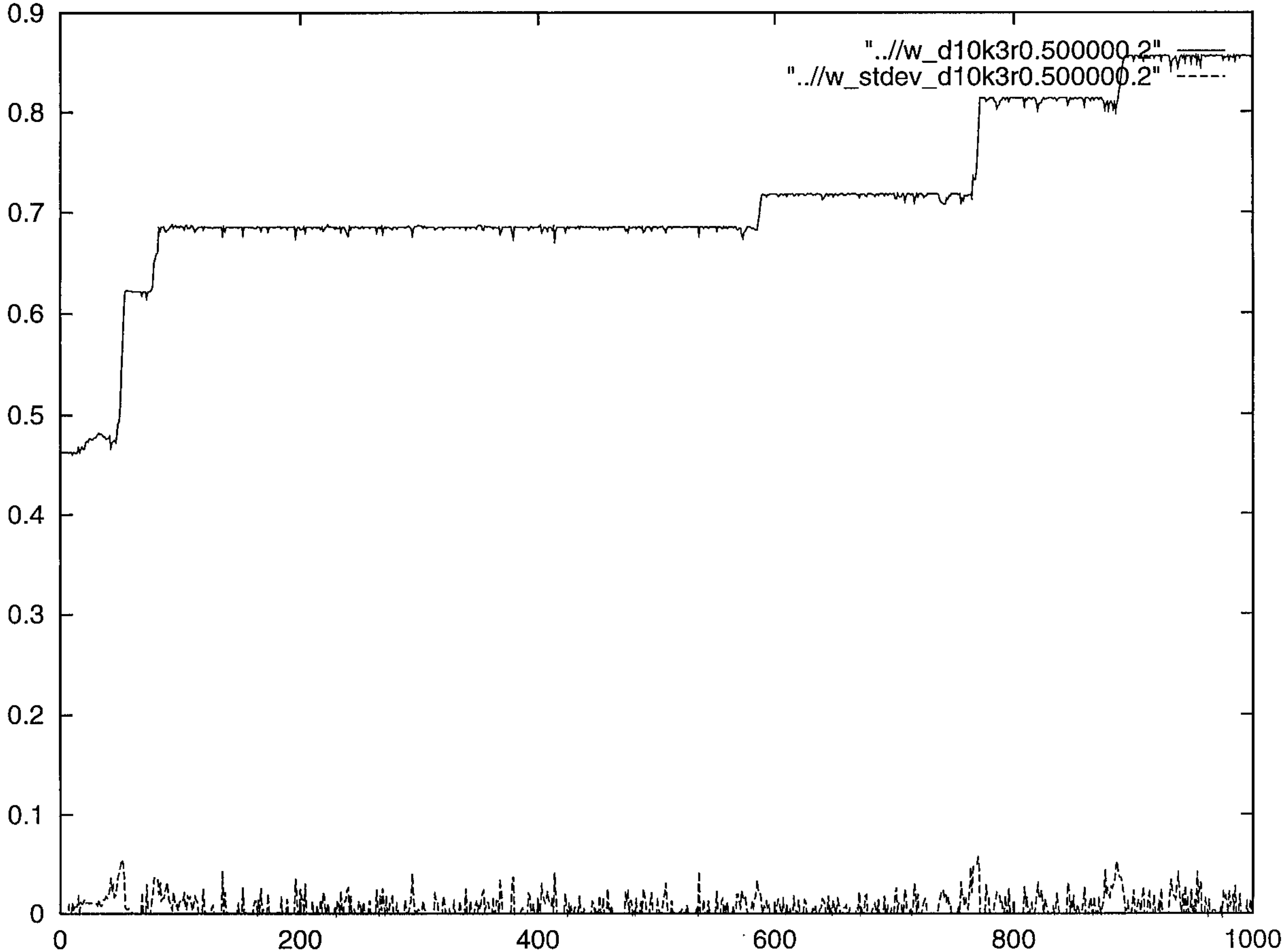

"..//w_d10k3r0.500000.2"
"..//w_stdev_d10k3r0.500000.2"
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
200
400
600
800
1000

Figure 8w

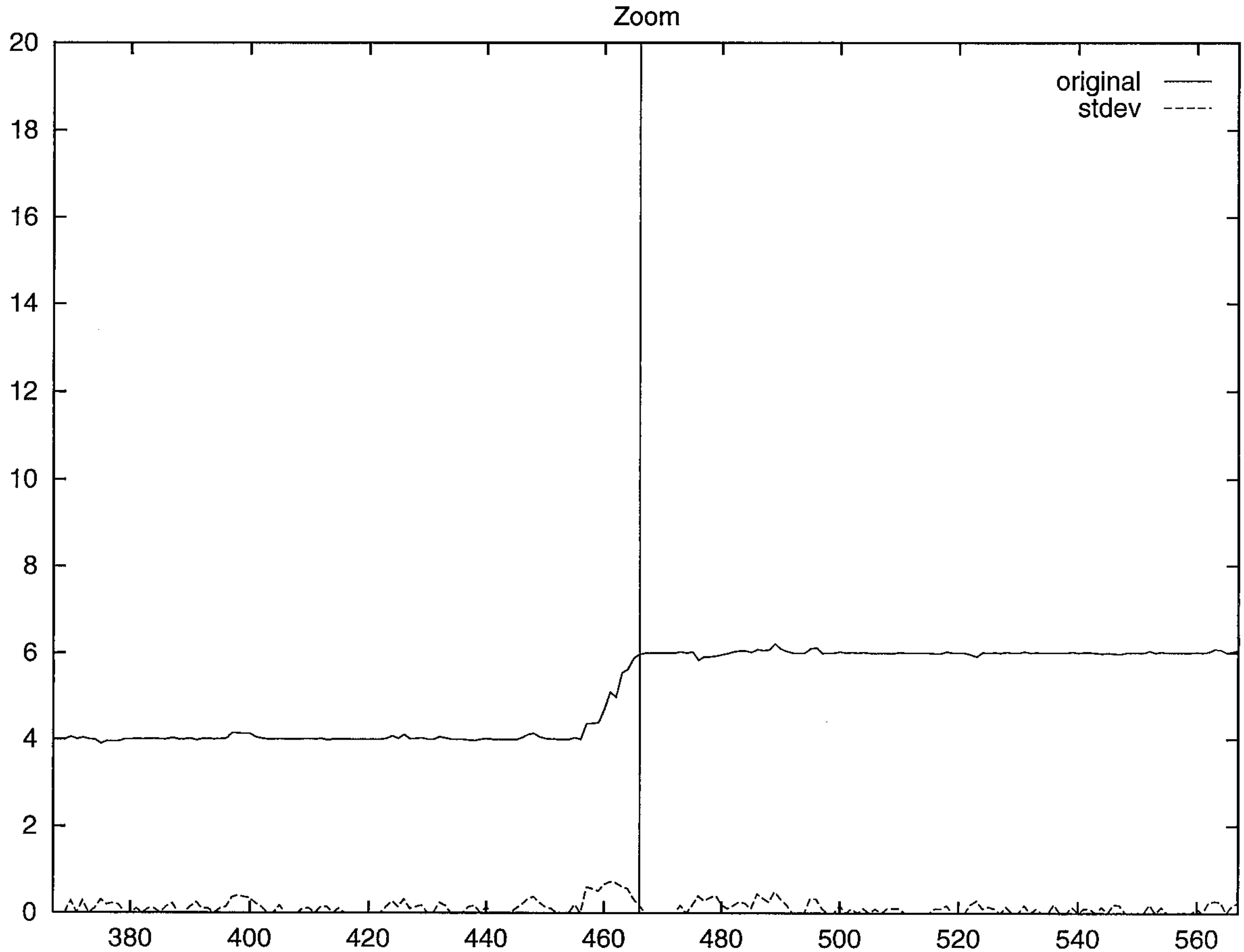

Zoom
original
stdev
20
18
16
14
12
10
8
6
4
2
0
380
400
420
440
460
480
500
520
540
560

Figure 9a(2)

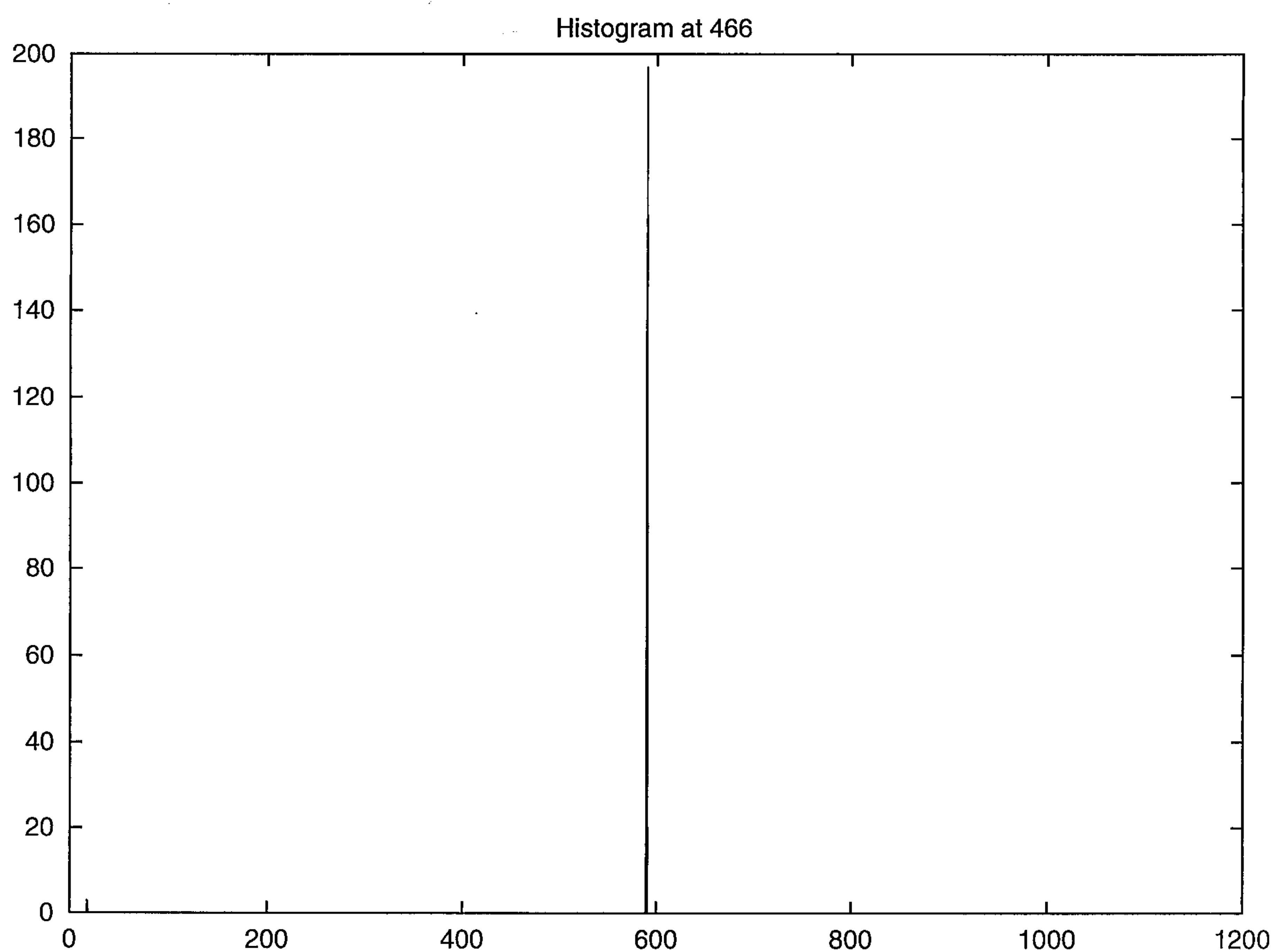

Histogram at 466
200
180
160
140
120
100
80
60
40
20
0
0
200
400
600
800
1000
1200

Figure 9c

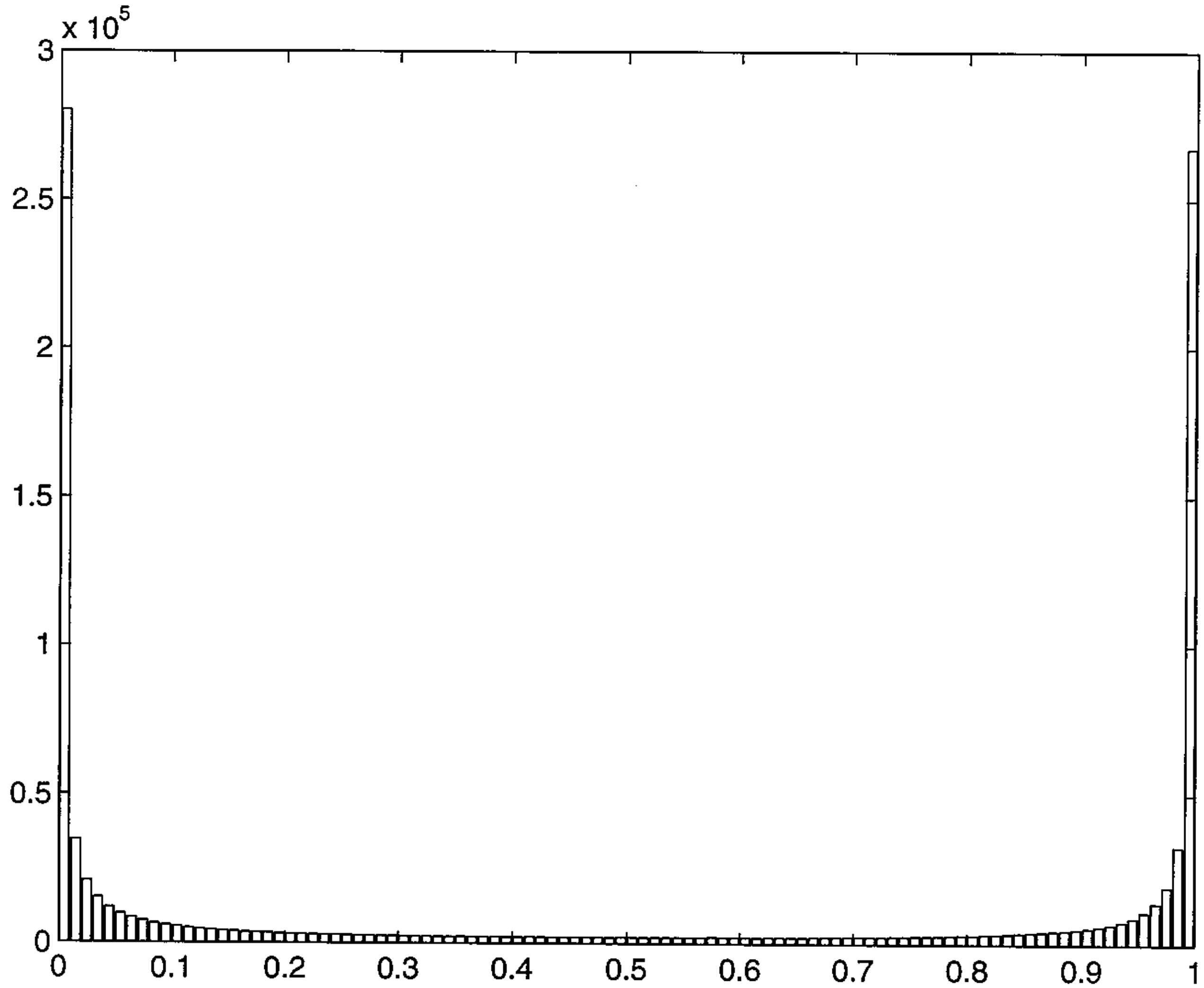


Figure 10b

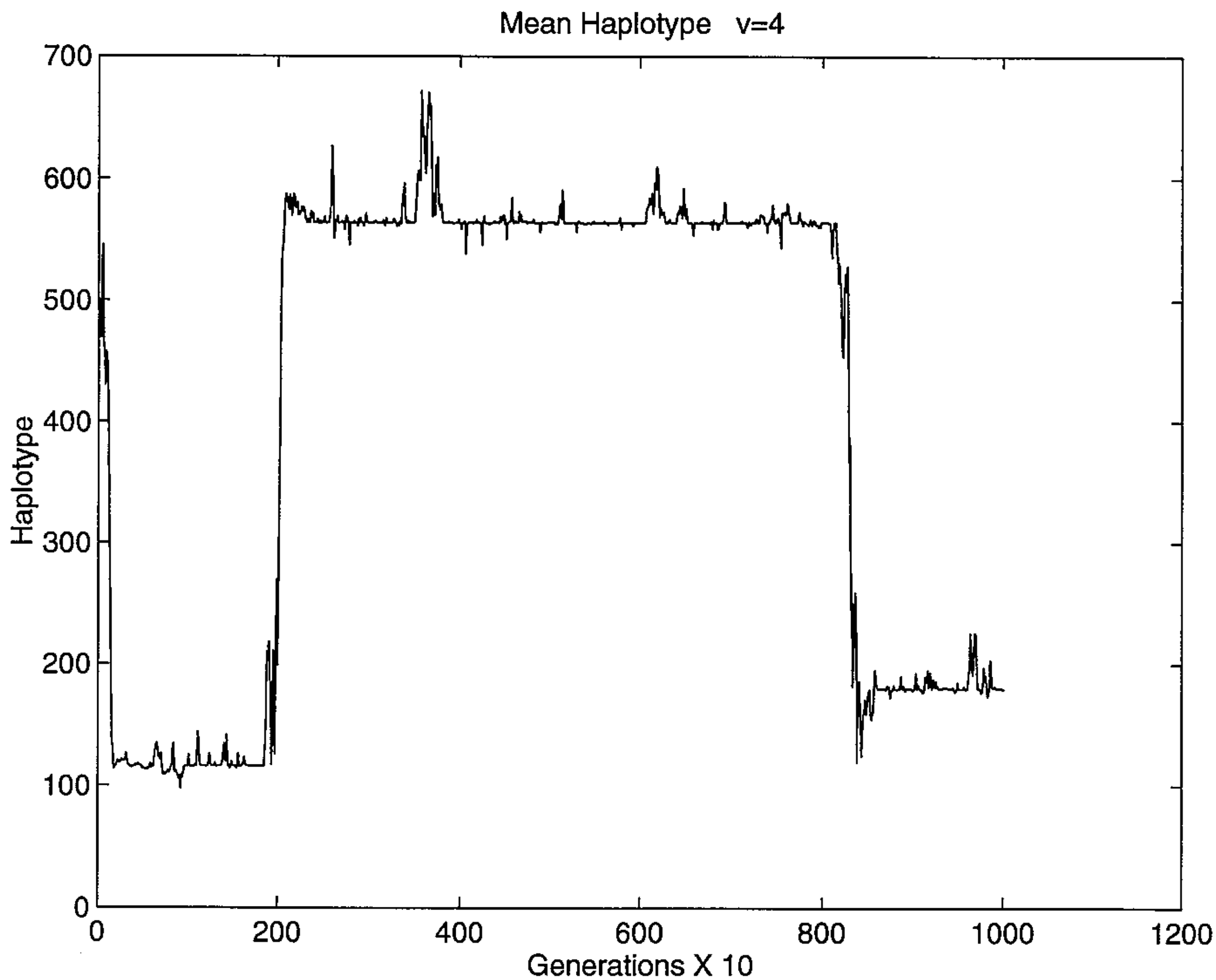

Mean Haplotype v=4
700
600
500
400
300
200
100
0
Haplotype
0
200
400
600
800
1000
1200
Generations X 10

Figure 11b