Interstrand distance distribution of DNA near melting

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The distance distribution between complementary base pairs of the two strands of a DNA molecule is studied near the melting transition. Scaling arguments are presented for a generalized Poland-Scheraga–type model that includes self-avoiding interactions. At the transition temperature and for a large distance r, the distribution decays as $1/r^{\kappa}$ with $\kappa=1+(c-2)/\nu$. Here ν is the self-avoiding walk correlation length exponent and c is the exponent associated with the entropy of an open loop in the chain. Results for the distribution function just below the melting point are also presented. Numerical simulations that fully take into account the self-avoiding interactions are in good agreement with the scaling approach.

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I. INTRODUCTION

Melting or denaturation of DNA, whereby the two strands of the molecule unbind upon heating, has been a subject of interest for several decades. In experiments carried out since the 1960's, calorimetric and optical melting curves have yielded information on the behavior of the order parameter (fraction of bounded complementary base pairs) near the transition [1]. This parameter gives a global measure for the average degree of opening of the molecule. With the recent advent of novel experimental techniques that allow for single-molecule manipulations, it has become possible to obtain more detailed information on the microscopic configurations of fluctuating DNA. For example, the time scale of opening and closing of loops of denaturated segments and some information about their steady-state distribution may be obtained by fluorescence correlation spectroscopy techniques [2]. Additional information is also gained by studies of the response of the molecule to stretching, unzipping, and torsional forces [3–7].

Theoretically, the melting transition has been studied within two main classes of models. The first, which we refer to as Poland-Scheraga–type (PS-type) models [8–11], considers the molecule as being composed of an alternating sequence of double-stranded segments and denaturated loops. Within the model, weights are assigned to bound segments and unbound loops from which the nature of the transition may be deduced. In a second approach that has been employed to study the melting transition [12], the DNA is considered as a directed polymer (DP). Here the two strands are described as directed random walks, and they interact through a short-range attractive potential. Using the transfer matrix method, the melting transition may be studied.

Within the directed polymer approach, the distance distribution of complementary base pairs is readily calculable. However, realistic geometrical restrictions (such as self-avoiding interactions) are not taken into account due to the oversimplifying directed polymer description. On the other hand, within the PS-type models, geometrical restrictions may be accounted for more realistically. It has recently been demonstrated [13–15] that a generalization of this model which includes the repulsive self-avoiding interactions between the various segments of the DNA chain may be analyzed. This is done using a scaling approach for general polymer networks introduced by Duplantier [16,17]. The results for the nature of the transition and for the loop-size distribution are in very good agreement with recent numerical studies [18–20]. In the PS-type models, the order parameter and the loop-size distribution near the transition are readily calculable. However, as defined, these models do not yield the interstrand distance distribution. It would be interesting to generalize the scaling picture of the PS-type models in order to study the interstrand distance distribution close to the melting point.

In this paper, we study the distance distribution between complementary base pairs of the two strands within the PS approach. We derive scaling results valid both at and below the melting temperature, and verify their validity by extensive numerical simulations of a model on a lattice that fully embodies excluded volume interactions.

The paper is organized as follows. In Sec. II we derive a scaling picture for the interstrand distance probability distribution both at and below the melting point. Scaling relations linking the exponents of the loop size and distance distributions are provided. The results of numerical studies of the distribution functions confirming the scaling picture are given in Sec. III. The main results are summarized in Sec. IV.

II. SCALING APPROACH

We start by briefly reviewing the main results of the PS approach. Within the framework of these models, one assigns length dependent weights to both bound and unbound segments. A bound segment is energetically favored over an unbound segment, while an unbound segment (loop) is entropically favored over a bound one. A bound segment of length l is assigned a weight w^l; where $w=\exp(-E_0/T)$, E_0 is the base pair binding energy, T is the temperature, and the Boltzmann's constant k_B is set to 1. Here it is assumed that only complementary base pairs interact with each other. The

binding energy E_0 is taken to be the same for all base pairs. An unbound segment (loop) of length l is assigned a weight

$$\Omega(l)=\frac{s^l}{l^c}, \tag{1}$$

where s is a nonuniversal geometrical constant and c is an exponent that is determined by some universal properties of the loop configurations. The nature of the melting transition depends on the value of the exponent c [11]. For $c\leqslant 1$, there is no transition, for $1<c\leqslant 2$, the transition is continuous; while for $c>2$, the transition is first order.

Early works [11] have evaluated the exponent c by enumerating random walks that return to the origin, yielding $c=d/2$ in d dimensions. The inclusion of excluded volume interactions within a loop gives $c=d\nu$ [10], where ν is the correlation length exponent of a self-avoiding random walk. Here the self-avoiding interactions between a loop and the rest of the chain are neglected. Both these estimates predict a continuous transition ($c<2$) for any $d<4$. Numerical simulations of chains of length of up to 3000 where self-avoiding interactions have been fully taken into account suggested that, in fact, the transition in the infinitely long chain limit is of first order [18]. Recently it has been suggested [13–15] that excluded volume interactions between a loop and the rest of the chain may be taken approximately into account using results for polymer networks of arbitrary topology [16,17]. It has been shown that for loops much smaller than the chain length, the entropy of the loop has the same form as in Eq. (1), but with $c=d\nu-2\sigma_3$. Here σ_3 is an exponent associated with an order three vertex configuration defined and evaluated in Refs. [16,17]. In $d=3$, the exponent c may be estimated to be $c\simeq 2.11$. Since $c>2$, the transition is of first order. Within the PS-type models, the weight of a loop of size l, $P_{\rm loop}(l)$, is given by

$$P_{\rm loop}(l)\sim\frac{e^{-l/\xi_l}}{l^c}, \tag{2}$$

where $\xi_l\sim|T-T_M|^{-1/(c-1)}$ for $1<c\leqslant 2$, and $\xi_l\sim|T-T_M|^{-1}$ for $c>2$. Here T_M is the melting temperature. In a recent numerical study [19], the loop-size distribution at the melting transition has been evaluated for chains of length up to 200 where self-avoidance is fully taken into account. These simulations yield $c\approx 2.10(4)$ in good agreement with the theoretical estimate.

We now use a scaling approach to study the complementary base-pair distance distribution $P_{\rm dist}(r)$. The probability that, within a loop of size $2l$, two complementary base pairs are separated by $\vec{r}$, scales as

$$P(\vec{r},l)=\frac{1}{l^{d\nu}}f\left(\frac{r}{l^\nu}\right), \tag{3}$$

where $r=|\vec{r}|$ and f is a scaling function. To obtain $P_{\rm dist}(r)$, we integrate over the contribution of all loops and over the angular degrees of freedom $d\omega$:

$$P_{\rm dist}(r)\sim\int_0^\infty dl P_{\rm loop}(l)\int d\omega r^{d-1}lP(\vec{r},l). \tag{4}$$

Note that the contribution of each loop is $lP(\vec{r},l)$, since each loop contains l matching pairs and thus contributes l times its average distance to the average of $P_{\rm dist}(r)$. Inserting Eqs. (2) and (3) into Eq. (4), one finds

$$P_{\rm dist}(r)\sim\int_0^\infty dl\frac{e^{-l/\xi_l}}{l^c}\frac{1}{l^{\nu-1}}\left(\frac{r}{l^\nu}\right)^{d-1}f\left(\frac{r}{l^\nu}\right). \tag{5}$$

At the transition, one has $\xi_l^{-1}=0$, and the integral scales with r as

$$P_{\rm dist}(r,\xi_l^{-1}=0)\sim\frac{1}{r^\kappa}, \tag{6}$$

where

$$\kappa=1+(c-2)/\nu. \tag{7}$$

The estimated values for the exponents $c\simeq 2.11$ and $\nu=0.588$ in $d=3$ yield $\kappa\simeq 1.19$.

Next we consider the distance distribution below the transition where $\xi_l^{-1}>0$. Simple scaling analysis cannot be carried out and one has to take a specific form for the function f. A general argument due to Fisher [21] for the end-to-end distance of a self-avoiding walk yields the following form of $f(x)$ for $x\gg 1$:

$$f(x)\sim x^\mu\exp(-Dx^{1/1-\nu}), \tag{8}$$

where μ is a known exponent. This argument may be generalized to consider the average distance between complementary pairs within a loop, or a loop embedded in a chain, yielding the same form but with a different exponent μ (to be discussed below). Using this form, the integral (5) may be evaluated using a saddle-point approximation. This gives

$$P_{\rm dist}(r)\sim\frac{\exp(-r/\xi_r)}{r^\eta}, \tag{9}$$

for $r\gg\xi_r$, with

$$\eta=c-1/2-(1-\nu)(\mu+d). \tag{10}$$

The characteristic distance ξ_r is related to the length ξ_l by

$$\xi_r\propto\xi_l^\nu \quad \text{for} \quad \xi_l\to\infty, \tag{11}$$

so that $\xi_r\propto|T-T_M|^{-\nu/(c-1)}$ for $1<c\leqslant 2$, and $\xi_r\propto|T-T_M|^{-\nu}$ for $c>2$. In our case $c\simeq 2.11$, and therefore we expect $\xi_r^{-1}\propto|T-T_M|^\nu$.

Within the approach introduced in Ref. [13], the exponent μ in the distribution function (8) should be evaluated by considering the average interstrand distance in a loop embedded in a chain. Here for simplicity we adopt the approach of Fisher [21] and consider the exponent μ in the interstrand distance distribution within an isolated loop. Thus the effect

of self-avoiding interactions between the loop and the rest of the chain on the exponent μ is not taken into account. The calculation is rather lengthy and it is outlined in the Appendix. The resulting exponent is found to be

$$\mu = \frac{1}{1-\nu}[1/2 + 2d(\nu - 1/2) - \gamma], \tag{12}$$

where γ is the exponent associated with the number of configurations of a random walk of length L as given by $s^L L^{\gamma-1}$. Thus, for a random, non-self-avoiding loop where $\gamma = 1$ and $\nu = 1/2$, one has $\mu = -1$ for any d. On the other hand, for a self-avoiding loop in $d = 3$ (where $\gamma \approx 1.18$), one has $\mu = -0.37$. An estimate for η may be obtained by using the c value of an isolated loop (namely, $d\nu$) in Eq. (10) together with the above value of μ to yield $\eta \approx 0.18$. It would be of interest to derive an expression for μ in the case of a loop embedded in a chain in order to fully take into account the effect of self-avoiding interactions.

It is instructive to compare these results with the distance distributions obtained within the DP approach. The exponent c characterizes the number of directed walks that return to the origin for the first time. This is known to be given by $c = 2 - d/2$ for $d < 2$ and $c = d/2$ for $d > 2$ (Ref. [22]). In $d = 2$, there are logarithmic corrections so that the number of configurations behaves as $s^l/(l \ln^2 l)$. Thus, one expects a continuous melting transition for $d < 4$ and a first-order phase transition for $d > 4$. Clearly, the correlation length exponent satisfies $\nu = 1/2$. Using these results, one obtains at criticality

$$\kappa_{DP} = d - 3 \quad \text{for} \quad d > 2, \tag{13}$$

$$\kappa_{DP} = 1 - d \quad \text{for} \quad d < 2. \tag{14}$$

Equations (13) and (14) are in agreement with calculations using a transfer matrix method for the DP model [23]. Below criticality, our results predict that the distance distribution decays exponentially with r, with $\xi_r \propto |T - T_M|^{-1/|2-d|}$ for $d < 4$ and $\xi_r \propto |T - T_M|^{-1/2}$ for $d > 4$. Also, using $\mu = -1$ for the DP model, one has $\eta = 0$. These results are again in agreement with known results for the DP model [23].

III. NUMERICAL SIMULATIONS

In order to test the predictions of this scaling picture, we carried out extensive numerical simulations of the loop size and interstrand distance distributions of a model of fluctuating DNA [18,19]. The DNA strands are represented by two self-avoiding walks of length N on a cubic lattice. The numerical simulations are carried out by using the pruned enriched Rosenbluth method (PERM) [24], that has already been employed in recent studies of DNA denaturation [18,20]. This method generates DNA chain configurations by a growth algorithm at fixed T. Each configuration consists of two complementary sequences of N unit steps between nearest-neighbor sites of the lattice, both starting from a common origin. Self avoidance is achieved by forbidding overlapping of sites. This constraint is relaxed only to introduce an interaction between complementary sites (with the same index along the two strands) that are allowed to overlap, with an energy gain $E_0 = -1$. In this way, the total number of these contacts gives the energy gain $-E$, and the Boltzmann weight of a DNA configuration is $\exp(E/T)$. In order to recover the equilibrium distribution in the simulation, one has to assign a suitable weight for each growth step of the chain [24,25]. In the present work we have modified the growth rules in order to achieve a better performance at lower T, where ordinary PERM yields slower convergence. In the usual PERM rules, long open segments that have low weights at low T are generated, and they are thus often pruned. This makes it difficult to generate sufficiently long and loop-rich chains by this procedure. In order to avoid this problem, we have introduced a small bias for the growing ends to recombine. This bias is compensated by a suitable reweighting of the generated chain, to yield a correct equilibrium distribution. The results of this study, which are described below, corroborate the scaling picture introduced above.

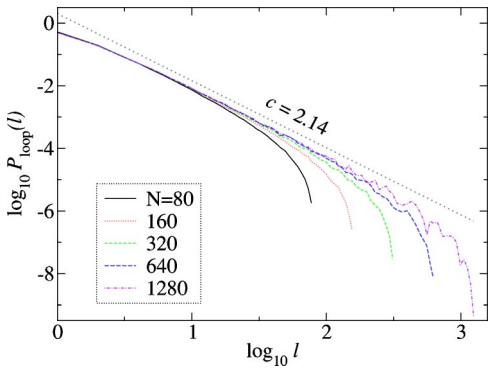

FIG. 1. Log-log plots of $P_{\rm loop}(l)$ at $T_M = 0.7455$ for several chain length N. l is measured in monomer units. One can identify a linear region (whose range increases with N) with slope $-c = -2.14(4)$ (dotted line).

We start by first considering the loop-size distribution at the melting temperature $T_M = 0.7455$. This distribution has been studied in the past for chains of length up to $N = 320$ monomers [19,20]. In Fig. 1 we present the results for chains of length up to $N = 1280$. We find $c = 2.14(4)$, which is in good agreement with the analytical estimate $c \simeq 2.11$ and the previous numerical estimates obtained from simulations of shorter chains.

The complementary-pair distance distribution at the melting point is plotted in Fig. 2 for systems of size up to $N = 1280$. We find that the decay exponent is given by $\kappa = 1.24(7)$, which is the expected value from the scaling relation (7), given the measured value of c. A direct estimate of κ from the data is not easy, since the power law behavior has a cutoff at values of r, which are much smaller than those for the l distribution. However, the algebraic decay of $P_{\rm dist}(r)$ is confirmed by the good collapse plot shown in Fig. 3.

We now consider the distribution functions below the melting temperature and study the behavior of the length scales ξ_l and ξ_r. Motivated by the asymptotic form (2) for the loop size distribution, we extract ξ_l by fitting $\ln P_{\rm loop}(l)$ to the form

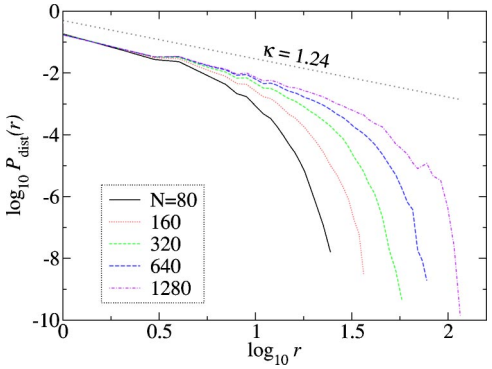

FIG. 2. Log-log plots of $P_{\rm dist}(r)$ at T_M for several chain length N. r is measured in lattice units, where the lattice spacing is set equal to 1. The slope $-\kappa=-1.24$, derived from Eq. (7) and plotted as a dotted line in the log-log scale, is consistent with the trend developing in the distributions of longer chains.

$$y_0 - l/\xi_l - c\ln l, \tag{15}$$

where y_0 is a constant. This fit is carried out for several values of the temperature near T_M using $c=2.14$. For each temperature T, the values of ξ_l is obtained at different chain lengths N and is then extrapolated to the limit $N\to\infty$. The resulting temperature dependence of the extrapolated ξ_l is displayed in Fig. 4. Indeed, the expected linear dependence of ξ_l^{-1} on the temperature difference $|T-T_M|$ is observed near T_M.

In order to obtain ξ_r, we carried out a similar fit of $\ln P_{\rm dist}(r)$ to the form

$$y_1 - r/\xi_r - \eta\ln r, \tag{16}$$

where the constant y_1 and the parameter η are left as free parameters. Unfortunately, the numerical estimate of η is rather crude, yielding $0.5\lesssim\eta\lesssim 1.2$. In Fig. 5, we present a plot of ξ_r^{-1} as a function of ξ_l^{-1}. This graph is consistent with the expected form (11).

Finally, we note that scaling relations (7) and (10) are rather general, and are not restricted to models where self-avoiding interactions are taken into account. Recently, Garel, Monthus, and Orland (GMO) [26] have introduced a model

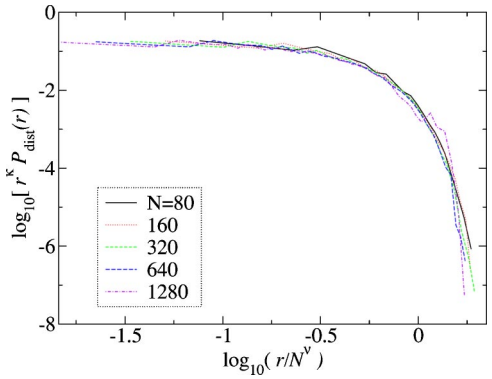

FIG. 3. Collapse plot of $P_{\rm dist}(r)$ according to a scaling form $P_{\rm dist}(r,N)\simeq r^{-\kappa}g(r/N^{\nu})$, where $\nu\simeq 0.59$. r is measured in lattice units, where the lattice spacing is set equal to 1.

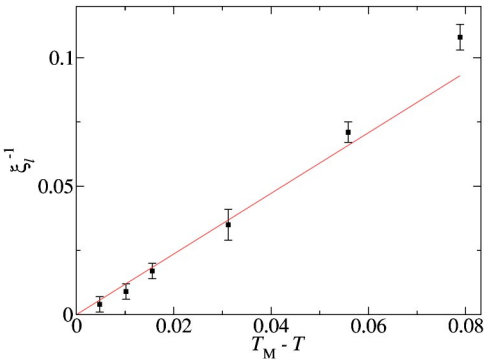

FIG. 4. The characteristic length ξ_l^{-1} (measured in monomer units) as a function of $|T-T_M|$, for $T<T_M$.

for DNA denaturation where self-avoidance within each strand is neglected while mutual avoidance is included. Each strand is a simple random walk, and thus $\nu=1/2$ for this model. Numerical results obtained with the PERM method for this model in $d=3$ dimensions yield $c=2.55(5)$ and $\kappa=2.1(1)$ [27]. It is readily seen that these exponents satisfy the scaling relation (7). In fact, for the GMO model, one can also develop a PS type of description [27] analogous to that of Refs. [13–15], but this time based on a block copolymer network picture [20]. This description gives analytical c estimates consistent with the numerical results.

IV. SUMMARY

In this paper we studied the interstrand distance distribution for DNA at and near the melting point. A scaling analysis within PS-type models where self-avoiding interactions are taken into account is presented. A scaling relation is derived [Eq. (7)] between the exponents c and κ, which govern the decay at the melting of probability distributions of loop lengths and of interstrand distances, respectively. Results of extensive numerical simulations are found to be in agreement with the scaling approach.

The DNA melting transition has been studied so far either with PS-type models or with the directed polymer approach.

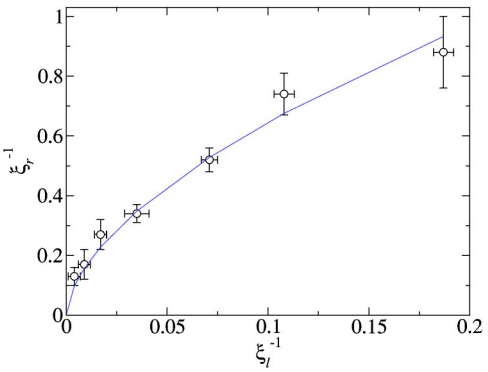

FIG. 5. Parameter ξ_r^{-1} as a function of ξ_l^{-1}, for $T<T_M$. ξ_l is measured in monomer units while ξ_r is measured in lattice units, where the lattice spacing is set equal to 1. Errors are indicated. For each T, we evaluate ξ_r by a nonlinear fit of $\ln P_{\rm dist}(r)$ of the form (16). The solid line is a fit using the form (11).

While in the latter case κ and c are easily computable, in the PS models the interstrand distance distribution, and thus the associated exponent κ, has not yet been discussed. Our analytical and numerical results for κ thus provide a valuable insight into the geometry of DNA at melting, enabling one to make more quantitative comparisons between the two types of approach. With the advent of new physical, single molecule techniques, such quantities may be measurable in the near future, yielding direct information on the fluctuations taking place in DNA.

ACKNOWLEDGMENTS

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APPENDIX: THE EXPONENT μ FOR A SELF-AVOIDING LOOP

The exponent μ may be evaluated for a self-avoiding loop by generalizing the approach of McKenzie and Moore [28] who calculated this exponent for a self-avoiding walk. This generalization closely follows the derivation in Ref. [28], and thus we will only briefly outline it here. The quantity of interest is the probability distribution for two complementary bases within a ring of length l. Equivalently, this may be viewed as the probability of two chains that are bound at one end, to reach the same point $\vec{r}$. In this probability, all possible lengths l_1 and l_2 (with $l_1+l_2=l$) are considered.

To this end, we first consider the generating function of two chains held together at one end and which are not restricted to return to the same point $\vec{r}$,

$$\Gamma(\vec{r}_1,\vec{r}_2,\theta)=\sum_{l_1,l_2=1}^{\infty} C_{l_1,l_2}P_{l_1,l_2}(\vec{r}_1,\vec{r}_2)s^{-(l_1+l_2)}e^{-\theta(l_1+l_2)}. \tag{A1}$$

Here C_{l_1,l_2} is the number of configurations of two chains held together at one end, and $P_{l_1,l_2}(\vec{r}_1,\vec{r}_2)$ is the probability that the free end of one chain is at $\vec{r}_1$ and the free end of the other chain is at $\vec{r}_2$. The distribution function is given by $\Gamma(\vec{r},\vec{r},\theta)$, where θ is a chemical potential that controls the chain length l_1+l_2 in the sum (A1).

The Fourier transform of the Green's function (A1) of the two chains can be assumed to have the Ornstein and Zernike form at small momenta $\vec{q}_1$ and $\vec{q}_1$,

$$\hat{\Gamma}(\vec{q}_1,\vec{q}_2,\theta)\sim\frac{\theta^{\nu\rho}}{(\theta^{2\nu}+q_1^2)(\theta^{2\nu}+q_2^2)}. \tag{A2}$$

Moreover, since the two chains are bound together at one end, their total number of configurations is just that of one chain of length l_1+l_2. Namely, $C_{l_1,l_2}=s^l l^{\gamma-1}$ where $l=l_1+l_2$ and $l^{\gamma-1}$ is the usual enhancement factor for a self-avoiding random walk. Using this in Eq. (A1), one can easily show that for small θ,

$$\hat{\Gamma}(0,0,\theta)=\sum_{l_1=1,l_2=1}^{\infty} C_{l_1,l_2}s^{-(l_1+l_2)}e^{-\theta(l_1+l_2)}\sim\theta^{-\gamma-1}, \tag{A3}$$

which after comparison with Eq. (A2), implies that $\rho=4-(\gamma+1)/\nu$.

The quantity of interest is the probability

$$P_l(\vec{r},\theta)=\sum_{l_1+l_2=l} P_{l_1,l_2}(\vec{r},\vec{r}). \tag{A4}$$

This can be calculated by first inverting Eq. (A2) to obtain $\Gamma(\vec{r}_1,\vec{r}_2,\theta)$. Setting $\vec{r}_1=\vec{r}_2=\vec{r}$ yields

$$\Gamma(\vec{r},\vec{r},\theta)\sim\theta^{\nu(\rho+d-3)}r^{1-d}e^{2\theta^{\nu}r}. \tag{A5}$$

One then has to carry out an inverse Laplace transform of Eq. (A5) in order to extract $P_l(\vec{r},\theta)$. One obtains

$$C_l P_l(\vec{r},\theta)s^{-l}=\frac{1}{2\pi i}\int_{X-i\pi}^{X+i\pi} d\theta e^{l\theta}\Gamma(\vec{r},\vec{r},\theta), \tag{A6}$$

where $C_l=C_{l_1,l_2}$ with $l=l_1+l_2$, and X is larger than the real part of any singularity of $\Gamma(\vec{r},\vec{r},\theta)$. The result of this calculation has the expected form (8) with

$$\mu=\frac{1}{1-\nu}[1/2+2d(\nu-1/2)-\gamma]. \tag{A7}$$

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