**A lower bound on the reversal and
transposition diameter**

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Abstract

One possible model to study genome evolution is to represent genomes as permutations of genes and compute distances based on the minimum number of certain operations (rearrangements) needed to transform one permutation into another. Under this model, the shorter the distance, the closer the genomes are. Two operations that have been extensively studied are the reversal and the transposition. A reversal is an operation that reverses the order of the genes on a certain portion of the permutation. A transposition is an operation that "cuts" a certain portion of the permutation and "pastes" it elsewhere in the same permutation. In this paper we show that the reversal and transposition distance of the signed permutation $\pi_n = (-1 \ -2 \ \ldots \ -(n-1) \ -n)$ with respect to the identity is $\lfloor n/2 \rfloor + 2$ for all $n \geq 3$. We conjecture that this value is the diameter of the permutation group under these operations.

1   Introduction

One possible model to study genome evolution is to represent genomes as **permutations** of genes and compute distances based on the minimum number of certain **operations** (rearrangements) needed to transform one permutation into another. Under this model, the shorter the distance, the closer the genomes are.

In general, genes are represented as integers from 1 to n, and a permutation π : $\{1, 2, \ldots, n\} \mapsto \{1, 2, \ldots, n\}$ by

$$(\pi_1 \ \pi_2 \ \ldots \ \pi_n),$$

where π_i denotes $\pi(i)$.

Permutations can be **signed**, in which case each π_i has a positive or negative sign to model the orientation of genes. We will call **permutation group** the set of all permutations of a given size n. The unsigned permutation group has $n!$ elements, while the signed group has $2^n n!$ elements.

In this note we are interested in the diameter of permutation groups, that is, the maximum distance possible between two permutations of size n, under several operation choices. Two operations that have been extensively studied are the *reversal* and the *transposition*. A **reversal** is an operation that reverses the order of the genes on a certain portion of the

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permutation. A **transposition** is an operation that "cuts" a certain portion of the permutation and "pastes" it elsewhere in the same permutation. (Refer to Section 2 for more formal definitions.) A transposition is also called a **block move** in the literature. A **block interchange** operation exchanges two portions of a permutation (Christie, 1996). Transpositions and block interchanges never affect the signs (if present) of a permutation. For this reason, they are studied in the unsigned case only. We could also conceive an operation that "cuts" a portion and "pastes" it elsewhere reversed. Call this a **transversal**.

Table 1 shows what is currently known about the diameter for signed and unsigned permutations under various combinations of the above operations. In this note we provide a lower bound for the diameter in the case of signed permutations evolving by transpositions and reversals.

Analyzing genomes evolving due to different mutational events represents today a great challenge. Hannenhalli and others (Hannenhalli et al., 1995) analyzed genomes evolving by different events, particularly reversals and transpositions. Hannenhalli and Pevzner (Hannenhalli and Pevzner, 1995) presented a polynomial time algorithm for comparing genomes evolving by reversals, translocations, fusions and fissions. Gu, Peng and Sudborough (Gu et al., 1996) gave approximation algorithms to compute the distance between two signed permutations, allowing three operations, reversal, transposition and transversal.

In this work we contribute to the analysis of reversals and transpositions acting on a single chromosome having genes with known orientation. We show a permutation π_n that needs at least $\lfloor n/2 \rfloor + 2$ steps to be sorted, thus obtaining a lower bound on the diameter of the signed permutation group under these operations.

2   Definitions

In this section we formalize the problem of computing the reversal and transposition distance of linear chromosomes.

We assume that the order and orientation of genes in a chromosome are represented by a permutation $\pi = (\pi_1 \ \pi_2 \ \ldots \ \pi_n)$, where each π_i is a signed integer such that $1 \leq |\pi_i| \leq n$ and $\pi_i \neq \pi_j$ for $i \neq j$.

A reversal $r(i, j)$ is defined by two integers i, j, such that $1 \leq i \leq j \leq n$, reversing the order and sign of π_k, $i \leq k \leq j$. Thus we have

$$r(i, j) \cdot (\pi_1 \ \ldots \ \pi_{i-1} \ \pi_i \ \ldots \ \pi_j \ \pi_{j+1} \ \ldots \ \pi_n) =$$

$$(\pi_1 \ \ldots \ \pi_{i-1} \ \overline{\pi}_j \ \ldots \ \overline{\pi}_{i+1} \ \overline{\pi}_i \ \pi_{j+1} \ \ldots \ \pi_n)$$

where $\overline{\pi}_k$ means π_k with opposite sign.

A transposition $t(i, j, k)$ is defined by three integers i, j, and k such that $1 \leq i < j \leq n + 1$, and $k \notin [i, j]$, in the following way. It "cuts" the portion between positions i and $j - 1$, including the extremes, and "pastes" it just before position k. Thus, if $i < j < k$, we can write

$$t(i, j, k) \cdot (\pi_1 \ \ldots \ \pi_{i-1} \ \pi_i \ \ldots \ \pi_{j-1} \ \pi_j \ \ldots \ \pi_{k-1} \ \pi_k \ \ldots \ \pi_n) =$$

$$(\pi_1 \ \ldots \ \pi_{i-1} \ \pi_j \ \ldots \ \pi_{k-1} \ \pi_i \ \ldots \ \pi_{j-1} \ \pi_k \ \ldots \ \pi_n)$$

Operations	Size	Degree	Diameter
Reversals (unsigned) [a]	$n!$	$\binom{n}{2}$	$D = n - 1$
Reversals (signed) [b]	$2^n n!$	$\binom{n}{2} + n$	$D = n + 1$
Transpositions [c]	$n!$	$\binom{n+1}{3}$	$\lfloor n/2 \rfloor + 1 \leq D \leq \lfloor 3n/4 \rfloor$
Reversals, transpositions [d]	$2^n n!$	$\binom{n+1}{3} + \binom{n}{2} + n$	$\lfloor n/2 \rfloor + 2 \leq D$
Block interchange [e]	$n!$	$\binom{n+1}{4}$	$D = \lfloor n/2 \rfloor$

[a] (Bafna and Pevzner, 1996)

[b] (Hannenhalli and Pevzner, 1999; Meidanis et al., 1997a)

[c] (Bafna and Pevzner, 1998; Meidanis et al., 1997b; Christie, 1998)

[d] This paper

[e] (Christie, 1996)

Table 1: Results known about the diameter of permutation groups under genome rearrangement operations. The column "Size" refers to the size of the graph, i.e., the total number of permutations for n elements. "Degree" is how many neighbors a permutation has. In the column "Diameter" either the diameter is given or the known bounds, with D representing the diameter.

Given two permutations π and σ, we want to compute a shortest series of reversals and transpositions that transforms π into σ, that is, we want to find $\varrho_1, \varrho_2, \ldots, \varrho_u$, where ϱ_i is a reversal or a transposition, such that $\varrho_u \cdot \varrho_{u-1} \cdot \ldots \cdot \varrho_2 \cdot \varrho_1 \cdot \pi = \sigma$ and u is minimum. We call u the **reversal and transposition distance** between π and σ and denote it by $d(\pi, \sigma)$. Without loss of generality we can fix σ. All our developments will be done with σ being the identity permutation, which is $\sigma = \iota_n = (+1 \ \ldots \ +n)$. In this case we denote $d(\pi, \iota_n)$ simply by $d(\pi)$.

In the following an **operation** can be a reversal or a transposition.

A powerful tool for studying the reversal and transposition distance is the *reality and desire diagram* of two permutations. In the literature (Bafna and Pevzner, 1998; Hannenhalli and Pevzner, 1999; Hannenhalli and Pevzner, 1996) this is called the *breakpoint graph* of two permutations, but we prefer to call it a diagram because its graph structure alone does not capture all the important information: the order of nodes is relevant too.

We first extend a permutation π by adding $\pi_0 = +0$ and $\pi_{n+1} = +(n+1)$. The extended permutation will still be denoted by π. We construct this diagram writing the original permutation π in the following way. Replace each integer i by a pair of points $-i$ and $+i$, in this order. For instance $+4$ is replaced by -4 and $+4$; -7 is replaced by $+7$ and -7. Add two extra points, one called $+0$ at the beginning of the sequence, and one called $-(n+1)$ at the end of the sequence. Now draw **reality** edges between $+0$ and $-\pi_1$, between $+\pi_{i-1}$ and $-\pi_i$, and between $+\pi_n$ and $-(n+1)$. Finally, draw **desire** edges between $+0$ and -1, between $+(i-1)$ and $-i$, and between $+n$ and $-(n+1)$ (see Figure 1). Again, in the literature, reality edges are called *black edges* and desire edges are called *gray edges*. We prefer the denominations reality and desire because they are more informative: reality edges refer to the current permutation, that is, where we are, and desire edges refer to the target permutation, that is, where we would like to be. We denote $G(\pi)$ the diagram of the permutation π (with respect to the identity).

Observe that the diagram is composed of a number of cycles, with each cycle alternating between reality and desire edges. The **length** of a cycle is the number of reality edges in it (which is the same as the number of desire edges in it). The decomposition of $G(\pi)$ into cycles is unique and we denote by $c(\pi)$ the number of cycles in $G(\pi)$.

The cycles of $G(\pi)$ are denoted by a bracket notation as follows. We number the reality edges of $G(\pi_n)$ from 1 to $n+1$ by assigning label i to the reality edge (π_i, π_{i-1}), with $1 \le i \le n+1$. Besides, we will assign to the label i from cycle c an orientation $+i$ or $-i$, defined with respect to the orientation of the greatest (in absolute value) label l from c, which is $+l$ by convention. So, taking these labels and their orientations, in the order they appear in around the cycle, the unique cycle of the diagram in Figure 1 (c) is

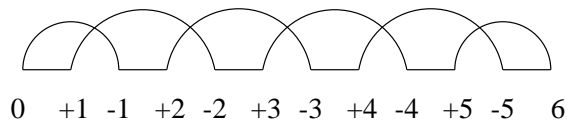$$[+(n+1), +(n-1), \ldots, +4, +2, -1, -3, \ldots, -n]$$

for n odd or

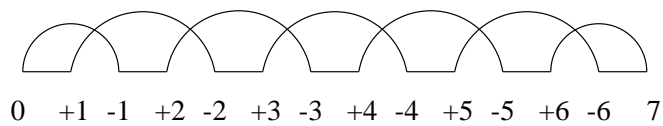$$[+(n+1), +(n-1), \ldots, +3, +1, -2, -4, \ldots, -n]$$

for n even.

The diagram has exactly $n+1$ reality edges and the same number of desire edges. The idea is that reality edges indicate the situation as it is now, and desire edges indicate the
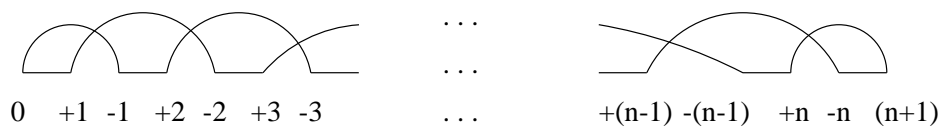
4

(a)

0　　+1　-1　+2　-2　+3　-3　+4　-4　+5　-5　　6

(b)

0　　+1　-1　+2　-2　+3　-3　+4　-4　+5　-5　+6　-6　　7

(c)

. . .

. . .

0　　+1　-1　+2　-2　+3　-3　　. . .　　+(n-1) -(n-1)　+n　-n　(n+1)

Figure 1: (a) The diagram for $\pi = (-1 \;\; -2 \;\; -3 \;\; -4 \;\; -5)$. (b) The diagram for $\pi = (-1 \; -2 \; -3 \; -4 \; -5 \; -6)$. (c) The general diagram for $\pi = (-1 \; -2 \; \ldots \; -(n-1) \; -n)$, for all n.

situation sought. When reality equals desire in all edges, we have $\pi = \iota_n$ and $d(\pi) = 0$. Therefore, our goal is to apply reversals and transpositions so that reality becomes desire.

Note that the diagram $G(\iota_n)$ is the only one having $n + 1$ cycles. So, the sequence of reversals and transpositions transforming π into ι_n must take the number of cycles from $c(\pi)$ to $n + 1$. For a permutation π, and an operation ϱ, denote by $\Delta c(\pi, \varrho)$ the difference $c(\varrho \cdot \pi) - c(\pi)$. This is the gain in the number of cycles due to operation ϱ applied to π.

Theorem 1 $\Delta c(\pi, \varrho) \in \{-2, -1, 0, 1, 2\}$

Proof: We note first that ϱ can be a reversal or a transposition.

Each reversal acts on two reality edges belonging to at most two cycles, creating or destroying at most one cycle. Hannenhalli and Pevzner (Hannenhalli and Pevzner, 1999) have shown that, for a reversal, $\Delta c(\pi, \varrho) \in \{-1, 0, 1\}$.

Each transposition acts on three reality edges belonging to at most three cycles. Figure 2 shows all possible actions of a transposition on a signed permutation. As we can see, there are cases where the number of cycles stays the same, or increases by one or two. So, for a transposition, $\Delta c(\pi, \varrho) \in \{-2, -1, 0, 1, +2\}$. □

For $x \in \{-2, -1, 0, 1, 2\}$, define an x-move on π as an operation ϱ such that $\Delta c(\pi, \varrho) = x$. Notice that, in Figure 2, there is only one pattern corresponding to a 2-move (or -2-move), three patterns corresponding to a 1-move (or -1-move), and the others corresponding to 0-moves.

The entire distance problem can be seen as finding shortest paths in a directed graph where a vertex corresponds to a permutation π, and there is an edge (π, σ) from π to σ when there is an operation (reversal or transposition) ϱ such that $\sigma = \varrho \cdot \pi$. We are interested in shortest directed paths from π to ι_n, where the length of a path is just its number of edges. However, we can assign weights to the edges in a way that will help us investigate the problem. In the sequel we will define the weight of an edge and of a path, on that graph.

Definition 1.1 *Given the permutations π and σ, such that $\sigma = \varrho \cdot \pi$ for some operation ϱ, we define the **weight** of the edge (π, σ) as*

$$w(\pi, \sigma) = 2 + c(\pi) - c(\sigma).$$

Notice that $w(\pi, \sigma) \geq 0$ for all edges (Theorem 1). The weight $w(\pi, \sigma)$ can be also written as $2 - \Delta c(\pi, \varrho)$, where ϱ is the operation that transforms π into σ. Since 2 is the highest value that $\Delta c(\pi, \varrho)$ can take, and we know that high values of $\Delta c(\pi, \varrho)$ will get us closer to our goal, we can think of the weight as a measure of "waste" in each operation we do.

Definition 1.2 *Given a path $p = \pi_0 \pi_1 \pi_2 \ldots \pi_{k-1} \pi_k$, we define the **weight** of p as*

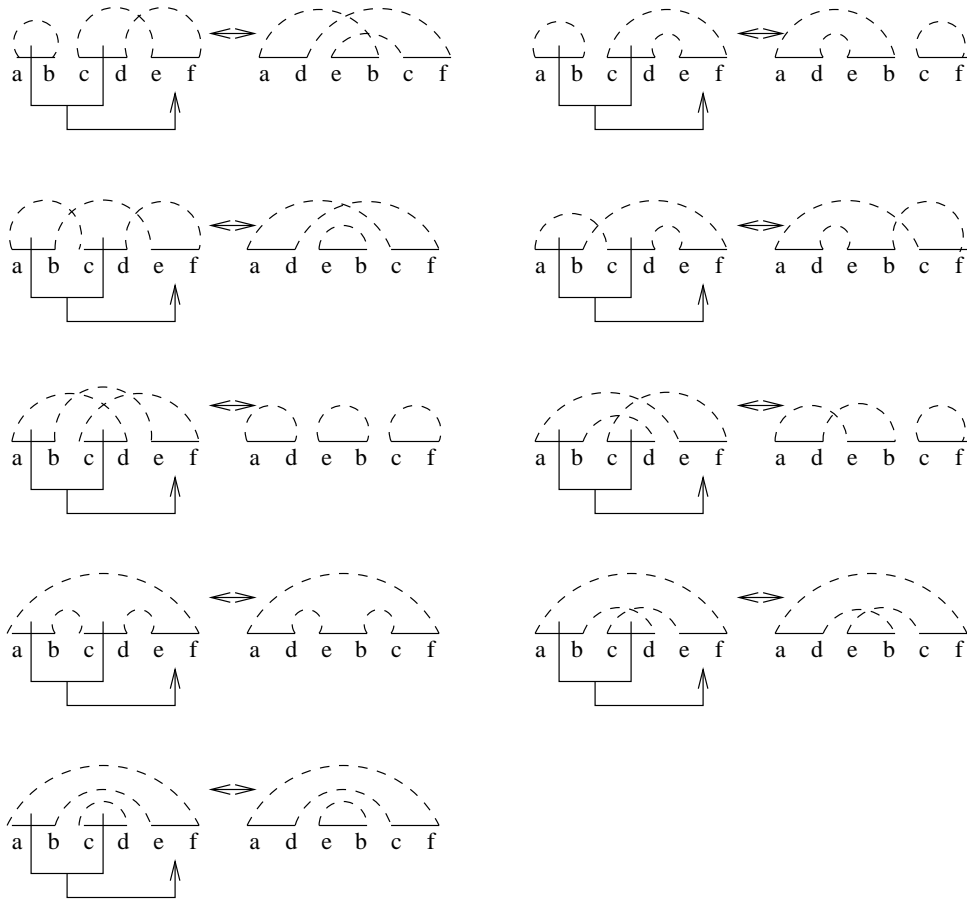$$w(p) = \sum_{i=1}^{k} w(\pi_{i-1}, \pi_i).$$

Figure 2: This figure shows all possible actions of a transposition on a signed permutation. Only affected cycles are shown. A dashed line indicates a path formed by one or more desire and reality edges. Since the inverse of a transposition is a transposition, the transformations are reversible.

Note that $w(p) \geq 0$ for all paths. We can now relate the length of a path with the weight of the same path, with important consequences on the distance. Let $|p|$ denote the length of a path p.

Theorem 2 *Let $p = \pi_0 \pi_1 \pi_2 \ldots \pi_{k-1} \pi_k$ be a path. We have*

$$w(p) = 2|p| + c(\pi_0) - c(\pi_k).$$

The proof is just an induction on k. An important corollary is the following.

Corollary 2.1 *For any permutation π and any shortest path p from π to ι_n we have*

$$d(\pi) = \frac{w(p) - c(\pi) + n + 1}{2}.$$

The proof is immediate from the theorem, using $\pi_0 = \pi$ and $\pi_k = \iota_n$.

3 The reversal and transposition diameter

Taking S_n as the set of all signed permutations with size n, define $D(n) = \max_{\pi \in S_n} d(\pi, \iota_n)$ as the **reversal and transposition diameter** of signed permutations. In this section we present a lower bound on this number, based on the distances of particular permutations for each integer n.

This particular permutation is $\pi_n = (-1 \ -2 \ \ldots \ -(n-1) \ -n)$. We will compute its reversal and transpositions distance, which will give a lower bound for the diameter $D(n)$. We start by showing an upper bound for $d(\pi_n)$, for all $n \geq 3$.

Theorem 3 *We have $d(\pi_n) \leq \lfloor \frac{n}{2} \rfloor + 2$ for $n \geq 3$.*

Proof: First we apply the reversal $r(1, n)$ on π_n, obtaining

$$\pi = r(1, n) \cdot \pi_n = (+n \ +(n-1) \ \ldots \ +2 \ +1),$$

a permutation with positive signs only.

After that we recall a result from Meidanis, Walter and Dias (Meidanis et al., 1997b), independently shown by Christie (Christie, 1998), proving that the transposition distance $d_t(\pi_n)$ is $\lfloor \frac{n}{2} \rfloor + 1$, for $n > 2$.

The total number of operations is then $\lfloor \frac{n}{2} \rfloor + 2$, which is an upper bound on the distance $d(\pi_n)$ for $n \geq 3$. □

Our strategy to show that this upper bound is a lower bound as well will be to prove that every path p from π_n to ι_n satisfies $w(p) \geq 3$. Then, by force of Corollary 2.1 and Lemma 3.1, we will have the desired result (see Theorem 6).

The general form of the diagram generated by this permutation is given in Figure 1 (c). The number of cycles is always 1, and we state this as our next lemma.

Lemma 3.1 *We have $c(\pi_n) = 1$ for all n.*

We need auxiliary results to support our claims. One that appears with frequency is a sufficient condition for the lack of 2-moves. Recall the format of the cycles in the diagram of π_n:

$$c = [+(n+1), +(n-1), \ldots, +2, -1, -3, \ldots, -n],$$

for n odd and

$$c = [+(n+1), +(n-1), \ldots, +3, +1, -2, \ldots, -n]$$

for n even. Notice that regardless of the parity of n these cycles are formed by two decreasing subsequences. We call **bimonotonous** the cycles formed by two decreasing subsequences, the first made of positive elements, and the second formed by negative elements. Such cycles cannot be broken by a transposition, as the following results show.

Lemma 3.2 *A permutation π admits a 2-move if and only if there are three reality edges labeled i, j and k with $i < j < k$, belonging to the same cycle in $G(\pi)$, and appearing in that cycle either in the order k, i, j (or i, j, k or j, k, i) with orientation $+$, or in the order k, j, i (or j, i, k or i, k, j) with orientation $-$.*

Proof: Theorem 1 shows that there is just one pattern corresponding to a 2-move. In this pattern (see Figure 2), we can verify that, taking the three labels (belonging to the same cycle) i, j and k such that $i < j < k$, and assigning to label k the orientation $+k$, we force the orientations of i and j to be respectively $+i$ and $+j$, implying that these three labels appear in the cycle with the order k, i, j (or i, j, k or j, k, i), and all three with the same orientation. Analogously, if we assign to k the orientation $-k$, the orientations of i and j become $-i$ and $-j$, implying the order k, j, i (or j, i, k or i, k, j), with i, j and k with the same orientation.

The proof on the other side is immediate. We apply $t(i, j, k)$ on π, with i, j and k following the conditions of the lemma, and obtain the desired result. □

Theorem 4 *Let π be a permutation for which all cycles in its reality and desire diagram are bimonotonous. Then $w(\pi, \varrho\pi) \geq 1$ for all operations ϱ.*

Proof: Of course, $w(\pi, \varrho\pi) = 0$ is equivalent to saying that ϱ is a 2-move on π. A 2-move has to be a transposition, and acting on three reality edges of the same cycle. However, by the bimonotonicity of the cycles of π, we cannot choose three labels following the conditions of Lemma 3.2, considering just one of these two subsequences. Another way to get these labels would be to choose them from both subsequences. But then they will not have the same orientation, so also in this case we cannot have the conditions of Lemma 3.2. □

We are now ready for our main theorem.

Theorem 5 *Let $p = \sigma_0\sigma_1 \ldots \sigma_k$ be any path from $\pi_n = \sigma_0$ to $\iota_n = \sigma_k$. Then we have, for $n \geq 3$:*

1. *$w(\sigma_0\sigma_1) \geq 1$*

2. *if $w(\sigma_0\sigma_1) = 1$, then $w(\sigma_1\sigma_2) \geq 1$*

3. if $w(\sigma_0 \sigma_1 \sigma_2) = 2$, then $w(\sigma_2 \ldots \sigma_k) \geq 1$

Proof: The first claim is true because the weight is always greater than or equal to zero, and it is zero only if the operation is a 2-move. However, $\sigma_0 = \pi_n$ has only one cycle, and this cycle is bimonotonous. Our claim then follows from Theorem 4.

For the second claim, observe that $w(\sigma_0 \sigma_1) = 1$ exactly when the operation ϱ that acted on $\sigma_0 = \pi_n$ was a 1-move. Both reversals and transpositions can be 1-moves in the signed case, so we need to analyze these two cases.

Let us deal with reversals first. It is well known (Meidanis and Setubal, 1997) that a reversal breaks a cycle (that is, is a 1-move) if and only if the two reality edges where it acts have opposite orientations. Since $r(i, j)$ acts on reality edges i and $j + 1$, this means that $r(i, j)$ is a 1-move if and only if i and j have the same parity. The diagram of the permutation $r(i, j) \cdot \pi_n$ in this case has two cycles. The exact pattern of the resulting cycles depends on the relative parity of i, j, and n, but in all cases they are bimonotonous. For instance, if i, j, and n are all odd, these cycles are

$$
\begin{aligned}
c_1 &= [+j, +(j-2), \ldots, +(i+2), +i, +(i-2), \ldots, +3, +1, \\
&\quad -2, -4, \ldots, -(i-1)], \\
c_2 &= [+(n+1), +(n-1), \ldots, +(j+1), +(j-1), +(j-3), \ldots, +(i+1), \\
&\quad -(j+2), -(j+4), \ldots, -n].
\end{aligned}
$$

It is apparent that these two cycles are bimonotonous. The other cases can be verified analogously. Therefore $w(\sigma_1 \sigma_2) \geq 1$ if ϱ is a reversal.

The case where ϱ is a transposition $t(i, j, k)$ also requires an analysis based on the parity of i, j, k, and n. From Figure 1 and Figure 2 we see that this operation is a 1-move if and only if i and k have the same parity, and j has the opposite parity from i and k. For instance, in the case of i, k, and n all odd and j even, we have a diagram $G(t(i, j, k) \cdot \pi_n)$ formed by two cycles, which are

$$
\begin{aligned}
c_1 &= [+(k-1), +(k-3), \ldots, +j, +(j-2), \ldots, +(i+1)] \\
c_2 &= [+(n+1), +(n-1), \ldots, +(k+1), +(i+k-j-1), \\
&\quad +(i+k-j-3), \ldots, +(i+2), +i, +(i-2), \ldots, +3, +1, \\
&\quad -2, -4, \ldots, -(i-1), -(i+k-j+1), \\
&\quad -(i+k-j+3), \ldots, -k, -(k+2), \ldots, -n].
\end{aligned}
$$

The first cycle is monotonous and therefore does not admit a 2-move. The second cycle is bimonotonous, and, by Theorem 4, does not admit a 2-move either. The other cases can be verified analogously.

Let us now turn to the third claim. Again we divide the proof into two cases: either there is a negative element in σ_2 or all elements there are positive. If there is at least one negative element, then $w(\sigma_2 \ldots \sigma_k) \geq 1$ because otherwise only transpositions would be applied until we reach ι_n, but ι_n does not have negative elements and transpositions do not change signs.

We concentrate then in the case where σ_2 has all elements positive. Since $\sigma_0 = \pi_n$ has all elements negative, there are only four possible ways of reaching an all-positive permutation in two steps:

1. $\sigma_2 = r(1,i) \cdot r(i+1,n) \cdot \sigma_0$, for some i between 1 and $n-1$, including extremes.

2. $\sigma_2 = r(i+1,n) \cdot r(1,i) \cdot \sigma_0$, for some i between 1 and $n-1$, including extremes.

3. $\sigma_2 = t(i,j,k) \cdot r(1,n) \cdot \sigma_0$, for some triple i, j, k with $1 \leq i < j < k \leq n+1$.

4. $\sigma_2 = r(1,n) \cdot t(i,j,k) \cdot \sigma_0$, for some triple i, j, k with $1 \leq i < j < k \leq n+1$.

The first two cases are actually the same, since $r(1,i)$ and $r(i+1,n)$ commute. In fact, we will show that all cases can be reduced to the third one. The key to this fact is to notice that any transposition can be written as the product of three reversals:

$$t(i,j,k) = r(i,k-1) \cdot r(i,j-1) \cdot r(j,k-1). \tag{1}$$

This can be easily verified from the definitions. If we use $i = 1$ and $k = n+1$ in this equation, we get:

$$t(1,j,n+1) = r(1,n) \cdot r(1,j-1) \cdot r(j,n),$$

showing that Cases 1 and 2 are indeed particular instances of Case 4 (recall that $r(1,n)^2 = I$). On the other hand,

$$r(1,n) \cdot t(i,j,k) \cdot r(1,n) = t(k',j',i'),$$

where $i' = n+2-i$, $j' = n+2-j$, and $k' = n+2-k$, which shows that Case 4 can be reduced to Case 3.

Let us then concentrate on Case 3. Notice that in this case σ_1 is the permutation $(+n\ +(n-1)\ \ldots\ +2\ +1)$. A consequence of the work by Meidanis, Walter, and Dias (Meidanis et al., 1997b) and that of Christie (Christie, 1998), which computed the transposition distance of such permutations, is that $w(\sigma_1 \ldots \iota_n) \geq 2$ for any path consisting of transpositions only. Now if $w(\sigma_2 \ldots \sigma_k) = 0$, this would refer to a path using transpositions only, and therefore we can conclude that $w(\sigma_1 \sigma_2) = 2$ and that $w(\sigma_0 \sigma_1) = 0$, a contradiction since the first step $r(1,n)$ was a reversal. It follows that $w(\sigma_2 \ldots \sigma_k) \geq 1$ as claimed. □

Theorem 6 *We have* $d(\pi_n) \geq \lfloor \frac{n}{2} \rfloor + 2$ *for* $n \geq 3$.

Proof: Theorem 5 guarantees that $w(p) \geq 3$ for any path from π_n to ι_n. Plugging this into the formula of Corollary 2.1 we conclude that

$$d(\pi_n) \geq \frac{n+3}{2},$$

which implies $d(\pi_n) \geq \lfloor \frac{n}{2} \rfloor + 2$ since $d(\pi_n)$ is an integer. □

The next theorem comes directly from Theorems 6 and 3.

Theorem 7 *Given the permutations π_n and ι_n, for all n, then we have*

$$d(\pi_n) = \begin{cases} \lfloor \frac{n}{2} \rfloor + 1 & \text{if } n = 1, 2 \\ \lfloor \frac{n}{2} \rfloor + 2 & \text{if } n \geq 3 \end{cases}$$

Proof: For $n = 1$ it is obvious that $d(\pi_n) = 1$ since $\pi_n \neq \iota_n$ and a reversal will do. For $n = 2$ a minimum series of operations transforming π_n into ι_n consists of two operations. For $n \geq 3$, the result follows from Theorems 3 and 6. $\qquad\square$

4 Conclusions

In this work we extend the analysis of transpositions done by Bafna and Pevzner (1995) to signed permutations, and compute the the reversal and transposition distance of the signed permutation $(-1 \ -2 \ \dots \ -(n-1) \ -n)$ with respect to the identity $(+1 \ +2 \ \dots \ +n-1 \ +n)$. The proof is based on the number of cycles that can be created, on the first two steps, in the diagrams generated on any sequence of operations transforming π_n on ι_n. Obviously this result gives a lower bound for the diameter. We conjecture that this is also an upper bound. We remark that the exact value of the transposition diameter is still unknown (see Table 1).

An interesting point to be studied later is the diameter of signed permutations under reversals, transpositions, and *transversals*. A transversal acts by moving a block of genes to another place on the permutation, but with the genes reversed. This operation is biologically as natural as the transposition.

Another line of study is to consider different weights for transpositions and reversals. With equal weights, as done here, the minimum path consists predominantly of transpositions. It would be interesting to use weights suggested by what has been observed in practice. Apparently, transpositions should weigh about twice as much as reversals.

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References

Bafna, V. and Pevzner, P. A. (1996). Genome rearrangements and sorting by reversals. *SIAM Journal on Computing*, 25(2):272–289.

Bafna, V. and Pevzner, P. A. (1998). Sorting by transpositions. *SIAM Journal on Discrete Mathematics*, 11(2):224–240.

Christie, D. A. (1996). Sorting permutations by block-interchanges. *Information Processing Letters*, 60(4):165–169.

Christie, D. A. (1998). *Genome Rearrangement Problems*. PhD thesis, Glasgow University.

Gu, Q.-P., Peng, S., and Sudborough, H. (1996). Approximating algorithms for genome rearrangements. In *Proc. 7th Worshop on Genome Informatics - GIW'96*.

Hannenhalli, S., Chappey, C., Koonin, E. V., and Pevzner, P. (1995). Genome sequence comparison and scenarios for gene rearrangements: A test case. *Genomics*, 30:299–311.

Hannenhalli, S. and Pevzner, P. (1995). Tranforming men into mice (polynomial algorithmic for genomic distance problem). In *Proc. 36th Annual IEEE Symposium on Foundations of Computer Science - FOCS'95*, pages 581–592.

Hannenhalli, S. and Pevzner, P. (1996). To cut... or not to cut (applications of comparative physical maps in molecular evolution). In *6th ACM-SIAM Sumposium on Discrete Algorithms*.

Hannenhalli, S. and Pevzner, P. A. (1999). Transforming cabbage into turnip: Polynomial algorithm for sorting signed permutations by reversals. *Journal of the ACM*, 46(1):1–27.

Meidanis, J. and Setubal, J. C. (1997). *Introduction to Computational Molecular Biology*. PWS Publishing Co.

Meidanis, J., Walter, M., and Dias, Z. (1997a). Distância de reversão de cromossomos circulares com sinais. In *Proc. XXIV Seminário Integrado de Software e Hardware - SEMISH'97*. In Portuguese.

Meidanis, J., Walter, M. E., and Dias, Z. (1997b). Transposition distance between a permutation and its reverse. In Baeza-Yates, R., editor, *Proceedings of the 4th South American Workshop on String Processing (WSP'97)*, pages 70–79, Valparaiso, Chile. Carleton University Press.