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A calculus for rational tangles: applications to DNA recombination

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1. *Introduction*

There exist naturally occurring enzymes (topoisomerases and recombinases), which, in order to mediate the vital life processes of replication, transcription, and recombination, manipulate cellular DNA in topologically interesting and non-trivial ways [**24**, **30**]. These enzyme actions include promoting the coiling up (supercoiling) of DNA molecules, passing one strand of DNA through another via a transient enzyme-bridged break in one of the strands (a move performed by topoisomerase), and breaking a pair of strands and recombining them to different ends (a move performed by recombinase). An interesting development for topology has been the emergence of a new experimental protocol, the topological approach to enzymology [**30**], which directly exploits knot theory in an effort to understand enzyme action. In this protocol, one reacts artificial circular DNA substrate with purified enzyme *in vitro* (in the laboratory); the enzyme acts on the circular DNA, causing changes in both the euclidean geometry (supercoiling) of the molecules and in the topology (knotting and linking) of the molecules. These enzyme-caused changes are experimental observables, using gel electrophoresis to fractionate the reaction products, and *rec A* enhanced electron microscopy [**15**] to visualize directly and to determine unambiguously the DNA knots and links which result as products of an enzyme reaction. This experimental technique calls for the building of knot-theoretic models for enzyme action, in which one wishes mathematically to extract information about enzyme mechanism from the observed changes in the DNA molecules.

This paper deals with the mathematics which arises in a topological model for enzyme mechanism [**25**, **26**, **27**]. The mechanism of many enzymes involves local (near the enzyme) interaction of two DNA strands. The mathematics which can be used to model this 2-strand interaction is that of the 2-string tangle. When bound to a circular DNA molecule, the enzyme naturally separates the DNA molecule into two complementary tangles. Enzyme action on circular DNA can be viewed as tangle surgery, in which the action of the enzyme is to delete one of these tangles, replacing it by another. One regards these tangles as enzyme mechanism variables, and experimental results pose equations relating these variables. One wishes to solve these equations. In general, solving tangle equations is a difficult task. The job is greatly simplified by the realization that most known DNA reaction products lie in a well-understood class, that of 4-plats (2-bridge knots and links) [**7**]. Moreover, a great deal can be said about the factorization of 4-plats into tangle summands. The summands of interest are rational tangles [**8**]. Rational tangles are formed from the trivial tangle by twisting pairs of strands about one another, and look a great deal like DNA electron micrographs, in which pairs of DNA strands wind about each other. In the analysis of certain DNA experiments, one can use recent results on Dehn Surgery on 3-manifolds [**9**] to prove that the solutions to the tangle equations which arise must be rational tangles. Once the solutions are known to be rational tangles, the analysis becomes a matter of calculating the rational solutions, in which the rational tangle calculus is employed.

In Section 2, we describe the rational tangle calculus, and develop methods for solving equations involving rational tangles and 4-plats. In Section 3, we discuss the general problem of proving that solutions to certain tangle equations must be rational tangles. Section 4 discusses site-specific recombination, and Section 5 describes the tangle model for site-specific recombination. Sections 6 and 7 use the tangle model to analyse experimental results for the site-specific recombinant enzymes *Tn*3 resolvase and phage λ integrase.

A more complete account of applications of the rational tangle calculus to molecular biology will appear elsewhere [**27**].

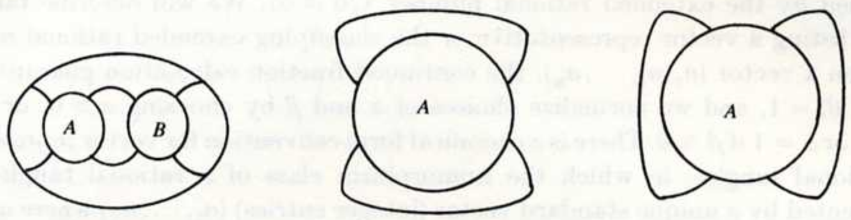
2. *Rational tangle calculus*

The following discussion takes place in the smooth category. Unless otherwise specified, all ambient 3-manifolds will come equipped with an orientation, and 1-submanifolds will be unoriented. All homeomorphisms of ambient spaces will be assumed to be orientation-preserving. A 2-string tangle (or just tangle) is a pair (B, t), where B is a 3-ball and t is a pair of (unoriented) arcs properly embedded in B [**8**, **16**]. We separate tangles into three types [**16**]. A tangle is rational if there exists a homeomorphism of pairs from (B, t) to the trivial tangle $(D^2 \times \mathbf{I}, \{x, y\} \times I)$, where D^2 is the unit 2-ball in $\mathbb{R}^2$ and $\{x, y\}$ are points interior to D^2. A tangle is locally knotted if there exists a local knot in one of the strands; that is, there exists a 2-sphere in B meeting t transversely in 2 points, and such that the 3-ball it bounds in B meets t in a knotted spanning arc. A tangle is prime if it is neither rational nor locally knotted. Since rational and prime tangles contain no local knots, we say that they are locally unknotted. Figure 1 shows tangle diagrams of the three types.

In order to compare tangles, we need to think of them as having 'the same' boundary. As in [**6**], we define the model 2-sphere S^2 in $\mathbb{R}^3$ to be the boundary of the unit 3-ball D^3 in $\mathbb{R}^3$, equipped with 4 distinguished equatorial points $P = \{\text{NE, SE, SW, NW}\}$. We require that every tangle comes equipped with a boundary parametrization, that is, a homeomorphism $\Phi: (\partial B, \partial t) \to (S^2, P)$. So a tangle is a triple $B = (B, t, \Phi)$. Two tangles (B, t, Φ) and (B', t', Φ') are isomorphic if there is a homeomorphism $H: (B, t) \to (B', t')$ such that $\Phi = \Phi' H$ on ∂B. If X and Y are isomorphic tangles, we write $X = Y$. Let p be the projection of D^3 into the equatorial plane, and choose a homeomorphism $\Psi: B \to D^3$ such that Ψ extends Φ and such that the image of the arcs t under $p\Psi$ is a regular projection in the interior of D^2. A tangle diagram is the image of (B, t) under $p\Psi$. Two tangle diagrams represent isomorphic

(a) Locally knotted (b) Prime (c) Rational $(3, 1, 1, -2) = -10/7$

Fig. 1. The three types of tangles.



(a) Addition $(A+B)$ (b) Numerator $N(A)$ (c) Denominator $D(A)$

Fig. 2. Tangle constructions.

tangles if and only if the diagrams are related by a finite sequence of Reidemeister moves in the interior of D^2.

Given two tangles $\{A, B\}$, we define tangle addition as shown in Figure 2 (*a*), and denote the result as $A+B$. Note that $A+B$ may contain a simple closed curve, in which case $A+B$ is not a 2-string tangle. Addition is an associative operation: $A+(B+C) = (A+B)+C$. The numerator and denominator constructions applied to tangle A are shown in Figure 2 (*b*, *c*), and denoted $\{N(A), D(A)\}$. If A and B are tangles, we define $N(A+B)$ and $D(A+B)$ in an analogous manner. If A is a tangle, then each of $\{N(A), D(A)\}$ is either a knot or a link of 2 components. We note that the knot (link) $N(A+B)$ is topologically equivalent to that obtained by glueing A to B along their 'common' boundary (after relabelling the 4 endpoints in ∂B). We say that a tangle A has the parity of (0) if the string which enters at the NW position exits at the NE position. Likewise, A has the parity of (1) if the string which enters at the NW position exits at the SE position, and A has the parity of ∞ if the string which enters at the NW position exits at the SW position. The concept of parity was considered in [3], where it was called string attachment class. Finally, if A denotes the isomorphism class of a tangle, then $(-A)$ denotes the isomorphism class of the mirror image of A, obtained by reversing every crossover in any projection of A.

Rational tangles admit very nice classification scheme (see [**8**, **11**]). They can be represented by rational numbers, by vectors with integer entries, or by 2×2 integer matrices of determinant $+1$.

Rational Tangle Classification Theorem ([**8**]). *There exists a* $1-1$ *correspondence between isomorphism classes of rational tangles and the extended rational numbers* $\beta/\alpha \in \mathbb{Q} \cup \{1/0 = \infty\}$, *where* $\alpha \in N \cup \{0\}$, $\beta \in \mathbb{Z}$, *and* $\gcd(\alpha, \beta) = 1$.

A proof of this Theorem 2·1 can be found in [**19**] or [**7**], p. 196. Every rational number

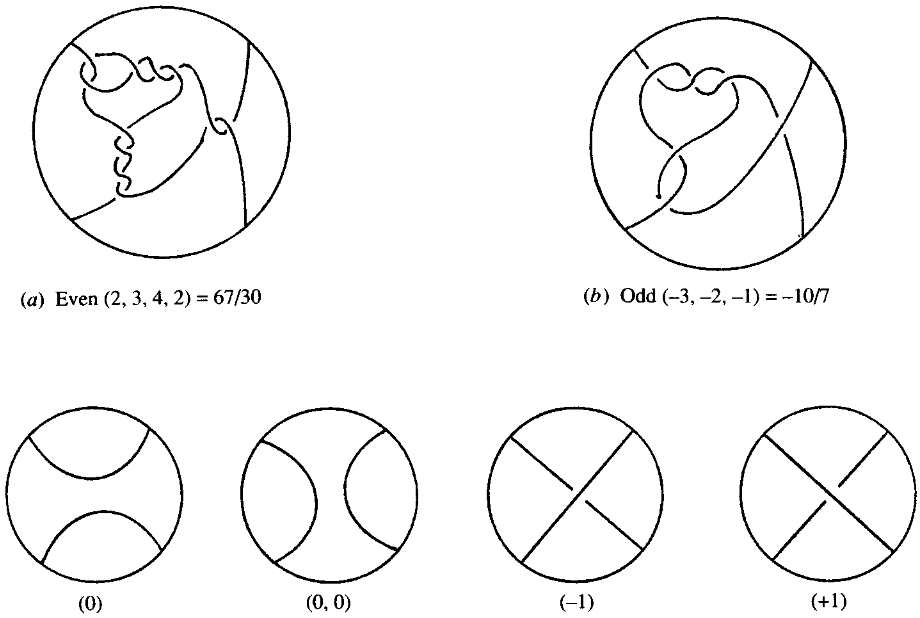
β/α can be expanded by means of a generalized euclidean algorithm (see [7], p. 187) into a continued fraction

$$\beta/\alpha = a_n + 1/(a_{n-1} + (1/a_{n-2} + \ldots)),$$

which yields the integer entry vector $(a_1, a_2, \ldots, a_n)$. By means of the same continued fraction formula, every vector $(a_1, a_2, \ldots, a_n)$ can be converted to an extended rational number. From any integer-entry vector one can construct a tangle diagram as in ([3], figure 3) or ([2], figure 5). Since the continued fraction expansion for β/α is not unique, there are many vectors representing the same tangle isomorphism class. For example, the vectors (0) and (0, 3, 0) represent the tangle classified by the rational number zero, and the vectors (0, 0) and (1, −1, 5) represent the tangle classified by the extended rational number $1/0 = \infty$. We will describe tangles by either listing a vector representative or the classifying extended rational number.

Given a vector $(a_1, a_2, \ldots, a_n)$, the continued fraction calculation guarantees that $\gcd(\alpha, \beta) = 1$, and we normalize choices of α and β by choosing $\alpha > 0$, or $\beta = 1$ if $\alpha = 0$, or $\alpha = 1$ if $\beta = 0$. There is a canonical form convention for vector representation of rational tangles, in which the isomorphism class of a rational tangle can be represented by a unique standard vector (integer entries) $(a_1, \ldots, a_n)$ where $a_i \neq 0$ for $1 \leqslant i \leqslant n-1$, all the non-zero a_i's have the same sign, and $|a_1| > 1$. Depending on the rational number β/α, the standard vector is of even or odd length, and the non-zero entries are either all positive or all negative. Figures 3(*a*) and 3(*b*) show canonical vectors and their diagrams; Figure 3(*b*) is the canonical form for the tangle in Figure 1(*c*). The above convention excludes the four exceptional tangles $\{(0), (\pm 1), (0, 0)\}$ which are shown in Figure 3(*c*). We will call the standard vector for a rational tangle the Conway symbol for the rational tangle, and take the four vectors above as the Conway symbols for the four exceptional tangles.

A 4-plat (2-bridge) knot or 2-component link is one which admits a projection which consists of a braid on four strings, closed up as in Figure 4(*a*). In [1] it is shown that every 4-plat admits a projection consisting of a braid on four strings in which one string is free from crossings, as in Figures 4(*b*, *c*). There are classification schemes for 4-plats analogous to those for rational tangles. Given any integer-entry vector of odd length $\langle d_1, \ldots, d_{2k+1} \rangle$, we can construct a 4-plat as shown in Figure 4. Every 4-plat has a canonical form vector representation by an integer-entry vector $\langle c_1, \ldots, c_{2k+1} \rangle$ where $c_i > 0$ for all i. We call this vector a Conway symbol for the 4-plat. This convention excludes the 4-plat $\langle 0 \rangle$, the unlink of two unknotted components, so we take $\langle 0 \rangle$ as the Conway symbol in this case. Figure 4(*b*) shows a canonical form for the 4-plat knots of Figures 4(*a*, *c*). Two 4-plats represent the same knot (link) type if and only if they admit identical Conway symbols, or their Conway symbols become identical if one of them is reversed. Analogous to the rational tangle case, a classifying rational number for the knot (link) equivalence class of the 4-plat can be obtained from any vector representing the 4-plat via a continued fraction calculation: $\beta/\alpha = 1/(c_1 + (1/c_2 + \ldots))$. If one performs this continued fraction calculation on a Conway symbol for the 4-plat $K (K \neq \langle 0 \rangle, \langle 1 \rangle)$, one obtains $0 < \beta < \alpha$. Unless otherwise specified in the following, we will always choose to compute a classifying rational number for the 4-plat from a Conway symbol, and (following [7]) we write the 4-plat as $b(\alpha, \beta)$. The numbers α and β have a geometric interpretation in terms of a 2-bridge projection of a 4-plat (see [7], p. 183). With the crossover sign



(*a*) Even (2, 3, 4, 2) = 67/30

(*b*) Odd (−3, −2, −1) = −10/7

(*c*) The exeptional tangles

Fig. 3. Canonical forms for rational tangles.

convention of Figure 4 (which agrees with the usual convention for representing generators of the braid group as in [**7**], and is opposite to that of [**8**, **25**]), the 2-fold branched cyclic cover of $b(\alpha, \beta)$ is the lens space $L(\alpha, \beta)$. For example, the unknot $b(1, 1) = \langle 1 \rangle$ has S^3 as 2-fold branched cover, and the unlink of 2 unknotted components $b(0, 1) = \langle 0 \rangle$ has $S^1 \times S^2$ as 2-fold branched cover. 4-plats are classified by means of their 2-fold branched cyclic covers (see [**7**], p. 185):

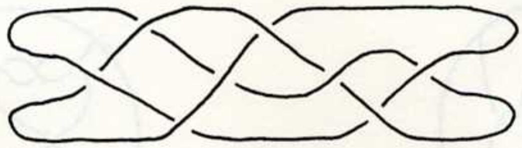
4-Plat Classification Theorem ([**21**]). *Two 4-plats $b(\alpha, \beta)$ and $b(\alpha', \beta')$ are equivalent (as unoriented knots or links) if and only if $\alpha = \alpha'$ and $\beta^{\pm 1} \equiv \beta' \pmod{\alpha}$.*

4-plats and rational tangles are closely related via the numerator and denominator constructions. For example, for any integer x,

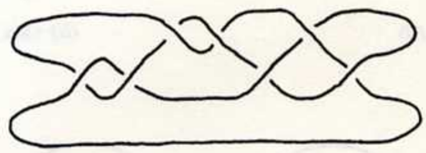
$$D((d_1, \ldots, d_{2k+1}, x)) = \langle d_1, \ldots, d_{2k+1} \rangle \text{ and } N((d_1, \ldots, d_{2k+1}, x, 0)) = \langle -d_1, \ldots, -d_{2k+1} \rangle.$$

Given a rational number β/α with $0 < \beta/\alpha < 1$, the denominator construction applied to the tangle β/α yields the 4-plat $b(\alpha, \beta)$; and the numerator construction applied to the tangle $\beta/\alpha \geqslant 1$ yields the 4-plat $b(\beta, -\alpha)$.

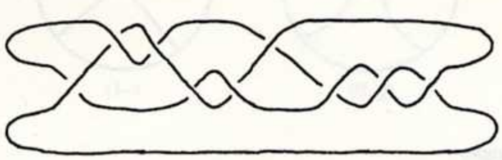
Our first lemma is a calculation (in terms of classifying rational numbers) for the 4-plat which results when the numerator construction is applied to the sum of two rational tangles. A 4-plat is the closure of a braid on 4 strings, in which only the first 3 strings form crossovers. The calculation below is based on the calculation in [**7**], p. 186, in which a 4-plat in S^3 is written in terms of generators $\{\sigma_1, \sigma_2\}$ of the braid group B_3. We write S^3 as two 3-balls $\{B_1, B_2\}$ connected by $S^2 \times I$, and with the braid contained in $S^2 \times I$. Lifting this picture to the 2-fold branched cyclic cover, the 3-balls lift to two solid tori $\{T_1, T_2\}$, connected by $(S^1 \times S^1) \times I$. The braid generators lift to Dehn twists on $S^1 \times S^1$, and in terms of oriented (meridian, longitude) generators for



(a) $b(19,8)$



(b) $\langle 2, 2, 1, 1, 1\rangle = b(19, 8)$



(c) $\langle 1, 2, -2, -1, 3\rangle = b(19, 8)$

Fig. 4. 4-Plats.

$H_1(S^1 \times S^1, \mathbb{Z})$, the Dehn twists are expressed by elementary 2×2 integer matrices. Every tangle β/α admits a (perhaps non-canonical) vector representation of even length $(a_1, \ldots, a_{2k})$. If the tangle is non-exceptional, one such vector representation can be obtained from the Conway symbol by relaxing the requirement that $|a_1| > 1$. We take the following vector representations for the four exceptional tangles: $(0) = (1, -1)$, $\infty = (0, 0)$, $(1) = (1, 0)$, and $(-1) = (-1, 0)$. An even-length vector representative for the tangle β/α determines a 2×2 matrix representative via the following equation:

$$\begin{pmatrix} u & v' \\ v & u' \end{pmatrix} = \begin{pmatrix} 1 & a_{2k} \\ 0 & 1 \end{pmatrix} \begin{pmatrix} 1 & 0 \\ a_{2k-1} & 1 \end{pmatrix} \cdots \begin{pmatrix} 1 & 0 \\ a_1 & 1 \end{pmatrix}. \tag{1}$$

Equation (1) expresses a homeomorphism (determined by the vector representative for the tangle β/α) from the boundary of the 2-fold branched cyclic cover of β/α to the boundary of a reference solid torus. In the above equation, the rational number $u/v = \beta/\alpha$ classifies the tangle, but it may not necessarily be in normal form. Note that $u'/v' = a_n + 1/(1_{n-1} + 1/(\ldots + 1/a_2))$.

Lemma 2·1. *Given two rational tangles $A_1 = \beta_1/\alpha_1$ and $A_2 = \beta_2/\alpha_2$, then $N(A_1 + A_2)$ is a 4-plat which is equal to $b(\alpha, \beta)$, where $\alpha = |\alpha_1 \beta_2 + \alpha_2 \beta_1|$ and β is determined as follows:*

(i) *if $\alpha = 0$ then $\beta = 1$;*

(ii) *if $\alpha = 1$ then $\beta = 1$;*

(iii) *if $\alpha > 1$, then β is uniquely determined by the following: $0 < \beta < \alpha$ and $\beta \equiv \sigma(\alpha_1 \alpha_2' + \beta_1 \beta_2') \pmod{\alpha}$, where $\sigma = \operatorname{sign}(\alpha_1 \beta_2 + \alpha_2 \beta_1)$ and α_2' and β_2' are the entries in the second column of any matrix representative for the tangle β_2/α_2.*

Proof. First we observe that conditions (i)–(iii) above imply that β is uniquely determined. In case (iii), substituting $\beta_2' = (1+\alpha_2\alpha_2')/\beta_2$ into the equation for β, we obtain $\beta \equiv (\sigma\beta_1+\alpha_2'\alpha)/\beta_2 (\mathrm{mod}\,\alpha)$. Since $(\alpha_2, \beta_2) = 1$, all possible values for α_2' are of the form $c+k\beta_2$, with c and k integers, and c a constant. This means that there is exactly one choice for β such that $0 < \beta < \alpha$.

Represent A_1 and A_2 by vectors of even length: $A_1 = (a_1, \ldots, a_{2k})$ and $A_2 = (b_1, \ldots, b_{2r})$. Then $N(A_1+A_2)$ is a 4-plat $b(\alpha, \beta)$, for some values of α and β. This 4-plat has a (possibly non-canonical) representation by one of the vectors $\langle b_1, \ldots, b_{2r-1}, (b_{2r}+a_{2k}), a_{2k-1}, \ldots, a_1\rangle$, or $\langle a_1, \ldots, a_{2k-1}, (a_{2k}+b_{2r}), b_{2r-1}, \ldots, b_1\rangle$, as shown in Figure 5. Figure 5(*a*) shows one of the main steps in this geometric calculation, in which the horizontal twists at the right-hand end of A_2 are converted to horizontal twists at the left-hand end of A_2 in order to facilitate addition. Note that the signs of a_i and b_i may differ, and that $(b_{2r}+a_{2k})$ may be zero. The 2-fold branched cyclic cover of $b(\alpha, \beta)$ is the lens space $L(\alpha, \beta)$, which is obtained by glueing together two solid tori $\{T_1, T_2\}$ by a homeomorphism $f: \partial T_1 \to \partial T_2$, where f is the product of Dehn twists given by a vector representation for the 4-plat. With respect to the (meridian, longitude) basis (μ_i, λ_i) for $H_1(\partial T_i, Z)$, for $i = 1, 2$, values (not necessarily normalized) for α and β are determined by the following matrix representation for f_*:

$$\begin{pmatrix} \beta & \alpha' \\ \alpha & \beta' \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ b_1 & 1 \end{pmatrix} \cdots \begin{pmatrix} 1 & b_{2r} \\ 0 & 1 \end{pmatrix} \begin{pmatrix} 1 & a_{2k} \\ 0 & 1 \end{pmatrix} \cdots \begin{pmatrix} 1 & 0 \\ a_1 & 1 \end{pmatrix}. \tag{2}$$

We have $\beta\beta' - \alpha\alpha' = 1$.

Applying Equation (1) above to the chosen vector representations for β_1/α_1 and β_2/α_2, we obtain

$$\begin{pmatrix} \beta & \alpha' \\ \alpha & \beta' \end{pmatrix} = \begin{pmatrix} \beta_2' & \alpha_2' \\ \alpha_2 & \beta_2 \end{pmatrix} \begin{pmatrix} \beta_1 & \alpha_1' \\ \alpha_1 & \beta_1' \end{pmatrix}. \tag{3}$$

From the matrix product in (3), we have

$$\alpha = \alpha_1\beta_2 + \alpha_2\beta_1, \quad \beta = \alpha_1\alpha_2' + \beta_1\beta_2'.$$

We can now determine normalized values for α and β as follows.

If $\alpha_1\beta_2+\alpha_2\beta_1 > 1$, since $L(\alpha, \beta) = L(\alpha, \beta+k\alpha)$ where $k \in \mathbb{Z}$, we set

$$\alpha = \alpha_1\beta_2+\alpha_2\beta_1 \quad \text{and} \quad \beta \equiv (\alpha_1\alpha_2'+\beta_1\beta_2')(\mathrm{mod}\,\alpha).$$

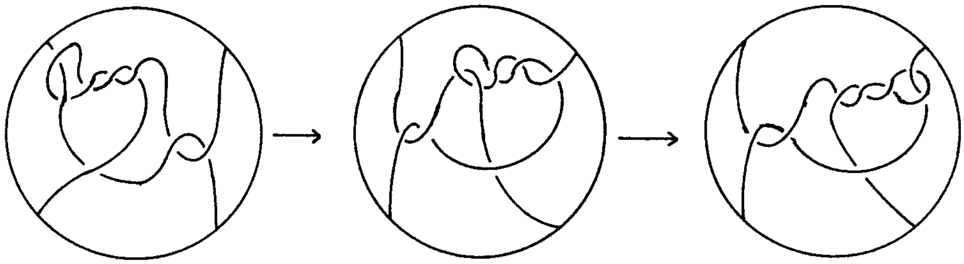
The conditions $0 < \beta < \alpha$, $\beta_2\beta_2' - \alpha_2\alpha_2' = 1$ and $(\alpha_2, \beta_2) = 1$ yield a unique choice for β.

If $-(\alpha_1\beta_2+\alpha_2\beta_1) > 1$, since $L(\alpha, \beta) = L(-\alpha, -\beta+k\alpha)$ where $k \in \mathbb{Z}$, we set

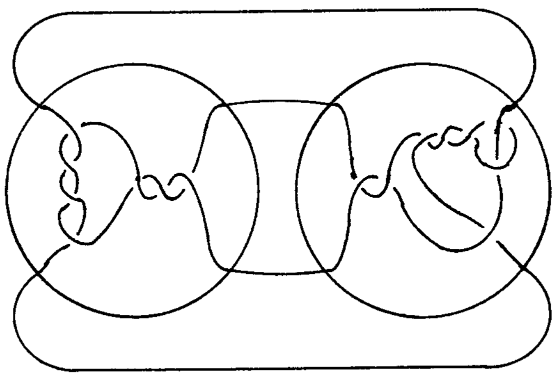
$$\alpha = -(\alpha_1\beta_2+\alpha_2\beta_1) \quad \text{and} \quad \beta \equiv -(\alpha_1\alpha_2'+\beta_1\beta_2)(\mathrm{mod}\,\alpha).$$

If $|\alpha_1\beta_2+\alpha_2\beta_1| = 1$, since $L(\pm 1, \beta) = S^3$, we set $\alpha = 1$ and $\beta = 1$. If $\alpha_1\beta_2 + \alpha_2\beta_1 = 0$, then $N(A_1+A_2)$ is the unlink of two unknotted components, with 2-fold branched cyclic cover $L(0, 1) = S^1 \times S^2$. In this case we set $\alpha = 0$ and $\beta = 1$. ∎

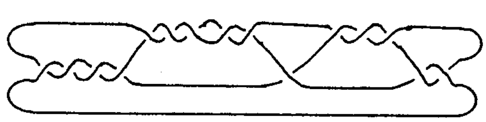
If A and B are tangles, and $N(A+B) = K$ (a knot or 2-component link), then we say that A and B are summands of K. If both A and B are rational tangles, and $N(A+B) = K$, then K is a 4-plat. Suppose, however, that A is a rational tangle, K is a 4-plat, and that we wish to solve the equation $N(X+A) = K$ for the unknown tangle X. Unfortunately, this data does not force X to be a rational tangle. For



(*a*) Isotropy of the tangle (–2, –3, –1, –2) = –25/9



(*b*) N(13/4 + –25/9) = *N*((4, 3) + (–2, –3, –1, –2))



(*c*) ⟨4, 1, –1, –3, –2⟩

Fig. 5. Tangle addition.

example if A is any integral tangle (a horizontal row of half-twists), and K = unknot, the equation $N(X+A)$ = unknot has infinitely many distinct prime tangle solutions of the form $(B+(-A))$, where B denotes any prime tangle with the property that $N(B+(0))$ = unknot. One such prime tangle is shown in Figure 1(*b*). Since B is prime, then $(B+(-A))$ is prime (see [**16**]), and

$$N((B+(-A))+A) = N(B+(0)) = \text{unknot}.$$

Although prime tangle solutions to these equations are in general difficult to enumerate, all rational tangle solutions to equations of this type are given by the following theorem:

THEOREM 2·2. *Let* $A = \beta/\alpha = (a_1, \ldots, a_{2n})$ *be a rational tangle and* $K = \langle c_1, \ldots, c_{2k+1}\rangle \neq \langle 0\rangle$ *be a 4-plat. The rational tangle solutions to the equation* $N(X+A) = K$ *are the following*:

$$X = (c_1, \ldots, c_{2k+1}, r, -a_1, \ldots, -a_{2n}), \quad \text{or} \quad X = (c_{2k+1}, \ldots, c_1, r, -a_1, \ldots, -a_{2n}),$$

with r *any integer. If* $K = \langle 0\rangle$, *then* $X = (-a_1, \ldots, -a_{2n})$ *is the unique solution.*

Proof. It is easily seen (from Lemma 2·1, or by drawing a picture), that for arbitrary r, each of the tangles X described above is a solution to the equation. The negative string of a_i's cancels out the tangle A, leaving

$$D(c_1, \ldots, c_{2k+1}, r) = \langle c_1, \ldots, c_{2k+1} \rangle = \langle c_{2k+1}, \ldots, c_1 \rangle = D(c_{2k+1}, \ldots, c_1, r).$$

We must show that the set of solutions described above is complete. The 4-plat $K = b(p,q)$ is represented by the rational number q/p, where either $0 < q < p$ are coprime integers, or $p = 1, q = 1$, or $p = 0, q = 1$. Suppose that $0 < q < p$. Let q' be the unique integer such that $0 < q' < p$ and $qq' \equiv 1 \pmod p$. Given a Conway symbol for K (either $\langle c_1, \ldots, c_{2k+1} \rangle$ or $\langle c_{2k+1}, \ldots, c_1 \rangle$), the integers $\{p, q, q'\}$ (and matrix representatives for K) are determined by one of the matrix equations below:

$$\begin{pmatrix} q & p' \\ p & q' \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ c_1 & 1 \end{pmatrix} \begin{pmatrix} 1 & c_2 \\ 0 & 1 \end{pmatrix} \cdots \begin{pmatrix} 1 & 0 \\ c_{2k+1} & 1 \end{pmatrix}; \tag{4}$$

$$\begin{pmatrix} q' & p' \\ p & q \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ c_{2k+1} & 1 \end{pmatrix} \begin{pmatrix} 1 & c_{2k-1} \\ 0 & 1 \end{pmatrix} \cdots \begin{pmatrix} 1 & 0 \\ c_1 & 1 \end{pmatrix}. \tag{5}$$

From the above matrix equations, we have $qq' - pp' = 1$. If $K = \langle 0 \rangle$ or $\langle 1 \rangle$, we use Equation (4) to produce a matrix representative. We wish to write down a general expression for the family of all 2×2 matrices which describe glueings which give rise to a lens space orientation-preserving homeomorphic to $L(p,q) = L(p,q')$. The lens space $L(p,q)$ is the result of glueing the solid torus T_1 to the solid torus T_2 by the glueing homeomorphism $f: \partial T_1 \to \partial T_2$. Suppose that the left-hand sides of Equations (4), (5) represent f with respect to a (meridian, longitude) basis for $\{T_1, T_2\}$. Then, all other glueings can be viewed as perturbations on these matrices, the perturbations coming from orientation-preserving change-of-coordinates on each of ∂T_1 and ∂T_2. That is, if $\{r, s\}$ are arbitrary integers, then from the left-hand-side of Equation (4) we obtain a 2-parameter family of glueing matrices:

$$\{G_q(r,s)\} = \epsilon \begin{pmatrix} 1 & r \\ 0 & 1 \end{pmatrix} \begin{pmatrix} q & p' \\ p & q' \end{pmatrix} \begin{pmatrix} 1 & s \\ 0 & 1 \end{pmatrix} \quad (\epsilon = \pm 1). \tag{6}$$

Similarly, using the left-hand side of (5), we obtain a 2-parameter family of glueing matrices:

$$\{G_{q'}(r,s)\} = \epsilon \begin{pmatrix} 1 & r \\ 0 & 1 \end{pmatrix} \begin{pmatrix} q' & p' \\ p & q \end{pmatrix} \begin{pmatrix} 1 & s \\ 0 & 1 \end{pmatrix} \quad (\epsilon = \pm 1). \tag{7}$$

Suppose now that X is a rational tangle such that $N(X+A) = K$. Suppose that tangles A and X admit the following matrix representatives:

$$A: \begin{pmatrix} \beta & \alpha' \\ \alpha & \beta' \end{pmatrix}, \quad \text{and} \quad X: \begin{pmatrix} u & v' \\ v & u' \end{pmatrix}.$$

Since $N(X+A) = K$, a glueing map for $L(p,q)$ is described by the matrix product (as in Equation (3))

$$\begin{pmatrix} \beta' & \alpha' \\ \alpha & \beta \end{pmatrix} \begin{pmatrix} u & v' \\ v & u' \end{pmatrix}.$$

This means that either

$$\begin{pmatrix} u & v' \\ v & u' \end{pmatrix} = \epsilon \begin{pmatrix} \beta & -\alpha' \\ -\alpha & \beta' \end{pmatrix} \begin{pmatrix} 1 & r \\ 0 & 1 \end{pmatrix} \begin{pmatrix} q & p' \\ p & q' \end{pmatrix} \begin{pmatrix} 1 & s \\ 0 & 1 \end{pmatrix} \quad (\epsilon = \pm 1) \tag{8}$$

or

$$\begin{pmatrix} u & v' \\ v & u' \end{pmatrix} = \epsilon \begin{pmatrix} \beta & -\alpha' \\ -\alpha & \beta' \end{pmatrix} \begin{pmatrix} 1 & r \\ 0 & 1 \end{pmatrix} \begin{pmatrix} q' & p' \\ p & q \end{pmatrix} \begin{pmatrix} 1 & s \\ 0 & 1 \end{pmatrix} \quad (\epsilon = \pm 1). \tag{9}$$

By multiplying out the right-hand sides of (8) and (9), we observe that the parameter s is irrelevant in the determination of $\{u, v\}$, so without loss of generality we take $s = 0$. The right-hand side of (8) (with $s = 0$) can be obtained from the vector representation $X = (c_1, \ldots, c_{2k+1}, r, -a_1, \ldots, -a_{2n})$. The right-hand side of (9) (with $s = 0$) can be obtained from the vector representation $X = (c_{2k+1}, \ldots, c_1, r, -a_1, \ldots, -a_{2n})$.

The 4-plat $K = \langle 0 \rangle$ is represented by the identity 2×2 matrix. In this case, Equations (8), (9) specify that $u/v = -\beta/\alpha$, so that $X = (-a_1, \ldots, -a_{2n})$ is the unique solution. ∎

In terms of classifying rational numbers, the rational solutions for X in the above theorem are given by the fractions

$$u/v = (\beta q - \alpha' p + r\beta p)/(\beta' p - \alpha q - r\alpha p)$$

and

$$u/v = (\beta q' - \alpha' p + r\beta p)/(\beta' p - \alpha q' - r\alpha p).$$

Although Theorem 2·2 says that one equation in one unknown has infinitely many rational solutions ($K \neq \langle 0 \rangle$), the next result says that two equations in one unknown have at most two rational solutions.

COROLLARY 2·3. *Let A_1, A_2 be distinct rational tangles, and K_1 and K_2 be 4-plats. There are at most two distinct rational tangle solutions to the equations* (i) $N(X + A_1) = K_1$, (ii) $N(X + A_2) = K_2$.

Proof. Let $X = u/v$, $A_1 = \beta_1/\alpha_1$, $A_2 = \beta_2/\alpha_2$, $K_1 = b(\alpha, \beta)$, and $K_2 = b(\alpha', \beta')$. Then, by Lemma 2·1, we have

$$\alpha = |u\alpha_1 + v\beta_1| \quad \text{and} \quad \alpha' = |u\alpha_2 + v\beta_2|.$$

In the (u, v)-plane, these equations describe two pairs of parallel straight lines. These lines intersect in at most 4 points. Since $u/v = -u/-v$, these 4 points of intersection describe at most two distinct rational tangle solutions for the equations in the hypothesis. ∎

Corollary 2·3 is sharp, as can be seen by taking $A_1 = 1/3$, $A_2 = 5/17$, $K_1 = b(5, 3)$, and $K_2 = b(29, 17)$. The two solutions for X are $X = -70/239$ and $X = -75/254$. It may happen that two equations of the above form have no rational solutions. For example, the pair of equations

$$\{N(X + (0)) = \langle 1 \rangle, \quad N(X + (1)) = \langle 1, 1, 1, 1, 1 \rangle\}$$

has no solutions of any kind (prime, rational, or locally knotted), as will be argued in Section 3.

LEMMA 2·4. *If R is a rational tangle, then $R + R$ is locally unknotted. Moreover, if $R + R$ is rational, then R is an integral tangle. Conversely, if R is not integral and does not have the parity of ∞, then $R + R$ is prime.*

Proof. The tangle $R+R$ ends in a number (possibly zero) of horizontal half-twists. By adding (if necessary) an extra half-twist at the right-hand end of $R+R$, we obtain $(R+R)_1$, which has the property that $N((R+R)_1)$ is a 4-plat link with two unknotted components, so $R+R$ is locally unknotted. If $R+R$ is rational, then $D(R+R)$ is a 4-plat, hence prime (or unknotted, or the unlink of two unknotted components). If R is not an integral tangle (a horizontal row of half-twists), then $D(R+R)$ is composite. ∎

3. *Detecting rationality*

Suppose that A and B are tangles, and that $N(A+B) = K$, where K is a 4-plat. If K is either a 2-component link or the unknot, then both A and B are locally unknotted. If K is a non-trivial knot, in general we cannot conclude that both A and B are locally unknotted. Since 4-plats are prime, at most one of the two tangles can be locally knotted, and if so, the other tangle can be either prime or rational.

LEMMA 3·1 ([**2**, **16**]). *Suppose that A and B are locally unknotted tangles, and that $N(A+B) = K$, where K is a 4-plat. Then at least one of $\{A, B\}$ is a rational tangle.*

Proof. A tangle X is prime if and only if its 2-fold branched cyclic cover X' is irreducible and boundary-irreducible, and rational if and only if its 2-fold branched cyclic cover is a solid torus (see [**16**]). If X is prime, then $\pi_1(\partial X')$ injects into $\pi_1(X')$ under inclusion. If both A and B are prime tangles, then the 2-fold branched cyclic cover of K is $K' = A' \cup B'$, identified along their common incompressible torus boundary. This means that $\pi_1(K') \supseteq \mathbb{Z} \oplus \mathbb{Z}$, which is never the case for the 2-fold branched cyclic cover of a 4-plat. ∎

It turns out that the cyclic surgery theorem [**9**] is very useful in proving that certain tangles which arise in models for DNA enzyme action are rational tangles. The strategy is to use the cyclic surgery theorem to prove that the 2-fold branched cover M of the tangle is a Seifert fibre space (or SFS) [**22**], and then to use facts about the lens space results of Dehn surgeries on M to prove that M must be a solid torus. Let M be a compact, connected, irreducible, orientable 3-manifold with ∂M a torus. The unoriented isotopy class of a non-trivial simple closed curve in ∂M will be called its slope (r). For any slope r, a closed 3-manifold $M(r)$ may be constructed by attaching a solid torus J to M, so that a curve of slope r bounds a disk in J. Given any two slopes $\{r, s\}$, let $\Delta(r, s)$ denote the minimal geometric intersection number for embedded representatives of r and s.

CYCLIC SURGERY THEOREM ([**9**]). *If M is not a Seifert fibre space (SFS), and if $\{r, s\}$ are slopes such that $\pi_1(M(r))$ and $\pi_1(M(s))$ are cyclic groups, then $\Delta(r, s) \leqslant 1$. Hence there are at most three slopes r such that $\pi_1(M(r))$ is cyclic.*

One corollary of the cyclic surgery theorem concerns the case when M is a knot complement. In this case, there is a unique coordinate system on ∂M, namely (meridian, longitude) on the boundary of the tube neighbourhood of the knot. If a slope is represented by (p, q) in this coordinate system, then the slopes on ∂M are parametrized by $p/q \in \mathbb{Q} \cup \{1/0\}$. Moreover M is a SFS if and only if M is the complement of a torus knot.

THEOREM ([9]). (i) *If M is the complement ... Moreover there are ... non-trivial and cyclic only if r is an integer. (ii) If M is the co... then they must be successive.* ... r, and if there are two, then $M(r)$ is not simply connected. Moreover ... *trivial knot and $r \neq \pm 1$, then $M(r)$ is simply-connected.*

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Lemma 3·1. One of the tangles ... the 2-fold branched cyclic covers of K, A, and B, respectively. The lens space K' is equal to $A' \cup B'$, with B' a solid torus. In other words, one obtains a lens space by attaching a solid torus to A'. The cyclic surgery theory says that if A' is not a SFS, then there are very few ways to do this.

LEMMA 3·2. *Suppose that X is a tangle, and that there exist tangles A_i, for $1 \leqslant i \leqslant 3$, with A_2 and A_3 locally unknotted, such that the following 3 equations hold:*

$N(X+A_1) = b(1,1)$ *(the unknot)*;

$N(X+A_2) = b(\alpha,\beta)$ *with* $\alpha > 1$;

$N(X+A_3) = b(\alpha',\beta')$ *with* $\alpha' > 1$.

If $|\alpha-\alpha'| > 1$, then the 2-fold branched cyclic cover X' is a torus knot complement.

Proof. Since $N(X+A_1)$ is the unknot, both X and A_1 are locally unknotted, and one of them must be rational. If X is rational, then X' is a solid torus and the proof is accomplished. Otherwise X is prime, and A_i is rational for $1 \leqslant i \leqslant 3$. The 2-fold branched cyclic cover X' is the bounded complement of a strongly invertible knot in S^3: see [**3**]. If X' is not a SFS, then the Dehn surgeries represented by A_2 and A_3 must be integral. The results of two integral Dehn surgeries along the knot which defines X' yields the Lens spaces $L(\alpha,\beta)$ and $L(\alpha',\beta')$, so the slopes of the surgeries are α and α'. Since the slopes are not successive integers by hypothesis, we conclude that X' is a SFS, and a torus knot complement. ∎

THEOREM 3·3. *Let M be a SFS with $\partial M = S^1 \times S^1$, and bounded orbit surface S. Suppose that there exists a boundary slope r such that $M(r)$ is a lens space. Then S is a disk with at most two exceptional fibres.*

Proof. Let k be the number of exceptional fibres of M, and S be the bounded orbit surface of M. If a curve C of boundary slope r is homologous to a fibre of ∂M, then $M(r)$ is a non-trivial connected sum if either $k > 1$ or S is not a disk. This is a slight generalization of proposition 2 of [**14**] (it includes the case of S non-orientable). Therefore if C is homologous to a fibre, then $k \leqslant 1$ and S is a disk. Otherwise C is not homologous to a fibre, and the Seifert fibration extends over the solid torus J. Let $S(r)$ be the orbit surface of $M(r)$. Then $S(r) = S \cup \text{disk}$. Since $\pi_1(M(r))$ is finite, this means that $S(r)$ is either a projective plane with at most one exceptional fibre, or a sphere with at most 3 exceptional fibres: see [**22**]. Since $\pi_1(M(r))$ is non-abelian if $S(r)$ is a projective plane or a sphere with 3 exceptional fibres, we conclude that $S(r)$ is a sphere with at most 2 exceptional fibres, so S is a disk with at most two exceptional fibres. ∎

The next two lemmas deal with proving that a SFS is actually a solid torus, given information about various lens spaces obtained from it by Dehn surgery. These results will be used in the next sections to analyse the results of some DNA

Theorem ([9]). (i) *If M is the complement of a non-torus knot, then $\pi_1(M(r))$ can be non-trivial and cyclic only if r is an integer. Moreover there are at most two such integers r, and if there are two, then they must be successive.* (ii) *If M is the complement of a non-trivial knot and $r \neq \pm 1$, then $M(r)$ is not simply connected. Moreover at most one of $M(1)$ and $M(-1)$ is simply-connected.*

These cyclic surgery results are useful to us in the situation of the hypothesis of Lemma 3·1. One of the tangles (say B) must be rational. Let K', A', and B' denote the 2-fold branched cyclic covers of K, A, and B, respectively. The lens space K' is equal to $A' \cup B'$, with B' a solid torus. In other words, one obtains a lens space by attaching a solid torus to A'. The cyclic surgery theory says that if A' is not a SFS, then there are very few ways to do this.

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If $|\alpha-\alpha'| > 1$, then the 2-fold branched cyclic cover X' is a torus knot complement.

Proof. Since $N(X+A_1)$ is the unknot, both X and A_1 are locally unknotted, and one of them must be rational. If X is rational, then X' is a solid torus and the proof is accomplished. Otherwise X is prime, and A_i is rational for $1 \leqslant i \leqslant 3$. The 2-fold branched cyclic cover X' is the bounded complement of a strongly invertible knot in S^3: see [3]. If X' is not a SFS, then the Dehn surgeries represented by A_2 and A_3 must be integral. The results of two integral Dehn surgeries along the knot which defines X' yields the Lens spaces $L(\alpha,\beta)$ and $L(\alpha',\beta')$, so the slopes of the surgeries are α and α'. Since the slopes are not successive integers by hypothesis, we conclude that X' is a SFS, and a torus knot complement. ∎

Theorem 3·3. *Let M be a SFS with $\partial M = S^1 \times S^1$, and bounded orbit surface S. Suppose that there exists a boundary slope r such that $M(r)$ is a lens space. Then S is a disk with at most two exceptional fibres.*

Proof. Let k be the number of exceptional fibres of M, and S be the bounded orbit surface of M. If a curve C of boundary slope r is homologous to a fibre of ∂M, then $M(r)$ is a non-trivial connected sum if either $k > 1$ or S is not a disk. This is a slight generalization of proposition 2 of [14] (it includes the case of S non-orientable). Therefore if C is homologous to a fibre, then $k \leqslant 1$ and S is a disk. Otherwise C is not homologous to a fibre, and the Seifert fibration extends over the solid torus J. Let $S(r)$ be the orbit surface of $M(r)$. Then $S(r) = S \cup$ disk. Since $\pi_1(M(r))$ is finite, this means that $S(r)$ is either a projective plane with at most one exceptional fibre, or a sphere with at most 3 exceptional fibres: see [22]. Since $\pi_1(M(r))$ is non-abelian if $S(r)$ is a projective plane or a sphere with 3 exceptional fibres, we conclude that $S(r)$ is a sphere with at most 2 exceptional fibres, so S is a disk with at most two exceptional fibres. ∎

The next two lemmas deal with proving that a SFS is actually a solid torus, given information about various lens spaces obtained from it by Dehn surgery. These results will be used in the next sections to analyse the results of some DNA recombination experiments.

LEMMA 3·4. *Let M be a torus knot complement. Suppose there is a boundary slope r for M such that $M(r)$ is one of $L(2,x)$, $L(3,x)$, $L(4,x)$ for some integer x. Then M is a solid torus.*

Proof. The results of Dehn surgery on torus knot complements are well known: see [**18**]. If one performs p/q surgery along an (r,s) torus knot, then one obtains a lens space if and only if $|rsq+p| = 1$. In this case, $L(|p|, qs^2)$ is the lens space obtained by the Dehn surgery. Now r, s are coprime positive integers, with $0 < s < r$, and a necessary condition for the torus knot to be non-trivial is $s \geqslant 2$, and so $rs \geqslant 6$. The condition $|rsq+p| = 1$ means that $|p| = rs|q| \pm 1$, so $|p| \in \{2,3,4\}$ is impossible if the torus knot is non-trivial. The hypothesis forces the torus knot to be trivial, and so its complement M is a solid torus. ∎

LEMMA 3·5. *Let M be a SFS with $\partial M = S^1 \times S^1$, and with bounded orbit surface S. If there exist boundary slopes r_j for $j = 1,2,3$ such that $M(r_1) = L(p,q_1)$, $M(r_2) = L(p+2,q_2)$, and $M(r_3) = L(p+4,q_3)$ for integers p, q_j, then M is a solid torus.*

Proof. Since at least one Dehn surgery on M produces a lens space, by Theorem 3·3 we know that S is a disk and that M has at most two exceptional fibres. If M has zero or one exceptional fibre, then M is a solid torus. Suppose then that M has two exceptional fibres of orders (α_i, β_i) with $0 < \beta_i < \alpha_i$ for $i = 1,2$, and with $\{\alpha_i, \beta_i\}$ coprime integers. Since no lens space admits a Seifert fibration with three exceptional fibres, the Seifert fibration must extend over the solid torus J which is glued to M to form the spaces $M(r_j), j = 1,2,3$. If we take a basis for ∂M consisting of F (a fibre in the SFS on ∂M) and Q (a curve on ∂M with intersection number $+1$ with F), then the glueing for each of the $M(r_j)$ is such that a meridian of J is homologous to $Q + b_j F$, for some integers b_j. In terms of the Seifert symbols (see [**22**]), we have $M(r_j) = (O, o, 0 \,|\, b_j, (\alpha_1, \beta_1), (\alpha_2, \beta_2))$ for $j = 1,2,3$. We have $|H_1(M(r_j))| = |b_j \alpha_1 \alpha_2 + \alpha_1 \beta_2 + \alpha_2 \beta_1|$. At least two of the b_j (say b' and b'') must have the property that the numbers $(b'\alpha_1\alpha_2 + \alpha_1\beta_2 + \alpha_2\beta_1)$ and $(b''\alpha_1\alpha_2 + \alpha_1\beta_2 + \alpha_2\beta_1)$ have the same sign (or that one of them is zero). Let r' and r'' denote the boundary slopes corresponding to b' and b''. Now $||H_1(M(r'))| - |H_1(M(r))|| = |b' - b''| \alpha_1 \alpha_2 \in \{2,4\}$. Since $\alpha_i \geqslant 2$, the only possibilities (after renumbering if necessary) are $\alpha_1 = 2$, $\alpha_2 = 2$, $\beta_1 = 1$, and $\beta_2 = 1$. However there are no integers $\{x, y\}$ such that $||4x+4| - |4y+4|| = 2$. ∎

The following example shows that Lemma 3·5 is sharp. The values $\alpha_1 = 5$, $\beta_1 = 3$, $\alpha_2 = 3$, $\beta_2 = 1$, $b_1 = -3$, $b_2 = 1$ produce a pair of lens spaces with $|H_1| \in \{29, 31\}$.

In the following we derive necessary algebraic conditions for two equations to have solutions. The next lemma is a generalization of a result of Lickorish [**17**]. Related results also appear in [**5**].

LEMMA 3·6. *Let X be any tangle, T and β/α be rational tangles, and $b(p,q)$ be a 4-plat, such that $N(X+T) = \langle 1 \rangle$ and $N(X+\beta/\alpha) = b(p,q)$.*

(1) *If $T = \infty$ then $L(p,q)$ can be obtained by $(\beta+s\alpha)/\alpha$ surgery along a knot in S^3, where s an integer and $p = \pm(\beta+s\alpha)$.*

(2) *If $T = (0)$ then $L(p,q)$ can be obtained by $(\alpha+s\beta)/\beta$ surgery along a knot in S^3, where s an integer and $p = \pm(\alpha+s\beta)$.*

Proof. The 2-fold branched cyclic cover of $\langle 1 \rangle$ is S^3, the 2-fold branched cyclic cover T' of T is a solid torus, so the 2-fold branched cyclic cover X' of X is a knot complement.

For the moment let us assume $T = \infty$. Then the arcs NW to SW and SW to SE on