Stochastic Cooling and the Accumulation of Antiprotons

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The large project mentioned in the motivation of this year's Nobel award in physics includes, in addition to the experiments proper described by Carlo Rubbia, the complex machinery for colliding high-energy protons and antiprotons (Fig. 1). Protons (p's) are accelerated to a momentum of 26 GeV/c (where GeV is gigaelectron volts and c is the velocity of light) in the Proton Synchrotron (PS) machine and are used to produce antiprotons $(\tilde{p}'s)$ in a copper target. The Antiproton Accumulator (AA) ring accepts a batch of these with momenta around 3.5 GeV/c every 2.4 seconds.

After, typically, a day of accumulation, a large number of the accumulated \tilde{p} 's (~10¹¹) are extracted from the AA, reinjected into the PS, accelerated to 26 GeV/c, and transferred to the large (2.2km diameter) Super Proton Synchrotron (SPS) ring. Just before, 26-GeV/c protons, also from the PS, have been injected in the opposite direction. Protons and antiprotons are then accelerated to high energy (270 or 310 GeV) and remain stored for many hours. They are bunched (in three bunches of about 4 nanoseconds duration each) so that collisions take place at six well-defined points around the SPS ring, at two of which experiments are located.

The process is of a complexity that could only be mastered by the effort and devotion of several hundred people. Only a small part of it can be covered in this lecture, and I will speak about stochastic cooling, a method used to accumulate the antiprotons.

Cooling: Why and How

A central notion in accelerator physics is phase space, well known from other areas of physics. An accelerator or storage ring has an acceptance that is defined in terms of phase volume. The antiproton accumulator must catch many antiprotons coming from the target and therefore has a large acceptance, much larger than that of the SPS ring, where

the p's are finally stored. The phase volume must therefore be reduced and the particle density in phase space increased. On top of this, a large density increase is needed because of the requirement to accumulate many p batches. In fact, the density in six-dimensional phase space is boosted by a factor 10⁹ in the AA machine.

This seems to violate Liouville's theorem that forbids any compression of phase volume by conservative forces, such as the electromagnetic fields that are used by accelerator builders. In fact, all that can be done in treating particle beams is to distort the phase volume without changing the density anywhere.

Fortunately, there is a trick-and it consists of using the fact that particles are points in phase space with empty space in between. We may push each particle toward the center of the distribution, squeezing the empty space outwards. The small-scale density is strictly conserved, but in a macroscopic sense the particle density increases. This process is called cooling because it reduces the movements of the particles with respect to each other.

We can only do this if we have information about the individual particle's position in phase space and if we can direct the pushing action against the individual particles. Without these two prerequisites, there would be no reason why particles rather than empty space would be pushed inwards. A stochastic cooling system therefore consists of a sensor (pick-up), which acquires electrical signals from the particles, and a so-called kicker, which pushes the particles and which is excited by the amplified pick-up signals.

Such a system resembles Maxwell's demon, which is supposed to reduce the entropy of a gas by going through a very similar routine, violating the second law of thermodynamics in the process. It has been shown by Szilard (1) that the measurement performed by the demon implies an entropy increase that compensates any reduction of entropy in the gas.

Moreover, in practical stochastic cooling systems, the kicker action is far from reversible; such systems are therefore even less devilish than the demon itself.

Qualitative Description of Betatron Cooling

The cooling of a single particle circulating in a ring is particularly simple. Figure 2 shows how it is done in the horizontal plane. (Horizontal, vertical, and longitudinal cooling are usually decoupled.)

Under the influence of the focusing fields, the particle executes betatron oscillations around its central orbit. At each passage of the particle a so-called differential pick-up provides a short pulse signal that is proportional to the distance of the particle from the central orbit. This is amplified and applied to the kicker, which will deflect the particle. If the distance between pick-up and kicker contains an odd number of quarter betatron wavelengths and if the gain is chosen correctly, any oscillation will be cancelled. The signal should arrive at the kicker at the same time as the particle; because of delays in the cabling and amplifiers, the signal path must cut off a bend in the particle's trajectory.

In practice, there will not just be one particle, but a very large number (for example, 10^6 or 10^{12}). It is clear that even with the fastest electronics their signals will overlap. Nevertheless, each particle's individual signal will still be there and take care of the cooling. However, we must now reduce the gain of the system, because all the other particles whose signals overlap within one system response time will have a perturbing (heating) effect, as they will in general have a random phase with respect to each other. Fortunately, the perturbing effect is, on average, zero; it is only its second-order term that heats (that is, increases the mean square of the amplitude). This is proportional to the square of the gain, whereas the cooling effecteach particle acting on itself-varies linearly with gain. As illustrated in Fig. 3, we may always choose the gain so that the cooling effect predominates.

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Simplified Analysis of

Transverse Cooling

I shall now analyze the process outlined above, neglecting several effects that will be discussed later. The purpose here is to get some feeling about the possibilities without obscuring the picture with too much detail.

In the first place, we shall assume a system with constant gain over a bandwidth W and zero gain outside this band. A signal passed by such a system may be described completely in terms of 2W samples per unit time. If we have N particles in the ring and their revolution time is T, each sample will, on average, contain

$$N_{\rm S} = N/2WT \tag{1}$$

particles. We may now consider the system from two viewpoints: (i) we may look at each individual particle and combine the cooling by its own signal with the heating by the other particles; and (ii) we may look at the samples as defined above and treat each sample as the single particle of Fig. 1, which is justified because the samples are just resolved by the system.

The two descriptions are equivalent and yield the same result. For the moment, we shall adopt description (ii). Incidentally, the name "stochastic cooling" originated (2) because from this viewpoint we treat a stochastic signal from random samples. However, viewpoint (i) is more fundamental; cooling is not a stochastic process. The pick-up detects the average position of each sample, \bar{x} , and the gain will be adjusted so that this is reduced to zero, so that for each particle x is changed into $x - \bar{x}$. Averaging over many random samples, we see that the mean square, \bar{x}^2 , is changed into

$$\overline{(x-\bar{x})^2} = \overline{x^2} - \bar{x}^2$$

Therefore, the decrement of x^2 per turn is $\bar{x}^2/x^2 = 1/N_s$, and the cooling rate (expressed as the inverse of cooling time) is $1/\tau = 1/N_{\rm S}T$. In fact, we have to divide this by four. One factor of 2 occurs because the betatron oscillation is not always maximum at the pick-up, as shown in Fig. 2. Both at the pick-up and at the kicker we therefore lose by a factor equal to the sine of random phase angle; the average of $\sin^2 is 1/2$. Another factor of 2 is needed because it is usual to define the cooling rate in terms of root mean square (rms) amplitude rather than its square. So we have, by the use of Eq. 1.

$$\frac{1}{\tau} = \frac{1}{4N_{\rm S}T} = \frac{W}{2N} \tag{2}$$

This result, although approximative, shows that stochastic cooling is not a practical technique for proton accelerators; for a typical accelerator, $N \approx 10^{13}$, so that even with a bandwidth of several gigahertz (GHz) the cooling would be much too slow compared to the repetition rate. In storage rings, however, the available time is longer and sometimes the intensity is lower, so that the technique may become useful.

Mixing and Thermal Noise

In deriving the cooling rate, we assumed that all samples have a random population, without a relation between successive turns. The main reason why the sample populations change is the spread in energy between the particles, which results in a revolution frequency spread. The particles overtake each other and, if the spread of revolution time is large compared to the sample duration, we speak of "good mixing"; in this case the derivation above is valid. In practice, it is rarely possible to achieve this ideal situation. In particular, with strongly relativistic particles, a large spread of revolution frequency can only be obtained by a large spread in orbit diameter. For a given aperture, this reduces the momentum spread that is accepted by the machine.

We may see how bad mixing influences the cooling by replacing the correction \bar{x} in the derivation of the cooling rate by a smaller amount $g\bar{x}$. As a result, we find in the same way

$$\frac{1}{\tau} = \frac{W}{2N} (2g - g^2)$$
(3)

Clearly, this is largest for g = 1.

The two terms correspond to the coherent cooling effect (each particle cooled by its own signal) and the incoherent heating effect from the other particles (3). It is the incoherent heating effect that increases with bad mixing, because of the relation between samples at successive turns. It may also increase





if thermal noise is added to the signal (usually orginating in the low-level amplifier attached to the pick-up). Thus, we may define a mixing factor M (with M = 1 for perfect mixing) and a thermal noise factor U (equal to noise divided by signal power) and obtain

$$\frac{1}{\tau} = \frac{W}{2N} \left[2g - g^2 (M + U) \right]$$

By optimizing g (now <1) we find

$$\frac{1}{\tau} = \frac{W}{2N(M+U)} \tag{4}$$

Frequency Domain Analysis

This qualitative analysis may be made much more precise by considering the process from the standpoint of the frequency domain instead of the time domain (4, 5).

Each particle produces in the pick-up (considered to be ideal) a delta-function signal at each passage. For a sum pickup, where the signal is independent of the transverse position, the Fourier transformation into the frequency domain results in a contribution at each harmonic of the revolution frequency (Fig. 4), whereas for a difference pick-up



Fig. 2 (left). Cooling of the horizontal betatron oscillation of a single particle. Fig. 3 (right). Variation with system gain of the coherent cooling and incoherent heating effects.

the modulation by the betatron oscillation splits each line into two components (5). For a collection of many particles with slightly different revolution frequencies, these lines spread out into bands, called Schottky bands because they represent the noise due to the finite number of charge carriers as described by Schottky (6).

The width of these bands increases toward higher frequency. The total power is the same for each band. The power density is therefore lower for the wider bands at high frequency up to the point where they start to overlap. Beyond that point the bands merge and their combined density is constant with frequency. This is illustrated in Fig. 5 for so-called longitudinal lines (from a sum pickup).

The cooling process may now be seen as follows. First, each particle will cool itself with its own (coherent) signal. This means that at the frequency of each of its Schottky lines the phase of the corresponding sine-wave signal must be correct at the kicker so that the kicker will exert its influence in the right direction. Second, the other particles produce an incoherent heating effect at each Schottky line proportional to the power density of the noise around that line (7).



To obtain optimum cooling, one should adjust the gain at each Schottky band to achieve an optimum balance between these two effects. If the bands are separated, the low-frequency ones have a higher density. This requires a lower gain and leads to less cooling for these bands. This is exactly the same effect that we called "bad mixing" in the time domain. At higher frequencies, where the bands overlap, we have good mixing, and the gain should be independent of frequency.

Note that the picture given here (that is, heating only caused by signals near the particle's Schottky frequencies) is completely different from the time-domain picture, where it seemed that particles in the same sample all contribute to the heating, independent of their exact revolution frequency. In fact, the latter is only true if the mixing is perfect and the samples are statistically independent. In the more general case, it turns out that both the optimum gain and the optimum cooling rate per line are inversely proportional to the density dN/dfaround that line, rather than to the total number of particles N. In the timedomain treatment, this was expressed by the mixing factor M, but the dependence of the parameters on frequency was lost.

Yet another mixing effect must be taken into account so far. While moving from the pick-up to the kicker, each sample will already mix to a certain extent with its neighbors. This harmful effect may be described in the frequency domain as a phase lag increasing with frequency (particles with higher revolution frequency arrive too early at the kicker, so that their signal is too late). It appears quite difficult to correct this by means of filters at each Schottky band; on the other hand, in practical cases, the effect is usually not very serious (8).

Another aspect that should be consid-

ered in the correct analysis of a cooling

system is the feedback loop formed by

the cooling chain and the beam response

(Fig. 6). Any signal on the kicker will modulate the beam coherently (in posi-

tion for a transverse kicker, in energy and density for a longitudinal one). The

modulation is smoothed by mixing, but

Beam Feedback



Fig. 4. Schottky signals in the time and frequency domains.

some of it will always remain at the pickup, closing the feedback loop.

The beam response is a well-known effect from the theory of instabilities in accelerator rings. For the purposes of cooling, because the points of excitation and detection are separated in space (5, 9), the treatment is slightly different. This is not the place to discuss the details; it may, however, be said that the response as a function of frequency can be calculated if the particle distribution versus revolution frequency is given as well as some of the ring parameters.

It is found that, for separated Schottky bands with negligible thermal noise, the optimum gain for cooling corresponds to an open-loop gain with an absolute value of unity and that the phase angle of the amplifier chain response must be opposite to the phase of the beam response (8). As a result, in the center of the distribution the optimum loop gain becomes -1 for transverse cooling. The coherent feedback will then halve the amplitude of the Schottky signals as soon as the system is switched on. This is a convenient way of adjusting the gain; the correct phase may be checked by interrupting the loop somewhere and measuring its complete response with a network analyzer (10).

Longitudinal Cooling

So far, I have mainly discussed transverse cooling, that is, reducing the betatron oscillations. Longitudinal cooling reduces the energy spread and increases the longitudinal density. This process, as it turns out, is most important for accumulating antiprotons.

One method of longitudinal cooling [sometimes called "Palmer cooling" (11)] is very similar to the one of Fig. 2. Again, we use a differential pick-up, now placed at a point where the dispersion is high, so that the particle position depends strongly on its momentum. The kicker must now give longitudinal kicks.

A different method is to use a sum pick-up (Fig. 7) and to discriminate between particles of different energy by inserting a filter into the system [the "Thorndahl method" (12)]. This works because the Schottky frequencies of particles with different energy are different; the filter must cause a phase change of 180° in the middle of each band, so that particles from both sides will be pushed toward the center. Such a filter may be made by using transmission lines whose properties vary periodically with frequency. The simple filter shown in Fig. 15 NOVEMBER 1985 8a may serve as an example. The line, shorted at the far end, behaves as a short-circuit at all resonant frequencies, which may be made to coincide with the centers of the Schottky bands. Just above these frequencies the line behaves as an inductance, just below as a capacitance; thus, the phase jump of 180° is achieved (Fig. 8b). For relativistic particles, the length of the line must be equal to half the ring's circumference. More complicated filters, with several lines or active feedback circuits, may sometimes be useful (10).

The advantage of the filter method,

especially for low-intensity beams, is that the attenuation at the central frequencies is now obtained after the preamplifier, instead of before it as with a difference pickup. The signal-to-noise ratio is therefore much better. Also, at frequencies below about 500 megahertz (MHz) where ferrites may be used, sum pickups may be made much shorter than differential ones, so that more may fit into the same space. This again gives a better signal-to-noise ratio. Of course, for filter cooling to be practical, the Schottky bands must be separated (bad mixing).



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Pick-ups and Kickers

Cooling systems often have an octave bandwidth, with the highest frequency equal to twice the lowest one. Pick-ups with a reasonably flat response may consist of coupling loops that are a quarter wavelength long in the middle of the band (Fig. 9a). At the far end, a matching resistor equal to the characteristic impedance prevents reflections (or, seen in the frequency domain, ensures a correct phase relationship between beam and signal). Two loops at either side of the beam may be connected in common or differential mode for use as a sum or differential pick-up. The same structure may function as pick-up or kicker. Sum pick-ups or kickers may also consist of a ferrite frame with one or more coupling loops around it (Fig. 9b).

At high frequencies (typically >1 GHz), slot-type pick-ups or kickers (13) become interesting (Fig. 10). The field from the particles couples to the transmission line behind the slots. If the latter are shorter than $\lambda/2$, the coupling is weak and the contributions from each slot may all be added together, provided the velocity along the line is equal to the particle velocity.

The signal-to-noise ratio at the pickups may be improved by using many of these elements and adding their output power in matched combiner circuits. A further improvement may be obtained by cryogenic cooling of the matching resistors or the preamplifiers.

Using many kickers reduces the total power required. The available power is sometimes a limitation to the cooling rate that may be obtained.

Accumulation of Antiprotons;

Stochastic Stacking

It is now possible to explain how the antiproton accumulator works. Tt should, however, be made clear that stochastic cooling is not the only method available for this purpose. In fact, in 1966, Budker (14) proposed a pp collider scheme where the cooling was to be done by his so-called electron cooling method. A cold electron beam superimposed on the p beam cools it by electromagnetic interaction (scattering). We originally also planned to use this idea; it turns out, however, that it requires particles with low energy to work well with large-emittance beams. An additional ring to decelerate the antiprotons would then have been needed. The simpler stochastic method, using a single ring at fixed field was preferred.



Fig. 10. Slot-type pick-up or kicker. One end of the transmission line is terminated with its own characteristic impedance.

In Fig. 11 we see how the particle density depends on revolution frequency (or energy, or position of the central orbit; the horizontal axis could represent any of these). On the right is the socalled stack, that is, the particles that have already been accumulated. On the left is the low-density beam that is injected every 2.4 seconds. The latter is separated in position from the stack in those regions of the circumference where the dispersion of the lattice is large. In such a place the injection kicker can therefore inject these particles without kicking the stack. Also, the pick-ups and kickers used for the first cooling operation (longitudinal precooling) are placed here so that they do not see the stack. They consist, in fact, of ferrite frames surrounding the injected beam. The pickups are therefore sum pick-ups (200 in total, each 25 mm long in beam direction) and the Thorndahl type of cooling, with a filter, is used (15). The distribution is reduced in width by an order of magnitude within 2 seconds. The number of antiprotons involved is about 7×10^6 ; the band used is 150 to 500 MHz.

After this precooling, one leg of the ferrite frames is moved downwards by a fast actuator mechanism (16) so that the precooled beam can be bunched by radio frequency (RF) and decelerated toward the low-frequency tail of the stack (Fig. 11). The whole process, including the upward movement of the "shutter" to restore the pick-ups and kickers, takes 400 milliseconds. The RF is then slowly reduced (17) so that the particles are debunched and deposited in the stack tail.

They must be removed from this place within the next 2.4 seconds because Liouville's theorem prevents the RF system from depositing the next batch at the same place without simultaneously removing what was there before. A further longitudinal cooling system, which uses the 250 to 500 MHz band, therefore pushes these particles towards higher revolution frequencies, up against the density gradient (18).

This so-called stack tail system should have a gain that depends on energy (or revolution frequency). In fact, the density gradient increases strongly toward the stack core (note the logarithmic scale), and the gain for optimum cooling should vary inversely with this. We achieve this by using as pick-ups small quarter-wave coupling loops, positioned underneath and above the tail region, in such a place that they are sensitive to the extreme tail but much less to the faraway dense core. This results in a bad signal-to-noise ratio for the region nearer to the core. Therefore, two sets of pick-ups are used, each at a different radial position and each with its own preamplifier and gain adjustment. With this setup we obtain fast cooling at the stack edge, where the particles are deposited, and slow cooling at the dense core, where we can afford it because the particles remain there for hours.

A problem is that the tail systems must be quite powerful to remove the particles fast enough. As a result, their kickers will also disturb the slowly cooled stack core (the Schottky signals do not overlap with the core frequencies, but the thermal noise does). The problem exists because the kickers must be at a point where the dispersion is zero to prevent them from exciting horizontal betatron oscillations. They therefore kick all particles (tail or core) equally.

We have found a solution by using transmission-line filters as described above to suppress the core frequencies in the tail cooling systems. These filters also rotate the phase near the core region in an undesirable way; this does not matter, however, because the cooling of the core is done by a third system of larger bandwidth (1 to 2 GHz).

While the particles move towards the core, they are also cooled horizontally and vertically, first by tail cooling systems, then by 1- to 2-GHz core systems. In the general view of Fig. 12, some of the transmission lines that transport the signals from the pick-ups to the kickers may be seen.

When the stack contains a sufficient number of antiprotons (typically 2 \times 10^{11}), a fraction of these (~30 percent) is transferred to the PS and from there to the SPS machine. This is done by bunching a part of the stack, of a width that may be adjusted by properly choosing the RF bucket area (19). These are accelerated until they are on the same orbit where normally particles are injected. They can then be extracted without disturbing the remaining stack. This process is repeated (at present three times); each time, one RF bucket of the SPS is filled. The remaining p's form the beginning of the next stack.

Design of Longitudinal Cooling Systems;

Fokker-Planck Equation

The main difference between transverse and longitudinal cooling systems is that the latter will change the longitudinal distribution on which the incoherent (heating) term depends as well as effects such as the beam feedback. This complicates the theory; still, everything can be calculated if all parameters are given.

It is convenient to define the flux ϕ as the number of particles passing a certain energy (or frequency) value per unit time. It may be shown (5) that

$$\phi = F\Psi - D\partial\Psi/\partial f_0 \tag{5}$$

where Ψ is the density dN/df_0 and F and D are slowly varying constants that depend on various system parameters as well as on the particle distribution. The first term represents the coherent cooling, the second one the incoherent (diffusion) effect that has the effect of pushing the particles down the gradient under the influence of perturbing noise.

By using the continuity equation

$$\partial \Psi / \partial t + \partial \Phi / \partial f_0 = 0$$

to express that no particles are lost, we find the Fokker-Planck-type equation

$$\frac{\partial \Psi}{\partial t} = -\frac{\partial}{\partial f_0} \left(F \Psi \right) + \frac{\partial}{\partial f_0} \left(D \frac{\partial \Psi}{\partial f_0} \right) \quad (6)$$

that allows us to compute the evolution of the density versus revolution frequency f_0 and time, given the initial distribution. The particles deposited at the edge are introduced as a given flux at that point.

The constants F and D depend on many system parameters (pick-up and kicker characteristics, amplifier gain, filter response, beam distribution, and so on). Their value is found through summing the contributions of all Schottky bands. Analytic solutions of Eq. 6 do not exist in practice, and a complicated numerical treatment is indicated.

Such calculations resulted in the design of the antiproton stacking system. At the time this was done, tests in a small experimental ring (ICE) had confirmed the cooling in all planes at time scales of the order of 10 seconds. However, it was not possible to check the stacking system (increasing the density by four orders of magnitude) in any way, and it may be argued that we took a certain risk by starting the project without being able to verify this aspect. Fortunately, everything behaved according to theory and, although the number of p's injected is smaller than was hoped for by a factor of 3.5, the cooling works largely as expected.



Fig. 11. Density distribution as a function of revolution frequency in the AA. On the right is the stack; on the left is the newly injected batch, before and after precooling.



Fig. 12. View of the AA ring before it was covered by concrete slabs. The silvered material around the vacuum tanks is insulation, needed because everything may be heated to 300° C to obtain ultrahigh vacuum. The transmission lines crossing the ring and carrying the cooling signals are also shown.



Fig. 13. The new CERN Antiproton Collector (ACOL) being constructed around the AA. The ACOL ring will increase the stacking rate by an order of magnitude. The stack will still be kept in the AA ring.

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Other Applications of Stochastic

Cooling; Future Developments

At present, stochastic cooling is used at CERN in the AA ring and in the Low Energy Antiproton Ring (LEAR) where the \bar{p} 's may be stored after deceleration in the PS. Before the Intersecting Storage Rings (ISR) were closed down last year, they also used the antiprotons and contained cooling equipment.

In the SPS where the high-energy collisions take place, cooling would be attractive because it would improve the beam lifetime and might decrease its cross section. However, a difficulty is formed by the fact that the beam is bunched in this machine; the bunches are narrow (3 or 4 nanoseconds). In fact, owing to the bunching, each Schottky band is split into narrow, dense satellite bands, and the signals from different bands are related (20). Nevertheless, a scheme is being considered that might improve the lifetime to a certain extent (21).

In the United States, a p accumulator complex similar to the one at CERN and also using stochastic cooling is being constructed (22). This machine is expect-

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ed to have a stacking rate an order of magnitude higher than the one at CERN, because it uses a higher primary energy to produce the antiprotons and higher frequencies to cool them.

In the meantime, we are building a second ring at CERN, surrounding the present accumulator (Fig. 13) with a similar performance. It will have stronger focusing, thereby increasing both transverse acceptances by at least a factor of 2 and increasing the longitudinal one by a factor of 4. The increased focusing strengths will diminish the mixing; consequently, higher frequencies (up to 4 GHz) will be used for cooling. The present AA will be used to contain the stack and its cooling systems will also be upgraded.

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 J. Peoples et al., Design Report, Tevatron I Project (Fermi National Accelerator Labora-
- tory, Batavia, Ill., 1983). The development of the stochastic cooling the ory owes much to H. G. Hereward, D. Möhl, F. Sacherer, and L. Thorndahl. The latter also made important contributions to the construction of most cooling systems at CERN, and it is doubtful if the accumulator would have been feasible without his invention of the filter methfeasible without his invention of the hiter meth-od. It is also a pleasure to acknowledge the invaluable contributions of G. Carron (hard-ware), L. Faltin (slot pick-ups), and C. Taylor (1- to 2-GHz systems). During the construction of the CERN Antiproton Accumulator, R. Bil-linge was joint project leader with me. It is mostly because of his contributions to the design ord his cable monagement that the machine was
- and his able management that the machine was ready in a record time (2 years) and worked so

Control of Directionality in Lambda Site Specific Recombination

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Site-specific recombination of DNA is an integral aspect of a wide range of biological processes such as viral development, transposition, antigen variation, immunoglobulin diversification, and oncogenesis. An important and interesting aspect of these processes is the mechanisms by which physiological factors are incorporated into the regulation of their timing and direction. The lysogenic pathway of bacteriophage lambda affords a tightly regulated recombination system that is particularly amenable to analysis of these questions. We show here that viral integration and excision make asymmetric use of protein binding sites and display marked differences in their dependence on the concentration of the relevant proteins. The two recombinations occur along discrete pathways that are different in several ways, some of which generate a mechanism for growth phase-dependent control of recombination.

During establishment of lysogeny, integrative recombination between a 250base pair (bp) site on the phage chromosome (attP) and a 25-bp site on the bacterial chromosome (attB) yields an

integrated prophage bounded by two prophage att sites, attL and attR (Fig. 1) (1, 2). The apparent reversal of this reaction leads to excision of the prophage by recombination between attL and attR to regenerate attP and attB. The exchange of DNA strands is accomplished by a 7bp staggered cut in each recombining partner within a region that is homologous in all four att sites (3). DNA homology within, but not beyond, the 7-bp overlap region is crucial for recombination, which is thought to proceed through a cruciform (or "Holliday") intermediate via a set of closely coupled strand exchanges (4-7).

Integrative recombination is executed by the phage-encoded protein integrase (Int) along with the bacterially encoded protein IHF (integration host factor). The integrase, Int, can bind sites flanking the overlap region in all four att sites (8). When bound at these "core-type" sites, Int effects strand exchange by nicking and ligating the DNA, one strand at a time (7), in the absence of any added energy source (9). It also binds several sites in the arm regions of attP. Because the consensus sequence for these armtype sites differs from that of the coretype sites, Int is postulated to have two distinct DNA binding domains (10). Al-

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