The Intramolecular Conformation of Adenosine 5'-Monophosphate in Aqueous Solution as Studied by Fast Fourier Transform $^1$H and $^1$H-$^{31}$P Nuclear Magnetic Resonance Spectroscopy*

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**SUMMARY**

Nuclear magnetic resonance spectra of 5'-AMP were examined over a concentration range of 0.001 to 2.2 M in the Fourier mode in the $^1$H and $^1$H-$^{31}$P configuration and were analyzed by computer simulation. The principal conclusions with respect to the solution conformation of 5'-AMP are as follows. (a) The exocyclic C(S')--O(S') and C(4')--C(5') bonds are flexible, and preferentially exist in the gauche-gauche conformation with a "W" relationship across H(4')--C(4')--C(5')--O(S')--P(5') in which the above atoms lie in one plane as in its crystal structure. (b) The ribose moiety exists as a flexible ring system undergoing interconversion between the $^E$ and $^Z$ conformations. The sugar ring conformation is strongly concentration dependent, being 63 ± 10% $^E$ and 37 ± 10% $^Z$ at concentrations below 0.01 M. At higher concentrations, the population of the $^Z$ form increases at the expense of the $^E$ form, and at 2.0 M, $^E$ is the preferred conformation. In the solid state the conformation of the sugar ring is $^Z$ for 5'-AMP.

Nuclear magnetic resonance spectroscopy has been used to study the conformation of 5'-AMP in solution (1-9). These studies have been conducted using continuous wave $^1$H NMR spectroscopy and the conclusions drawn were based on concentration dependence of a few nonexchangeable protons in a narrow concentration range. Further, the complete intramolecular solution conformation of 5'-AMP was not known. The available ability of a large Fourier transform system in our laboratory enabled us to obtain both $^1$H and $^1$H-$^{31}$P magnetic resonance spectra of 5'-AMP, superior to any hitherto reported in the concentration range of 0.001 to 1.0 M. Computer line shape simulations enabled complete analysis of the spectra giving the most precise concentration dependence of the chemical shifts and coupling constants of all the nonexchangeable protons. These data are used to propose the intramolecular conformations of 5'-AMP in aqueous solution.

**EXPERIMENTAL PROCEDURE**

The $^1$H and $^1$H-$^{31}$P NMR spectra were recorded at 100 MHz on a Varian HA100D spectrometer interfaced to a Digilab FTS-3 Fourier transform data system. This system has a total memory of 128K and is capable of performing a maximum of 64K single precision (16 bits per word length) or a 32K double precision (32 bits per word length) transform and possesses an adequate dynamic range.

The frequencies for the proton (observing) channel and fluorine (lock) channel were derived from a Digilab 10-94 frequency synthesizer and a Digilab 400-2 pulser. Hexafluorobenzene in a 1-mm capillary served as an external reference as well as providing the signal for the $^1$H lock. The internal reference was tetramethylammonium chloride. The sample temperature was 30.5°. Those spectra where the phosphorus nuclei were decoupled were recorded with irradiation derived from a Digilab 50-80 PD plug-in amplifier.

Spectra were obtained in the concentration range of 0.001 to 2.2 M for 5'-AMP. Spectra in the range of 0.005 to 1.0 M were analyzed by the computer program LACGON III using a UNIVAC 1108 computer, and line shape simulations were generated using a program developed by Che-Hung Lee of this laboratory. The commercial samples of 5'-AMP were lyophilized two times from 99.8% D$_2$O and the spectra were taken in commercial 100% D$_2$O. The pH reported are pH meter readings from a Fisher Accumet.

A detailed study on 5'-AMP was undertaken because of its ubiquitous nature in biochemistry. Not only is it one of the important building blocks of polynucleotides, it is also part of high energy compounds such as ATP and oxidation reduction enzymes such as NAD, NADH, FAD, and FADH; it even occurs as part of cofactors involved in glycogen synthesis such as adenosine diphosphoglucose. It is our belief that a thorough understanding of the dynamic three-dimensional solution geometry of 5'-AMP will enable one to understand the conformation of similar 5'-nucleotides. This information, in conjunction with the "concept of conformational rigidity" advocated by Sundaramlingam should be of considerable help in unraveling the stereochemical basis of conformational biology.

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The term torsional diastereomer (10) is used to describe the various rotational isomers of a nucleoside or a nucleotide.

The combined contributions from \( g't' \) and \( t'g' \) can be computed from Equation (1).

Fractional population of

\[
g'g' \approx \frac{(24 - \Sigma')}{18} \tag{1}
\]

where \( \Sigma' = J_{VP} + J_{VP} \). Because of the uncertainty in the magnitude of pure \textit{trans} and \textit{gauche} couplings (11-16) there may be an error of at least 10% in the computed populations. Further, it should be pointed out that in deriving Equation 1 it is assumed that energy minima occur with dihedral angles centered near 60, 180, and 300° (Structures I to III), and that the fraction of time spent outside these minima, i.e., during interconversion, is small.

The value of \( \Sigma' \) in Equation 1 can be obtained from the 5' region of the spectrum. However, at concentrations above 0.1 M, an exact value of \( \Sigma' \) cannot be obtained because the 5' region shows unusual broadening at higher concentrations and the derived data cannot be fitted unequivocally by line shape computer simulation. The observed values for \( \Sigma' \) at 0.1, 0.05, and 0.005 M 5'-AMP (pD 8.0) are 9.0, 9.2, and 9.2 Hz, respectively. These values when used with Equation 1 indicate that 5'-AMP, on a time average basis, at biological pH exists predominantly (≈80%) with a \( g'g' \) conformation (Structure I) about the C(5')—O(5') bond with a small contribution (≈20%) from \( g't' \) and \( t'g' \) conformers (Structures II and III). Further, this population distribution appears to be independent of concentration, at least at levels below 0.1 M. At concentrations above 0.1 M, as stated earlier, an unequivocal data fitting is not possible; however, the shape of the 5' region is inconsistent with any predominance of \( t'g' \) and \( g't' \) conformation. At pD 5.4, \( \Sigma' \) is 10.0 Hz. The change in phosphate ionization probably has some effect on the H-C-O-P Karplus relationship, but the observed value of \( \Sigma' \) indicates the population could not have been greatly changed in going to the monoanion.

Torsional Diastereomers Constrained to C(4')—C(5') Bond of 5'-AMP—The minimum energy torsional isomers constrained to the C(4')—C(5') bond of 5'-AMP are shown by Newman projections in Structures I, II, and III. The magnitude of the coupling constant for coupling across \( ^3P \) and the C(5') protons should enable one to distinguish among the above three possibilities. This is because molecules containing the system H-C-O-P have been reported to show an angular dependence of spin-spin coupling similar to that found in H-C-H systems. The \textit{gauche} coupling is in the range of 3 Hz and the \textit{trans} in the range of 21 Hz (11-16). One of the difficulties in determining the conformational preferences of the C(5')—O(5') bond in \( \beta \)-5'-nucleotides is that an unambiguous assignment by NMR of the 2 C(5') protons cannot be made at present and hence one cannot distinguish between the \textit{gauche-trans} (Structure II, \( g't' \)) and \textit{trans-gauche} (Structure III, \( t'g' \)) rotamers. By manipulation of Equations 1 to 3 in Hruska et al. (17) it has been shown (18-20) that the percentage of \textit{gauche-gauche} (Structure I, \( g'g' \)) conformer and the 5'-AMP monoaion.
constrained to C(4')—C(5') is not significantly dependent on concentration, at least below 0.5 m. The observed value for Σ is 6.5 Hz which when used in conjunction with Equation 2 indicates that 5'-AMP, on a time average basis, at biological pH exists predominantly (≥65%) with a gg conformation (Structure IV) about the C(4')—C(5') bond and with a significant contribution (≥25%) from gt and tg conformers. At pD 5.4, Σ is 6.1 Hz indicating phosphate ionization has little if any effect on the population about this bond.

The above discussion does not mean that the conformations about the C(4')—C(5') and C(5')—O(5') bonds are totally independent of concentration; rather, the limited range of concentration in which the proton NMR data can be accurately analyzed does not show any detectable variation which is significant with respect to the errors in the calculations or the measurements.

Evidence for Preferred gg-g'g' (Structures IV and I) Conformation for Exocyclic CH₂OPO₂⁻ Group of 5'-AMP from Four-Bond ¹H-¹H Coupling—One of the important stereochemical consequences of the C(4')—C(5') and C(5')—O(5') bonds being simultaneously oriented gg and g'g' is that the atoms H(4'), C(4'), C(5'), O(5'), and P(5') lie in one plane and the geometric relationship between H(4') and P(5') is an in-plane "W" (Structure VII). Hall and co-workers (12, 13, 22) have shown that in phosphate esters such an in-plane "W" relationship will generate a maximum J₁H-¹P of 2.7 Hz and this value reduces to zero when the planarity is destroyed. We have observed a J₁H₁P of magnitude greater than 1 Hz in pyridine nucleotides (23-25) in 5'-UMP (17, 19) and in several mononucleotide components of DNA and RNA (19) and in such bio logically important cofactors as adenosine diphosphoglycine, uridine diphosphoglycine, and α-glucose 1-phosphate (26). We have argued, based on our treatment of Σ and Σ', that the observed J₁H₁P in these compounds reflects the preference of the C(4')—C(5') and C(5')—O(5') bonds to orient gg and g'g', respectively. We substantiated this contention by showing that in such conformationally aberrant nucleotides as 6-aza-5'-UMP (18, 20) in which the C(4')—C(5') predominantly exists in gt-tg conformations, the J₁H₁P is zero. A discussion on the J₁H₁P is published elsewhere (27).

Based on all of the above observations, we feel confident in presenting the observed J₁H₁P in 5'-AMP (1.4 to 1.7 Hz in the concentration range 0.1 to 0.005 m at pH 8, and 2.1 for 0.01 m at pH 5) as an important and additional piece of data to support contention that the C(4')—C(5') and C(5')—O(5') bonds of 5'-AMP exist preferentially, but clearly not completely, in gg and g'g' conformations, respectively. The small differences in J₁H₁P between pH 8 and 5 may be caused by the change in phosphate ionization.

Conformation of β-Ribose Ring—Among all the fragments of nucleosides and nucleotides the solution conformation of the β-ribofuranose system has probably received the maximum attention and controversy from NMR spectroscopists. Sarma and Mynott (23, 28) have reviewed the status on this subject and have suggested that, in a qualitative sense, perhaps it is best to treat the ribose ring coupling constant data just in terms of two modes, viz. C(3') endo (4E) and C(2') endo (2E) undergoing interconversion via pseudorotation (Fig. 1). For 5'-AMP, the parameters J₁V₁, J₂V₂, and J₃V₃ have been extracted by computer simulation (±0.1 Hz) at the following concentrations: 1.0, 0.5, 0.1, 0.05, and 0.005 m. The data are plotted as a function of concentration in Fig. 2. A remarkable feature observed is that as J₁V₁ increases with dilution, the value of J₂V₂ correspondingly decreases, with J₃V₃ and the sum J₁V₁ + J₂V₂ remaining essentially constant. Earlier work on 5'-AMP (6, 7, 29) has shown that J₁V₁ is concentration dependent. No concentration dependence of J₂V₂ or concentration independence of J₁V₁ + J₂V₂ and J₃V₃ has been demonstrated before. In Fig. 3 we illustrate the ¹H-¹P spectra of 0.5 and 0.005 m 5'-AMP along with computer simulations. Ionization of the phosphate had no detectable effect on the ring coupling constants. Qualitatively speaking, the data are consistent with the existence of ¹E and ³E (Fig. 1) conformations in equilibrium (23, 28) and, at concentration levels higher than about 0.01 m, increases in 5'-AMP concentration cause a depopulation of ³E and an increase in ¹E conformation.

One may attempt to describe the sugar puckering in quantitative terms using the concept of pseudorotation (30-37). Altona and Sundaralingam (36, 37) argue that accurate quantitative information about the conformational dynamics of the ribose ring...
where $P$ and $r_m$ represent the phase angle of pseudorotation and the amplitude of pucker and the letters $N$ and $S$ stand for the two types of pucker. This approach, which *prima facie* sounds precise, has a number of pitfalls.

1. Granted, exact quantitative relationships exist among endo-
cyclic torsion angles, $P$ and $r_m$, for the pseudorotational
behavior of cyclopentane, and all endocyclic torsion angles
which occur in the entire pseudorotational pathway can be exactly
obtained by maintaining a constant $r_m$ while varying $P$. How-
ever, there is no evidence that the same quantitative rela-
tionships will exactly hold true for the projected pseudorotational
interconversion of an asymmetrically substituted ribose of a
nucleoside or nucleotide; there is likely only a qualitative re-
semblance.

2. The pseudorotational treatment (36, 37) relies on the basic
Karplus equation ($J_{HH} = A \cos \phi - B \cos \phi + C$) to dis-
tinguish accurately between small changes in dihedral angles;
we have reported earlier that an adjusted, more complex form of
the equation is required to obtain the conformational dynamics
of the ribose ring (23).

3. Any attempt to utilize the Karplus equation to extract
precise quantitative information on conformational equilibria
will be fruitless unless the values of the constants $A$, $B$, and $C$
are precisely determined for the system. The Altona-Sundara-
ingam method of obtaining the above constants has serious de-
faults. Using crystalline data for a large number of nucleosides
and nucleotides, the authors determined average torsion angles
between carbon, oxygen, and nitrogen atoms (hydrogen atoms
cannot be located accurately) for both $N$ and $S$ conformations,
and then assumed that in the Newman projection the carbon-
hydrogen vectors are centered in the middle. An error of only
$2.5^\circ$ between two such vectors may produce an error up to $5^\circ$
in the corresponding hydrogen-hydrogen vectors $\phi$. These solid
state angles ($\phi$ values) were then assumed to be equal to the
average solution $\phi$ angles of a collection of nucleosides and nu-
cleotides, and from the average coupling constants Altona and
Sundaralingam derived $A$ and $B$ values of 10.5 and 1.2, re-
spectively. They further assumed that the value of $C$ is zero. Using
this procedure (36, 37), we have altered several of the six $\phi$
values of interest in Refs. 36 and 37 by $5^\circ$ and calculated different values of $A$ and $B$ pairs, e.g. 10.7 and 3.6, and 10.2 and 1.43.

4. Even if all of the above objections were not taken into
account, the conservatively estimated experimental error of
$\pm 0.1$ Hz in coupling constants for the computer-simulated spec-
trum (Fig. 3) greatly affects the predicted pseudorotational
parameters (36, 37). An error of $\pm 0.1$ Hz means an uncer-
tainty of 0.4 Hz in the sum $J_{TV} + J_{TV'}$, and 0.2 Hz in $J_{TV'}$,
when included in the pseudorotational calculations (36, 37), typi-
cally produces an uncertainty of $\pm 2^\circ$ in $r_m$ and $\pm 7^\circ$ in $P$. Con-
sequently, if the pseudorotational computations yielded a value
of $P$ of say $18^\circ$, it would not mean that the conformation of the sugar
must be $E$, but rather it may be $T_3$, $E$, or $T_4$ (see Fig. 4 of
Ref. 36). Further, the calculated $r_m$ values for the $N$ and $S$
conformations typically differ by $3^\circ$, yet for a cyclopentane pseu-
dorotational scheme, they should be the same. Here having only three couplings to solve five unknowns is a problem (36).

We have used our data for 5'-AMP to calculate its solution pseudorotational parameters. For the S conformation of 5'-AMP, the resulting mean amplitude of pucker $r_m$ is $35^\circ$ and the phase angle $P_s$ is $175^\circ$. For $N$, $r_m$ is $35^\circ$ and $P_s$ is $5^\circ$. Taking the above uncertainty into account, it would mean that 5'-AMP may exist as $3T'$, $3^2T'$, or $3^2T_2$ conformations on the S side and as $3^1T$, $3^2T'$, or $3^2T_2$ conformations on the N side, i.e. on the N side the atoms C(2') and C(3') may be symmetrically puckered or they may be unsymmetrically puckered with either C(2') or C(3') undergoing major puckering. It is obvious that the pseudorotational treatment (36, 37) does not enable one to pinpoint the exact conformational status of a sugar ring.

5. In the pseudorotational treatment (36, 37) one must assume $J_{a'b'}$ of $N$ and $S$ conformations to be equal; experimentally a spread of 1 Hz in $J_{a'b'}$ values is observed upon inspection of data from several nucleosides and nucleotides. It is possible that this approximation (36, 37) may be valid. However, we caution, if a difference of about 1 Hz exists in the value of $J_{a'b'}$ between pure N and pure S conformations, this alone causes uncertainty of about $6^\circ$ in $r_m$ and $10^\circ$ in $P$.

It is clear from the above discussion that there is inaccuracy and uncertainty in the pseudorotational treatment of coupling constants. The pseudorotational approach of Altona and Sundaralingam enabes one to compute the population of the percentages of $N$ and $S$ conformations from the experimental coupling constants because such a treatment yields the magnitude of the various coupling constants in the pure $N$ and $S$ conformations. It is necessary to incorporate an uncertainty of 1 Hz in these calculations which in turn generates an error of about $10^\circ$ in the computed populations. For example, 5'-AMP data so treated indicate that at all concentrations below 0.01 M, the ribose ring conformation exists $63 \pm 10^\circ$ $E(S)$, the remainder being $E(N)$. As the concentration increases, the fraction of $E(S)$ decreases and $E(N)$ correspondingly increases. At high concentrations, i.e. 2.0 M, an estimated value of $J_{a'b'}$ of less than 4 Hz indicates the ribose ring is greater than 50%; $E(N)$ conformation. The computed $E$ population of 5'-AMP at concentrations below 0.1 M, using the simple Karplus equation as employed by Schleich et al. (39), Hruska et al. (40), and Smith and Jardetzky (41) vary from 63 to 73%.

In concluding we wish to point out that the description of the sugar puckering in terms of the precise values of $P$ and $r_m$ as an entity in the pseudorotational itinerary is very articulate and elegant with respect to the solid state data and most certainly an improvement over the traditional description of sugar pucker. To exclude the Karplus approach in describing the ribose ring conformation in solution. Finally, we wish to restate that in solution the ribofuranose system exists as an envelope of continuously changing conformations. For the sake of simplicity in description it may be treated as a two-state $E \leftrightarrow S$ equilibrium. See Ref. 42 for a discussion of sugar-base torsion.

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