graphically. Electrical stimulation was administered through another suction electrode. Although McFarlane (*6*) described a number of conducting systems for anemones, in our study only the nerve net pulses (NNP's) and the potentials of the retractor muscle were examined (*7*).

Preliminary studies of anemones in aerobic conditions revealed NNP's of 10 μV or less (Fig. 1A). Threshold was 5 to 7 V when a 1-msec stimulus was given. Anemones that had been kept in sealed anaerobic chambers for 1 week were placed in recording chambers with nitrogen bubbling through the seawater; as before, the oxygen levels were less than 0.1 ppm. The contracted posture of the animals made it difficult to attach the suction electrodes; however, one or two tentacles were usually exposed.

The NNP's recorded from the anoxic anemones were identical in configuration and threshold to NNP's seen in anemones in aerobic conditions (Fig. 1C). Also, two shocks 0.5 second apart induced the muscle potential that is usually associated with the second stimulus (Fig. 1, B and D). Thus the neuromuscular system does not fatigue any more rapidly in anaerobic conditions.

It is generally accepted that nerve cells require oxygen to function. The sodium ion pump requires adenosine triphosphate (ATP) generated by the electron transport system. One well-known exception is found in the sea turtle. The central nervous system of this animal functions anaerobically for hours during dives (*8*). Glycolysis is thought to generate sufficient ATP for the turtle to survive. To my knowledge, the anaerobic function of the nervous system of a facultative anaerobic invertebrate has not been reported until now. The *B. cavernata* nerve net and retractor muscle function normally in the absence of oxygen or in the presence of the cytochrome inhibitor KCN. There is sufficient ATP stored or, more likely, produced by anaerobic metabolic pathways for an anemone to execute a protective withdrawal response in anaerobic conditions. Invertebrates that survive anoxic environments maintain important behavioral and physiological functions despite lower production of ATP.

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Antibody to Spermine: A Natural Biological Constituent

Abstract. *A protein that binds spermine specifically was separated from normal rabbit serum by affinity chromatography. Immunoelectrophoresis, the Ouchterlony immunodiffusion test, and gradient gel electrophoresis indicated that this protein has immunoglobulin characteristics and consists of several populations of antibodies to spermine. These were sequentially released from Sepharose-spermine gel by stepwise elution with solutions ranging in* pH *from 4 to 1. The binding constants varied from* 5.0×10^8 *to* 11.1×10^8 *liters per mole. These globulins did not react with monoacetylputrescine,* L*-ornithine,* L*-lysine, and histamine. Negligible cross-reactivity was detected with spermidine, putrescine,* N^8*-monoacetylspermidine, cadaverine, and diaminopropane. Since perturbations in polyamine metabolism have been identified in several diseases, the study of extracellular polyamine homeostasis may reveal an important regulatory function for this protein.*

Intracellular aliphatic polyamines and diamines in micromolar quantities facilitate tissue growth, hypertrophy, and regeneration (*1–5*). By contrast, no more than picomolar levels of extracellular polyamines (free, acetylated, and bound) are observed normally (*6–10*). In a number of systems, extracellular free polyamines may promote or inhibit cell growth depending on their concentration (*11–15*). Body polyamine homeostasis may be seriously disturbed under conditions of uncontrolled production, tissue damage, or renal retention (*16–18*). These organic cations may bind nonspecifically or specifically to cell membrane components (*19, 20*). Similar intracellular interactions have been described for proteins, nucleic acids, and cell organelles (*21–23*).

During the purification of induced rabbit antibodies to spermine with affinity chromatography (*24*), we noted that control rabbit serum treated in the same way as serum from immunized animals contained a protein fraction with strong binding affinity for spermine. As a consequence, we completed the separation and characterization of this active

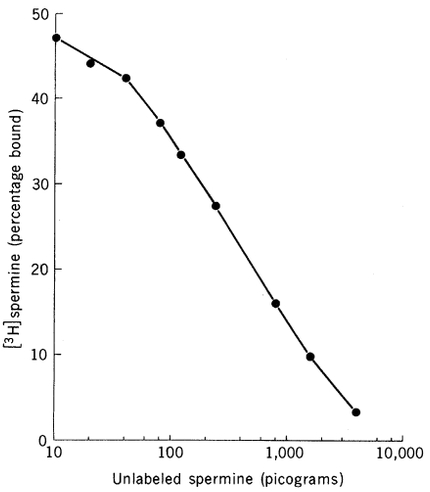

Fig. 1. Inhibition curve for isolated antispermine antibody (pool 4). Thirty thousand DPM of [^{3}H]spermine was used per assay test tube (incubation volume, 1 ml). Binding at 0 pg of unlabeled spermine was 48 percent; at 10 pg, 47.2 percent. Charcoal dextran solution (0.1 ml per assay test tube) (*38*) was used for separating bound and free spermine. After being mixed and incubated at 4°C for 20 minutes, the charcoal was centrifuged at 3000 rev/min for 25 minutes in radioimmunoassay test-tube carriers in a Beckman J-6B refrigerated centrifuge; the supernatant fraction, containing bound ligand, was then counted.

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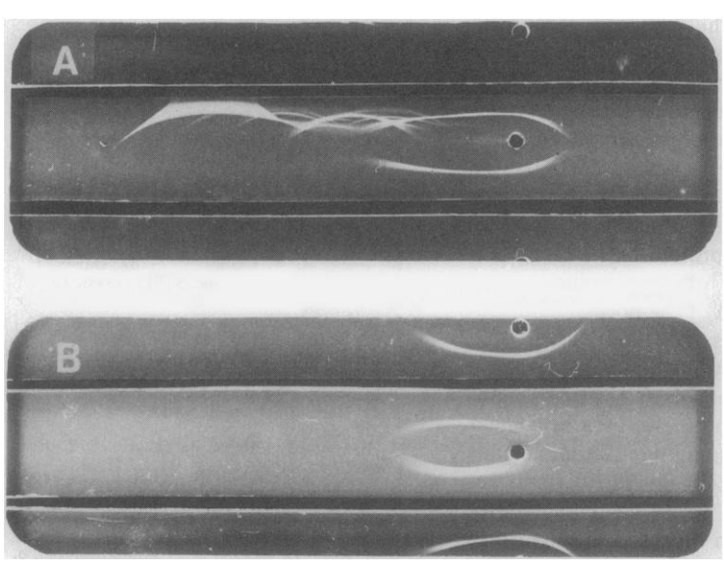
fraction from larger volumes of normal rabbit serum. In this study, we report the detection, separation, and characterization of a natural antispermine immunoglobulin (Ig) in normal rabbit serum.

Protein A-Sepharose CL-4B (3.0 g; Pharmacia), which selectively reacts with the Fc part of IgG, was used for separating IgG from four 10-ml portions of pooled normal rabbit serum. Eluted IgG (for its purity, see legend to Fig. 2, B and C) was immediately dialyzed against distilled water, pooled, and lyophilized. It was then dissolved in 10 ml of 0.01*M* borate buffer (*p*H 8.0) containing 0.14*M* NaCl and 0.02 percent sodium azide, centrifuged, and applied on spermine-Sepharose gel in a 15-ml polystyrene Sarstedt column (*24*).

Two grams of dry activated CH-Sepharose 4B (Pharmacia) was used to prepare the spermine-Sepharose complex (*24*). With purified [^{3}H]spermine as the tracer, we found that 3.4 μmole of spermine was bound per milliliter of gel. After application of a 10-ml solution of IgG on the spermine-Sepharose column, unreacted proteins were washed out with an excess of the borate buffer. Antispermine IgG was eluted with solutions of different *p*H (3.8 to 1.0), and 1-ml fractions were collected into test tubes containing neutralizing buffers (*24*). Protein content was monitored by ultraviolet spectrophotometer. Four distinct protein peaks were obtained and identified as pools 1, 2, 3, and 4. All were dialyzed against distilled water for 48 hours at 4°C, lyophilized, dissolved in 5 ml of distilled water, centrifuged to eliminate denatured protein, and stored frozen in 0.5-ml portions. Each IgG pool was tested for (i) [^{3}H]spermine binding in serial dilutions (titer determination); (ii) displacement of [^{3}H]spermine by unlabeled spermine (inhibition curve); and (iii) cross-reactivity with other polyamines, diamines, and compounds of similar structure (*24*, *25*). In all these tests, 0.1*M* borate buffer (*p*H 8.0) containing 20 mg of KCl, 20 mg of $CaCl_2$, and 21 mg of $MgCl_2 \cdot 6H_2O$ per liter was used as incubation medium (total incubation volume, 1.0 ml). A [^{3}H]spermine solution (in distilled water) containing 30,000 disintegrations per minute (DPM) per 0.1 ml was prepared fresh daily from highly purified stock solution (specific activity, 56 Ci/mmole; New England Nuclear) (*26*, *27*). Bound and free spermine were separated by adding 0.1 ml to each assay test

Table 1. Percentage of cross-reactivity of polyamines and other compounds of similar structure with antispermine IgG from normal rabbit serum, eluted in fraction pools 1, 2, 3, and 4.

Compound	Cross-reactivity (%)			
	Pool 1	Pool 2	Pool 3	Pool 4
Spermine	100	100	100	100
Spermidine	1.7	1.9	1.7	1.5
Putrescine	0.002	0.05	0.03	0.08
N^8-acetylspermidine	0.13	0.16	0.13	0.17
Monoacetylputrescine	0	0	0	0
Cadaverine	0	<0.001	0.001	0.003
Diaminopropane	0.01	0.02	0.03	0.04
L-lysine	0	0	0	0
L-ornithine	0	0	0	0
Histamine	0	0	0	0



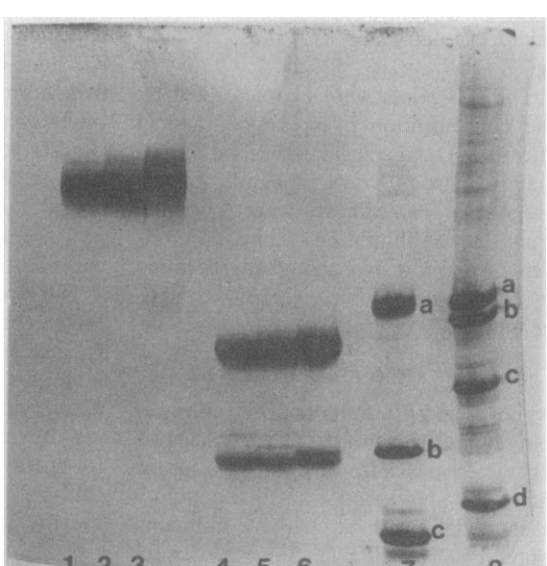


Fig. 2 (left). (A) Immunoelectrophoresis on 2 percent agar gel (*29*). Whole rabbit serum was used in the middle well; goat antiserum to whole rabbit serum, in the upper trough; and goat antiserum to rabbit IgG, in the lower trough. (B) Upper and lower wells show migration of rabbit IgG after passage through Protein A-Sepharose column; middle well shows rabbit IgG separated by Protein A-Sepharose after affinity chromatography on spermine-Sepharose column (antispermine IgG pool concentrated by lyophilization). Goat antiserum to whole rabbit serum was used in the upper trough; goat antiserum to rabbit IgG, in the lower trough. Fig. 3 (right). Gel electrophoresis on Pharmacia PAA 4/*30* gradient gel in 0.04*M* tris (*p*H 7.4) with 0.02*M* sodium acetate, 2 m*M* EDTA, and 0.2 percent sodium dodecyl sulfate. Sample buffer was 0.01*M* tris-HCl (*p*H 8.0) with 0.001*M* EDTA, 1 percent sodium dodecyl sulfate, and with or without 1 percent β-mercaptoethanol. Electrophoresis was performed at 150 V for 4 hours at 18°C. Samples treated with sample buffer containing β-mercaptoethanol were boiled for 5 minutes at 100°C. Samples: *1*, rabbit IgG standard; *2*, rabbit IgG separated by Protein A-Sepharose before affinity chromatography; *3*, rabbit IgG after passage through spermine-Sepharose column (antispermine IgG pool concentrated by lyophilization); *4*, rabbit IgG standard treated with β-mercaptoethanol; *5*, rabbit IgG separated by Protein A-Sepharose treated with β-mercaptoethanol; *6*, rabbit IgG after passage through spermine-Sepharose column (antispermine IgG pool concentrated by lyophilization) treated with β-mercaptoethanol; *7*, standard mixture containing (*a*) bovine serum albumin [molecular weight (MW) 67,000], (*b*) α-chymotrypsinogen (MW 25,000), and (*c*) lactalbumin (MW 14,400), and treated with β-mercaptoethanol; and *8*, standard mixture (Pharmacia) containing thyroglobulin, ferritin, albumin, catalase, and lactate dehydrogenase, and treated with β-mercaptoethanol. Standard mixture shows bands for (*a*) bovine serum albumin and subunit bands for (*b*) catalase (MW 60,000), (*c*) lactate dehydrogenase (MW 36,000), and (*d*) ferritin (MW 18,500).

Table 2. Affinity constant (K_a), concentration of binding sites [AB_0], and heterogeneity index (α) for the four protein pools. Total volume of each pool was 5 ml, which represented 40 ml of original normal rabbit serum. The error is expressed as ± 1 standard deviation.

Pool	Dilution	K_a (liter/mole × 10^8)	[AB_0] (mole/liter × 10^{-9})	α
1	1 : 10	5.0 ± 0.3	2.9 ± 0.1	0.92
2	1 : 7.5	6.5 ± 0.3	2.0 ± 0.05	0.95
3	1 : 7.5	7.8 ± 0.5	2.3 ± 0.1	1.00
4	1 : 10	11.1 ± 0.5	0.8 ± 0.05	1.00

tube of charcoal dextran solution, which is used routinely in radioimmunoassay procedures. Dilutions of separated IgG that bound 30 to 50 percent of [^{3}H]spermine were used in further tests (inhibition curve and cross-reactivity). Figure 1 is a representative inhibition curve showing the competition of labeled and unlabeled spermine for binding sites of isolated IgG.

The separated IgG pools were highly selective (see Table 1). They reacted specifically with spermine. The average cross-reactions with other substances of similar structure were as follows: spermidine, 1.7 percent; putrescine, 0.04 percent; N^8-monoacetylspermidine, 0.15 percent; cadaverine, 0.003 percent; and diaminopropane, 0.02 percent. The other compounds tested (monoacetylputrescine, histamine, L-lysine, and L-ornithine) did not react with these isolated IgG's at all.

The IgG pools were characterized by the concentration of spermine binding sites [AB_0], the spermine-antibody association constant K_a, and the index of heterogeneity (α). These were obtained from data on inhibition of binding of labeled spermine by unlabeled spermine by using the Sips model (*28, 29*) for antigen-antibody interaction:

$$B/F^{\alpha} = K_a{}^{\alpha}([AB_0] - B)$$

where B and F are the concentrations of bound and free antigen. The association characteristics were determined from the fit of the above equation to the experimental data with an Olivetti minicomputer P6060 (Table 2). Since $\alpha = 1$ for pools 3 and 4, we assume that these contained homogeneous antibody. Although the association constant varied slightly among the pools, the last fraction had the highest value.

The presence of spermine-binding IgG in the protein pools was also confirmed by immunoelectrophoresis (*30*). Clear single bands of IgG were found in a mixture of all four pools by using goat antiserum to "whole rabbit serum" and to rabbit IgG (Fig. 2, A and B). The Ouchterlony test showed a line of identity when we compared purified antispermine Ig with pure rabbit IgG standard (*31*). Gel electrophoresis of separated antispermine Ig showed migration identical to that of standard rabbit IgG. Similarly, protein fragments of about 50,000 and 23,000 daltons were identified after treatment of standard rabbit IgG and separated antispermine Ig's with 1.0 percent β-mercaptoethanol (Fig. 3). We identified a similar spermine-binding protein in eight other samples of normal rabbit serum when Rivanol (*32*) or ammonium sulfate (final concentration, 40 percent at 4°C) (*33*) were used for separating gamma globulins. No spermine-binding IgG's were recovered after passing the samples through the ethanolamine-Sepharose gel column (prepared by the same procedure as for the spermine-Sepharose column).

These unexpected findings lead us to conclude that the naturally occurring spermine-binding protein recovered from normal rabbit serum is a member of the IgG class. Moreover, the high K_a values derived for each of the tested pools suggest that the binding reactions are specific. The cross-reactivity data support the possibility of a specific biological role for this protein.

The presence of a spermine-binding IgG in the serum of the normal laboratory rabbit raises questions about the molecule's function. It could act as a detoxifying agent for excess free spermine, or, more routinely, as a scavenger for spermine-containing macromolecules released from cells. A reservoir of reversibly bound spermine available for tissue utilization on demand might also prove useful. With respect to detoxification, a protein with the capacity to bind spermine, the most toxic of the free polyamines (*34*), could serve as a biological buffer during periods of rapid rise in extracellular spermine. Further, under conditions of trauma or tissue necrosis, the antibody, acting as a scavenger, could initiate complex formation with protein molecules or large cellular fragments containing bound but exteriorized spermine. There is probably also reticuloendothelial clearance of these complexes and induction of Ig in a fashion analogous to that of antibodies to DNA and histone (*35, 36*).

It is unlikely that the antispermine Ig's described in this report are species-specific. This view is based on the preliminary results of our study of spermine-binding serum fractions in normal human serum. Moreover, Roch *et al.* (*37*) recently conducted studies that indicate that natural antibodies to polyamine are present in normal human serum.

The inducibility of this natural Ig, its possible role in ontogeny, and its susceptibility to quantitative change under the stresses of disease are of theoretical and practical concern. The availability of naturally occurring, high-affinity, high-specificity antibody to spermine in normal rabbit serum should make possible wide experimental and clinical applications.

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Acquisition of a Memory Skill

Abstract. *After more than 230 hours of practice in the laboratory, a subject was able to increase his memory span from 7 to 79 digits. His performance on other memory tests with digits equaled that of memory experts with lifelong training. With an appropriate mnemonic system, there is seemingly no limit to memory performance with practice.*

One of the most fundamental and stable properties of the human memory system is the limited capacity of short-term memory. This limit places severe constraints on the human ability to process information and solve problems (*1*). On the other hand, this limit (about seven unrelated items) stands in apparent contrast to documented feats of memory experts (*2*). Whether these memory skills are the result of extensive practice or of exceptional ability has often been disputed. The goal of this research is to analyze how a memory skill is acquired.

An undergraduate (S.F.) with average memory abilities and average intelligence for a college student engaged in the memory span task for about 1 hour a day, 3 to 5 days a week, for more than $1\frac{1}{2}$ years. S.F. was read random digits at the rate of one digit per second; he then recalled the sequence. If the sequence was reported correctly, the next sequence was increased by one digit; otherwise it was decreased by one digit. Immediately after half the trials (randomly selected), S.F. provided verbal reports of his thoughts during the trial. At the end of each session, he also recalled as much of the material from the session as he could. On some days, experiments were substituted for the regular sessions.

During the course of 20 months of practice (more than 230 hours of laboratory testing), S.F.'s digit span steadily improved from 7 to almost 80 digits (Fig. 1). Furthermore, his ability to remember digits after the session also improved. In the beginning, he could recall virtually nothing after an hour's session; after 20 months of practice, he could recall more than 80 percent of the digits presented to him. On one occasion (after 4 months of practice), we tested S.F.'s memory after the session with a recognition test (because recognition is a much more sensitive measure of retention than recall is); he not only recognized perfectly 3- and 4-digit sequences from the same day, but also recognized sequences from earlier in the week.

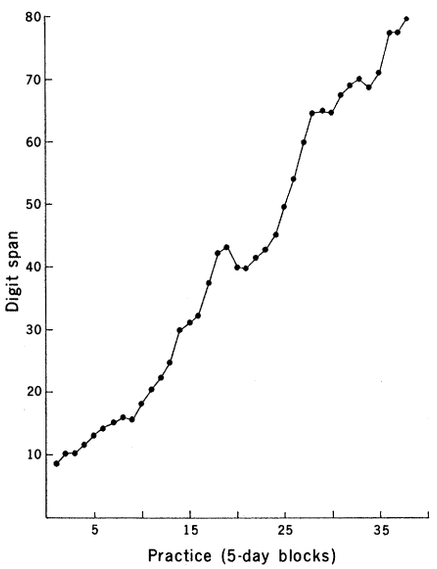

Fig. 1. Average digit span for S.F. as a function of practice. Digit span is defined as the length of the sequence that is correct 50 percent of the time; under the procedure followed, it is equivalent to average sequence length. Each day represents about 1 hour's practice and ranges from 55 trials per day in the beginning to 3 trials per day for the longest sequences. The 38 blocks of practice shown here represent about 190 hours of practice; interspersed among these practice sessions are approximately 40 hours of experimental sessions (not shown).

With only a few hundred hours of practice, S.F. would be classified as a beginner at most skills. However, in his field of expertise, memory for random digits, he compares favorably with the best-known mnemonists, such as Luria's S. and Hunt and Love's V.P. (*2*). For example, after about 6 months of practice, we set S.F. the task of recalling a matrix of 50 digits because data on this task are available for both S. and V.P. S.F.'s study times and recall times were at least as good as those of the lifetime memory experts.

The key to understanding this skill comes from analyses of S.F.'s verbal reports and his performance on various experimental tests. We will first describe two essential components of this skill: (i) his mnemonic associations and (ii) his retrieval structures. Then we will address the question of whether or not S.F. was able to increase his short-term memory capacity.

The most essential part of S.F.'s skill is his mnemonic associations, which he described in great detail in his verbal reports. The principle of a mnemonic is to associate unknown material with something familiar; the advantage is that it relieves the burden on short-term memory because recall can be achieved through a single association with an already-existing code in long-term memory. What S.F. did was to categorize 3- and 4-digit groups as running times for various races (*3*). For example, 3492 was recoded as "3 minutes and 49 point 2 seconds, near world-record mile time" (*4*). During the first 4 months, S.F. gradually constructed an elaborate set of mnemonic associations based initially on running times and then supplemented with ages (893 was "89 point 3, very old man") and dates (1944 was "near the end of World War II") for those sequences that could not be categorized as times. Running times (62 percent) and ages (25 percent) account for almost 90 percent of S.F.'s mnemonic associations.

There are several lines of evidence concerning the mnemonic associations. On the basis of S.F.'s verbal reports, we were able to simulate his mnemonic associations, that is, to abstract a set of rules that categorizes a sequence of digits as 3- and 4-digit running times. When we compared the simulation to the verbal reports, between 85 and 95 percent of the time the computer categorized the digit sequences as S.F. did. By means of the simulation, we were also able to determine which sequences of digits would be categorized as running times and

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