Methodology article

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Combination of native and denaturing PAGE for the detection of protein binding regions in long fragments of genomic DNA Kristel Kaer, Kert Mätlik, Madis Metsis and Mart Speek*

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Abstract

Background: In a traditional electrophoresis mobility shift assay (EMSA) a ³²P-labeled doublestranded DNA oligonucleotide or a restriction fragment bound to a protein is separated from the unbound DNA by polyacrylamide gel electrophoresis (PAGE) in nondenaturing conditions. An extension of this method uses the large population of fragments derived from long genomic regions (approximately 600 kb) for the identification of fragments containing protein binding regions. With this method, genomic DNA is fragmented by restriction enzymes, fragments are amplified by PCR, radiolabeled, incubated with nuclear proteins and the resulting DNA-protein complexes are separated by two-dimensional PAGE. Shifted DNA fragments containing protein binding sites are identified by using additional procedures, i. e. gel elution, PCR amplification, cloning and sequencing. Although the method allows simultaneous analysis of a large population of fragments, it is relatively laborious and can be used to detect only high affinity protein binding sites. Here we propose an alternative and straightforward strategy which is based on a combination of native and denaturing PAGE. This strategy allows the identification of DNA fragments containing low as well as high affinity protein binding regions, derived from genomic DNA (<10 kb) of known sequence.

Results: We have combined an EMSA-based selection step with subsequent denaturing PAGE for the localization of protein binding regions in long (up to10 kb) fragments of genomic DNA. Our strategy consists of the following steps: digestion of genomic DNA with a 4-cutter restriction enzyme (*Alul, BsuRI, Trul,* etc), separation of low and high molecular weight fractions of resultant DNA fragments, ³²P-labeling with Klenow polymerase, traditional EMSA, gel elution and identification of the shifted bands (or smear) by denaturing PAGE. The identification of DNA fragments containing protein binding sites is carried out by running the gel-eluted fragments alongside with the full "spectrum" of initial restriction fragments of known size. Here the strategy is used for the identification of protein-binding regions in the 5' region of the rat p75 neurotrophin receptor (*p75NTR*) gene.

Conclusion: The developed strategy is based on a combination of traditional EMSA and denaturing PAGE for the identification of protein binding regions in long fragments of genomic DNA. The identification is straightforward and can be applied to shifted bands corresponding to stable DNA-protein complexes as well as unstable complexes, which undergo dissociation during electrophoresis.

Background

Electrophoretic mobility shift assay (EMSA), developed by Fried and Crothers [1], and Garner and Revzin [2], is a popular method used for detection of protein-DNA interactions [3]. It is highly sensitive and may be used to obtain qualitative as well as quantitative information in determination of protein binding parameters of various DNA molecules [4-6]. In traditional EMSA, a DNA oligonucleotide or a restriction fragment, generally within the size range of 20-400 bp [7], is radiolabeled and complexed with purified protein or mixture of proteins (nuclear or whole cell extract). This complex is separated from the naked DNA by using polyacrylamide gel electrophoresis (PAGE) under native conditions. Because of the "caging" effect within the gel matrix [8,9], the DNA-protein interactions can be stabilized and the corresponding shifted complexes can be detected as discrete bands. Although in some cases, complexes may dissociate and do not produce detectable shifted bands.

Previously, two similar high-throughput methods were developed for the identification of protein binding regions using a large population of fragments derived from DNAs (plasmids, bacteriophages, bacterial chromosome and human genome fragment) ranging in size from 3 kb to 4,700 kb [10,11]. These methods are relatively laborious because, in addition to the initial two-dimensional PAGE separation step, they require several additional steps (linker addition, PCR amplification, cloning and sequencing) for fragment identification.

Here we describe an alternative and straightforward strategy which is based on a principle of the selection method, known as SELEX [12,13] and uses a combination of native (EMSA) and denaturing PAGE for the identifications of protein binding regions in long (up to 10 kb) fragments of genomic DNA. With this strategy, unique protein binding fragments, which give rise to shifted bands, can be "fished out" and identified. Moreover, DNA fragments which dissociate from the complexes during electrophoresis may be also identifed.

Methods

Cells and nuclear extract preparation

Rat pheochromocytoma PC-12 cells (CRL-1721; ATCC, Manassas, VA, USA) [14] were grown in a humidified 5% CO2 incubator at 37 °C in Dulbecco's modified Eagle's medium (DMEM) supplemented with 5% fetal bovine serum, 10% horse serum and 100 U/mL of penicillin and streptomycin. All cell culture reagents were purchased from Gibco, Invitrogen, Carlsbad, CA, USA. For nuclear extract preparation, PC-12 cells were washed with $1 \times PBS$ (10 mM Na₂HPO₄, 2 mM KH₂PO₄, pH 7.4, 137 mM NaCl and 2.7 mM KCl) and lysed in ice-cold buffer containing 10 mM Tris-HCl (pH 8.0), 10 mM NaCl, 1 mM EDTA, 10

mM DTT, 10% glycerol 0.5% NP-40 supplemented with 1 mM PMSF and 1× protease inhibitor cocktail (10 mM Benzamidine, 10 μ g/ml Antipain, 2 μ g/ml Aprotinin, 10 μ g/ml Leupeptin) (Sigma-Aldrich, Bellefonte, PA, USA). Nuclei were pelleted by low speed centrifugation at 350 RCF for 3 min and proteins were extracted with the high salt buffer as described in [15].

Digestion of genomic DNA and size selection of fragments

A 9.3 kb BamHI fragment of rat genomic DNA derived from the 5' region of neurotrophin receptor (p75NTR) gene was cloned into Bluescript KS vector (Stratagene, La Jolla, CA, USA) and digested with restriction enzyme BsuRI or AluI (Fermentas, Vilnius, Lithuania). The fragments obtained were separated on a 1% low gelling temperature agarose (SeaPlaque; FMC, BioProducts Rockland, ME, USA) together with the DNA molecular weight marker (1 kb ladder, Stratagene) run in parallel lane. Two fractions, with approximate sizes of fragments 30-300 bp and 300-700 bp, named low (L) and (H) molecular weight fractions, respectively, were cut out and allowed to diffuse into TE (10 mM Tris-HCl, pH 7.5, 1 mM EDTA; 3 volumes per gel-slice) at 37°C for 8-12 h. These fractions were further concentrated by precipitation with ethanol (2.5 volumes) in the presence of 0.15 M NaOAc (pH 5.5) at room temperature. After centrifugation, the DNA pellets were dissolved in TE at concentration of 100 ng/ μ l.

Labeling of DNA fragments

Fragments (400 ng of each fraction) were 3' end-labeled with 20 μ Ci of $[\alpha^{-32}P]$ dCTP (GE Healthcare, Amersham, Buckinghamshire, England) using 1 unit of Klenow polymerase (Fermentas, Vilnius, Lithuania) in a 10 µl reaction volume containing 50 mM Tris-HCl (pH 8.0), 5 mM MgCl₂ and 10 mM DTT. To favor 3'end-labeling of blunt-ended fragments by 3'-5' exonuclease and 5'-3' polymerase activities of Klenow fragment, the reaction was first incubated in the presence of $[\alpha^{-32}P]dCTP$ at 37 °C for 10 min. Then all unlabelled dNTPs were added to a final concentration of 0.1 mM for each and the reaction was continued for 25 min. Finally, the reaction was terminated by phenol extraction, ³²P-labeled fragments were precipitated with 2.5 volumes of ethanol in the presence of 1.5 M NH₄OAc and dissolved in TE at a concentration of 40 ng/ μ l.

EMSA

³²P-labeled fractions of fragments (80 ng of each) were incubated with PC-12 nuclear extract (1 μ g total protein per reaction) in 3 mM Hepes-KOH at pH 7.9, 60 mM KCl, 0.15 mM EDTA, 1.5 mM DTT, 1.5% glycerol, poly (dI-dC) (final concentration 200 ng/ μ l for low and 400 ng/ μ l for high molecular fractions, respectively) at room temperature for 20 min. After addition of 20% glycerol (1/5 volume), samples were subjected to electrophoresis on a 3% polyacrylamide gels run with 50 mM Tris-borate buffer, pH 8.3, 1 mM EDTA at room temperature for 2 h. The following electrophoresis reagents were used Tris (ultrapure, Duchefa, Haarlem, The Netherlands), boric acid (ACS grade, AMRESCO, Solon, OH, USA), acrylamide (>99%), N,N'-methylene bisacrylamide (>98%) and EDTA (ACS reagent) from Sigma, St. Louis, MO, USA

Labeled fragments and their shifted complexes with proteins were visualized in wet (preparative) or dried gels by phosphoimaging using Personal Molecular Imager FX system (Bio-Rad Laboratories, Hercules, CA, USA). Shifted bands or zones were located, cut out from the preparative gels and the corresponding labeled fragments were allowed to diffuse into TE as described above. Fragments were concentrated by ethanol precipitation, dissolved in sample buffer containing 90% formamide and 10 mM EDTA and treated at 95 °C for 2 min.

Denaturing PAGE

EMSA-positive shifted fragments, together with ³²Plabeled L and H molecular weight fractions of fragments and appropriate DNA marker were subjected to electrophoresis on a 40 cm-long 6% denaturing polyacrylamide gel containing 50 mM Tris-borate buffer, pH 8.3, 1 mM EDTA and 7 M urea. After electrophoresis, gel was transferred to the Whatman 3 MM paper, dried and radioactive fragments were visulized by phosphoimaging.

Sequence analysis and fragment identification

Sequence of the 9.3 kb BamH1 fragment derived from the rat *p75NTR* 5' region was obtained from the Genbank[®] (accession numbers AABR03076992.1 and AABR03076383.1) [16]. Restriction mapping with *Bsu*RI and *Alu*I, and identification of shifted fragments corresponding to protein-DNA complexes were carried out using DNAMAN software package (Restriction analysis) version 4.0 (Lynnon Biosoft, Quebec, Canada).

Results and Discussion

A Strategy for the detection of protein binding regions in genomic DNA

Based on a traditional EMSA and selection of DNA fragments containing protein binding regions from the population of restriction fragments (similar to the SELEX methodology [13]), we have developed a strategy for the detection of protein binding regions in long (<10 kb) fragments of genomic DNA (Fig. 1). This strategy consists of the following steps: fragmentation of genomic DNA with a frequent-cutter restriction enzyme recognizing a 4 bp sequence, isolation of the L and H molecular weight fractions of fragments, ³²P-labeling with Klenow fragment, EMSA, elution of the shifted fragments and their identification by denaturing PAGE (for details see Methods). The main difference from the traditional EMSA is that instead of using a single labeled oligonucleotide or restriction fragment, a large number of fragments (from 10-50) are used in a single experiment. However, because smaller fragments may give rise to complexes which may be masked by longer fragments, a prior separation of L and H molecular weight fractions of fragments is necessary. After localization and elution of the shifted bands (or smear) from the preparative EMSA-gel, identification of the corresponding protein-bound fragments is carried out by high resolution PAGE. Generally, each shifted DNA fragment can be identified when running it in gel in parallel with the initial pool of labeled fragments of known size (Fig. 1). However, if two fragments of the same size are present among the shifted fragments, their identity may be revealed by the presence or absence of a diagnostic restriction enzyme site, determined from a separate experiment.

Determination of the protein binding regions in the 5' region of rat neurotrophin receptor (p75NTR) gene

To test the strategy, based on a combination of native and denaturing PAGE, we used a 9372 bp fragment corresponding to the nucleotide positions -9,645 to -274 of the upstream (promoter) region of the rat p75NTR gene (Fig. 2). Fig. 3A shows the preparation of L and H molecular fragment fractions (30-300 bp and 300-700 bp, respectively). As determined by in silico restriction analysis, BsuRI generated 41 fragments in L and 11 in H molecular range. Similarly, AluI generated 43 and 12 fragments in L and H molecular fractions, respectively (Fig. 3B; see also Fig. 2). Representative fractions (L for BsuRI with about 40% coverage and H for AluI with about 70% coverage) were selected for further analysis. Fig. 4 shows the results obtained by using these fractions in EMSA and denaturing PAGE experiments. In the case of BsuRI L fraction, a band with reduced mobility was identifed as a 200 bp fragment derived from a region -6417 to -6617 bp relative to the transcriptional start site (+1) of the *p75NTR* gene (Fig. 4; see also Fig. 2). However, in the case of AluI H fraction, a smear was observed in EMSA gel (Fig. 4A). A zone covering most of this smear was cut out and analyzed on a denaturing gel (Fig. 4B). This zone contained fragments from 359 to 737 bp in length (Fig. 4B; see also Fig. 2). Comparison of the band intensities between lanes + and -, corresponding to the incubations with and without nuclear proteins, revealed enrichment of two fragments 359 and 737 bp (derived from -1.7 kb and -6.5 kb regions of p75NTR; see Fig. 2) suggesting that these fragments contain binding sites for nuclear proteins.

Therefore, this result shows that DNA fragments which dissociate from the complexes during electrophoresis and produce a smear can be identified by denaturing PAGE.

It is important to note that fragments with sizes greater than 500 bp tend to have nonspecific interactions with Genomic DNA fragment <10 kb





BsuRI digestion:

 11, 16, 18, 18, 23, 25, 28, 31, 38, 38, 39, 41, 42, 45, 48, 51, 55, 56, 56, 58, 73, 79, 80, 82, 83, 101, 101, 102, 103, 113, 134, 135, 142, 145, 155, 156, 168, 174, 180, 185, 200, 219, 232, 243, 249, 267, 293, 293, 321, 434, 458, 485, 488, 563, 576, 593, 605, 650, 949, 984

AluI digestion:

7, 8, 9, 12, 14, 16, 16, 21, 21, 22, 25, 32, 33, 33, 39, 42, 46, 46, 54, 57, 63, 64, 71, 72, 80, 81, 89, 90, 95, 96, 100, 104, 108, 109, 118, 121, 123, 133, 138, 147, 200, 218, 218, 226, 237, 254, 255, 257, 257, 257, 263, 281, 297, 298, 310, 359, 416, 449, 515, 521, 540, 563, 595, 623, 629, 737

Individual fragments used in EMSA:

F202, a 202 bp Bg/II-NdeI fragment derived from positions -1653 to -1855 F395, a 395 bp PstI fragment derived from positions from -5958 to -6353 F514, a 514 bp PstI fragment derived from positions -6353 to -66867

9,372 bp BamHI fragment cloned in pBS SK+

1	GGATCCTGCC	AGCTTCCTGC	CACACCAGCC	CATTAGCAAA	ACCACTGTGG	CIGCACACCA	AACCCTTGCC	CATAGCCTCA	CCCACCTGCC	TAGCAGGGCC	CCCCTCCCAG	GCACCTGCCT	TTCCCACACA	TCTTAAATCT
141	CCTGAGGGTT	GCTGCCTCCT	GCTGCTTCCC	CGGACATTGT	CTGTACACAG	CATCCTGGGC	CACCCCTGTG	CTTGTGGGGA	GTTAGTCATC	CACTTTCTTT	ACAGTCAGTC	AGTCTCTGTC	AGTCTCCAGT	GTCTGGTCCT
421	ACCACCACA	TECCOTACTC	CTCAGTACTG	CAGGTCTGTC	AGCTCTTTCC	CACAGCAGCT	CACACCAGTT	CCAGAGIGIG	CATGCCAGTG	CCTCAGCCCA	GUGGUUTUUA	GGCTGGACCC	TGGGCAGGGC	TECTENCARC
5.61	CGAGAGCACA	TTTTTATTA	AAGTGGAAAAA	AGAGCTGAAA	ATCTGCTCGC	ATTTAATCAT	CTTGACGACC	TTTTTGCTTA	AGAGTTTCCA	GCTGAGGGGG	GAGCIGCICC	GATGGGTTGT	GAAGGCATTT	CTGAGCTGAG
701	CCTGGGTCTG	GAGGGGAGGG	TGAGGGATGA	ATAAACTTAC	CCAGCCAGGT	GGCTGGGCTA	AAAGTGTCAA	GTCAGCACTT	CCTCATGGGC	TGGCTCCTCC	AGGGGCCCTC	CCTCCCATCT	TCTCTCCACC	CCCACCCTCC
841	CGGGCACCCA	GCACACTGGA	CAAGAACCCT	GCTACATGGC	ACAGGAGCAA	GGACAGTGTG	AGGAGGGGTC	TTTCCTTTTG	TCACAAGTTG	AAAAGTAGAC	CCTGGAGGGG	CCAGTGTCCT	CCTAGGAACT	GGGCAAGGCC
981	TCCTTGAATA	CTATTGAAAC	CTCTCTCTAT	CACTCCTTTT	CTCTCACCAT	CCCACGGAAA	GGTTTGAACC	TGTCACCAGG	CCTCAACTCC	CCCAGTAACT	TCTGGGTAAC	TTTTCACATC	CCTGAAATCT	GCCTACCACT
1121	TTCCAATGTG	TAAATGAATG	CCATGTTCCC	ATCCCAGGTA	TACACTGATT	GGGGGAAACC	CCTAAGATGA	GAAGATCACC	AAGGCTACAG	CTATGGCCCT	GTCCAGTAGA	GGGGGGACAAC	AGCAGCAGAG	GAAGTCCCTC
1261	TCCACTGTCT	GGACCACCTC	GATGCTCCCA	AGGACCCGAG	ACTTAGAATA	AGAATAAGAG	ATGGCGGGCT	GGAGAGATGG	CTCAGTGGTT	AAGAGCATGG	ATTGCTCTTC	CAGAGGTCCT	GAGTTCAAAT	CCCAGCAACC
1401	ACATGGTGGC	TCACAACCAT	CTGTAATGAG	TTCTGATGCC	CTCTTCTGGT	GTGTCTGAAG	ACAGCTACAG	TGTACTTATA	TATAAATAAA	TAAATCTTTA	АААААААААА	АААААААААА	AAAAGAGAGA	TGGGAGAATC
1541	TGCCTTCTGC	TCCTCTCAGG	AAGGAGGTCC	GCTGGTACAT	GCAGAGACAG	ACTCTGTAGG	AAGATCTGGT	GCCTCTGGTC	TTCTGTCCCC	CAAAGCCCCT	CTCTCTTCAT	TTCTGCTTGG	GACTTGTGCA	TTTGAACAGA
1001	GCCICCCICC	TCCAAACCAA	GCCIAGGAAG	TRECORTIONS	GCGAIGCIIG	ACACATCCCC	CATCAGAGGG	AGICCICICI	CIGIAAGGGA	AAGGCACAGG	GAATAIGACI	CTCCTCCTCC	ACTGATCGG	CTCCCDATTT
1961	CTCTGAAGCC	AGAGGCCTGC	CCCAGCTCTA	TCTCTTATCT	ACAGCAGGAA	GGACCCTGGG	CCCAGTCCCC	AGTGTTGAGA	TGTCATCTTA	CCCCTCATCC	GGTTTCTTGC	TAGAAGCCAC	CATCAATGGC	AGCATCAAAC
2101	ATGAGACTAA	TGACATCTTT	CCGGTTCTCC	CTGACTTTCA	AAGCGCACTG	ACCCACACTC	TTTTCTTGAC	TGCTCATTCT	GTGAGGCTCT	CTCTCATCTT	ATGCCTATGT	TAGGGAGAAA	GACACTGAGG	CTCAGAGCAA
2241	GAGAGAGACG	GGCCGGTCAC	CACTCATCAG	TACACAGACA	GGCACCTGGG	CCTCAGACAG	TTCATTTTCT	CTTCCTCTAC	ACTGACTTCA	TGATGTTCTG	GCCATGGAAT	AGGTTAACCT	CATTTTTCTT	TTTTCTTTCT
2381	TCTTTTTTTT	TTTTTCCGGA	GCTGGGGACA	GAACCCAGGG	CCTTGCGCTT	GCTAGGCCAG	CGCTCTACCA	CTGAGCTAAA	TCCCCAACCC	CTCATTTTTC	TTTAAAACAT	GTTGCATGCC	CTTGGACATA	GGCTGGGAAG
2521	AGAGGACTGA	ATCTAGCTGG	ACATGGCGGT	ACACATCTGT	AATTTCTGTC	TGTGGAGTCA	AAGTAAGAAA	ATCAGTTCAG	GATCATCCTT	GGCTGGCTAC	ACCGGATGCC	CAAGTCTAAC	CCCATTTCAA	ATAAATGAGC
2661	AAAACATAAG	AATCAGGTCA	GAGCTGGAGA	CACAGTTCAG	TTGATAAAGT	GTTTACCCAG	CATGCCCCAA	GCCCCAGATT	CATCCCCCAG	TATCCCGTAA	ACTGTCCACG	ATGCTGCAGG	TCTTGGTACT	TGGGAGGTAG
2801	GCAGGAGGGT	CAGAAGCTAG	AGGTCATCCT	CAGTTACAGA	TAAAGTTCAG	GACAGACCTG	AGATTCCGCA	GACTGTATCG	CAACAGACAA	AAGGCTAGAG	AGATGGCTCA	GTGGTAAAGA	GTATTTGCTG	GCTTTGCAGC
2941	GGGCTAAAGG	TTEEGTTTET	AGCACCCACA	TGCCAGTTCA	CAGCGGTCTT	TAACTCCAGT	TCCATGAACT	CCTCCATACC	CTCTTCTGGC	CTCTTTAGGC	ACCAGACGTG	ACACACATGC	ACATATGCCA	GACAGACATT
2221	ACCELETATE	CTACACCTAC	ACTCCANACC	AGAGAGIGIAI	ACAACCOTTC	CCCCANTCCT	ACTENCECTE	CAGGAAAACA	CONCONCTO	CTTCTCCCCC	ATCCCCTCTC	TCCCCCTCAC	ACCCCCCCCC	GACAGCCATA
3361	GGGGAAAGGG	CTGGTGGGGT	TACATGGGCT	TCTACAGAGC	AGCGGAGTGG	AGGCAGGGAG	GCGGCAGTGG	CTGCCATATT	TGGGCAGGCA	GTTGGGGGGAG	GGCACTGCCA	AAAGTGCCCA	TTTTGATGCT	TGAGTTAATC
3501	TAACTGGACT	CCAAAGTTGC	TAATCCTTCC	CATCCCCCTC	ACTACCGATT	CAGCTCCAGA	ATGAAAGCTC	AAGAACCCCA	AACCAATTTC	TGGCCTCCAC	CGTCCATCTG	CCATCCCCCT	ATGGAACAGG	CTCCGCCTTC
3641	ATTTCTCAGA	GGTGTCAGTT	TAGAGGCAAC	CAGGACGTCG	TGCTGCAGCA	AAGCCGCCAA	GCCAGCTCCT	GAAGGGGAGG	GGTGGGTTTC	ACTTACCTTG	CCTGGCTGCC	TGACCCCGGG	GGCAGATGGG	ATTCAGCTGG
3781	AAAGGGCTAA	CACTTCCTCT	TTCCTCGCCT	CIGGICICCC	TGCTGACACC	CTGCCTCTGG	TTAGACATGG	AACTGGAGAA	ATGGATGAAA	CIGICATAGG	GCAAGAAAGG	TGGGCGCTAG	CAGAGTTCAC	CCCTCCTTTC
3921	TGACACAGTG	TGCCTATCTG	AGCAGCCCAC	TTAGCCTCTA	AGCCTGTATT	TTGCCTTGGA	CACCAAGAGG	GAGCAGCCAG	GGACCTGGAG	ACAGGACTGA	GCCCCTCTCA	GGTGGAGATC	CTTCCTCCCC	AGTCTAGAGG
4061	CTGGGGAGTT	GGGCTGGAAC	AGGGGAGTAC	CTTGGATCAG	GTGTTAGTGG	GGAGAGGTGT	GAGCGTTTGT	GCTTTGTGCA	GAGCAGAACC	ATTGGTAATG	GGTGCCACAA	TTTGCTTCTG	AGCCAAGAGG	CTTCACCTCT
4201	TCAAGTCCCA	GACACCICAC	CTACGAAGTG	GTTACAAGCA	CGGCCTTCCT	GGGGTGGAAA	TGGGAATGTG	GGAGACTITC	CTGGCCTGTG	GGTGATGGTA	GUGTGUATUT	CCAGCCTATA	GAAAGGCTCT	GGCAGTGAGC
4481	AATGGAATGG	CAAGAGAAGG	AGAGGACATT	AGCGGACATC	TTCCTGGAGG	GTGAGGTAGG	GAGGTGAATG	GTGTGGGGGGG	GAGGGCTTGC	CCCCCCCTATA	TEGACTCCTE	ATAATGCATC	TTCCCAACGA	GCCCCCACTC
4621	CCGCCAGCTC	ATGCTGAACT	AAGCCTATAT	TATCCAATCC	TTTTGCCTTG	AAGTCACTGT	AGTCTAGGAA	GCCTCTGTGT	GTGTGTGTGTGT	GIGIGIGIGIGI	GTGTGTGTGTGT	GTGTGTGTGTGT	TTACAGAGAG	GGGAAGAGGG
4761	GGGGAGAGAG	AGAGGAGAGA	GACAGAGACA	GAGAGAGGGG	GAGAGAGAGA	GAGAGAGAGA	GAGAGATCCT	CTCTAAGTGC	TGCTTTATCA	CGGGAGACAG	TTCTAAAATC	CCTTCAGGAA	TAACTATTGC	CACCTTGGTG
4901	CIGCCAAGCI	GGTCATTTTT	CAGTCTTCCC	CCCTTGTCCC	ATCTCTCAAT	GGTTAGGCTG	AGAAGAAGGT	GTCTTGTGGA	GTCTGGGGTA	GGACCACTTA	TTGCTTGGTT	TGGGGCCAGG	AGTCACTGTC	GGGCAGCAGT
5041	GGTTCTAAGG	GATGAGTAGA	GGTAGGTAAG	ATGGCGGTGG	TCACGATTGC	TTTAGGGTTT	TTTTGGTGAT	GGTCATGGTG	AGGGTGGGTG	GTGGTGGTCG	TGCAGTACTG	GACTTGGTAA	ATCGTCTGTG	ACAGAAAATG
5181	GTGGCAATGG	TTTATTAGTT	ACTTTTCTTT	ATTTTTTAAT	TGGATATTTT	TTATTTACAT	TTCAAATGTT	ATCCCCTTTC	CTGATTTCCT	GTCCATAAAC	CCCCTATCCC	ACCCCCTCTC	CCTCTTTTTC	TATGAGGGTG
5461	TCTGTCCATG	TGTAACTCTT	TGGATGGTGG	CTTAGTCCCT	GGGGGGTCTGT	TGGTTGGTAT	TGTTGTTCTT	ATGGAGTTGC	AAATCCCTTC	AGCTCCTTCA	ATCCTTTCTC	TAGCTCCTCC	ACTGGGGGACC	CCATTCTCAG
5601	TTCAATCAGT	TACTTTTCTA	ATTGCTATGA	CAAAGTACCC	AATAAAGCAA	ATTAATAAGG	AAGGTTTAGG	GGGCTGGAGA	GATGGCTCAG	CGGTTAAGAG	CACTGACTGC	TCTTCCAGAG	GTCCTGAGTT	CAATTCCTTG
5741	TAACCACATG	GGTGACTCAC	AACCATCTGT	AACCGGTAAT	CIGGIGCCCC	TTTTTCGGGG	TGTGTTCTGA	AGAGAGGTGG	ACAGTGGTAT	TCATATGAAT	AAAACAAATA	AATCTTAGAA	AAGAAAAGAA	GGGAGGATTA
5881	TTTTACCTCC	CTATTCAAAC	ATGCAATGAA	TCTGGAAGGC	ACATGTCTCA	GTTACTTTTC	TATTGCTGTG	GTTAGACACC	ATGGCCAGGG	CAACAAGATT	TTTTGGGGGC	TTTCAGGTCA	GAGGGATAGG	GGTCTATCAC
6021	CATCTCCATG	GGGAGAATGG	CAGCAGACAG	CAGGCAGCAG	GCAGCAGGCA	GCAGGCAGCA	GGCAGCAGGC	AGCAGGCAGC	AGGCAGCAGG	CAGCAGGCAG	CAGGCAGAAG	GCAGCAGGCA	GCCGGCAGCA	GGCAGCAGGC
6161	AGCAGTAGCT	GAGAGCTCAC	ATTTCAGACC	CTCAAGCTGG	AGGCTGAGAA	ACCACACCTC	TAGGGTTGGT	GAGAGGCTTC	TGAAGCCCTT	AGACCACCCC	TAGTGACACA	CCTTCTCTAT	CAAGGCCAGA	CCTCCTAACC
6161 6301 6441	GGAGAAACGC	GAGAGCTCAC AAGCACCAAC TGGTACTTGC	ATTTCAGACC TGAGGTCCAA CATCCTGCCC	CTCAAGCTGG GTATTAAAAT TTTGACTTCT	AGGCTGAGAA GCCCGAGACT ATATGGTGCC	ACCACACCTC TTTTGTGGGA CAGCTCATGG	TAGGGTTGGT AGACATCTCA GAGGCCACCG	GAGAGGCTTC TTCAAACCAC CCTGTGTGCT	TGAAGCCCTT CACAGCATGG GGTGGCTTTC	AGACCACCCC AAACATGAGG TTCCTGTCTG	TAGTGACACA GATCTTGGAC TTAAAAACTT	CCTTCTCTAT ACATTGTATC CTGCAAAAAC	CAAGGCCAGA AGCAGCCTGG CCTCATAGAA	CCTCCTAACC AAGCAGAGAG ACACCCAGAG
6161 6301 6441 6581	AGCAGTAGCT CTTCCCAAAC GGAGAAACGC TTGTGCTTCC	GAGAGCTCAC AAGCACCAAC TGGTACTTGC TGGGTGACTC	ATTTCAGACC TGAGGTCCAA CATCCTGCCC TAAATCCAGG	CTCAAGCTGG GTATTAAAAT TTTGACTTCT CAAGCTGACA	AGGCTGAGAA GCCCGAGACT ATATGGTGCC ATGAGAGTTA	ACCACACCTC TTTTGTGGGA CAGCTCATGG ATGATACCCA	TAGGGTTGGT AGACATCTCA GAGGCCACCG TGGTCAGGGT	GAGAGGCTTC TTCAAACCAC CCTGTGTGTGCT CACGATGATT	TGAAGCCCTT CACAGCATGG GGTGGCTTTC TGGGAGGTAT	AGACCACCCC AAACATGAGG TTCCTGTCTG GGGGGGGTGGG	TAGTGACACA GATCTTGGAC TTAAAAAACTT TAGAGAAACT	CCTTCTCTAT ACATTGTATC CTGCAAAAAC GCAGTCTAGG	CAAGGCCAGA AGCAGCCTGG CCTCATAGAA ATTCGCCATC	CCTCCTAACC AAGCAGAGAG ACACCCAGAG GTGGTGTGAA
6161 6301 6441 6581 6721	AGCAGTAGCT CTTCCCAAAC GGAGAAACGC TTGTGCTTCC TTGAGGCCGGT	GAGAGCTCAC AAGCACCAAC TGGTACTTGC TGGGTGACTC GATGGAGATG	ATTTCAGACC TGAGGTCCAA CATCCTGCCC TAAATCCAGG GTGGTGGTCA	CTCAAGCTGG GTATTAAAAT TTTGACTTCT CAAGCTGACA CAGTGGTGTG	AGGCTGAGAA GCCCGAGACT ATATGGTGCC ATGAGAGTTA TGCGGGTTTG	ACCACACCTC TTTTGTGGGA CAGCTCATGG ATGATACCCA GAGGTAGGTG	TAGGGTTGGT AGACATCTCA GAGGCCACCG TGGTCAGGGT GTTGCGGTCA	GAGAGGCTTC TTCAAACCAC CCTGTGTGCT CACGATGATT TGGTGACACG	TGAAGCCCTT CACAGCATGG GGTGGCTTTC TGGGAGGTAT GGCAACTCGA	AGACCACCCC AAACATGAGG TTCCTGTCTG GGGGGGTGGG CAGAGGACTA	TAGTGACACA GATCTTGGAC TTAAAAACTT TAGAGAAACT TTTGGATCAC	CCTTCTCTAT ACATTGTATC CTGCAAAAAC GCAGTCTAGG AGCTGTGCCA	CAAGGCCAGA AGCAGCCTGG CCTCATAGAA ATTCGCCATC GCTATAGTGT	CCTCCTAACC AAGCAGAGAG ACACCCAGAG GTGGTGTGAA GGTTAAGCTA
6161 6301 6441 6581 6721 6861	AGCAGTAGCT CTTCCCAAAC GGAGAAACGC TTGTGCTTCC TTGAGGCGGT AGGCGTCACA	GAGAGCTCAC AAGCACCAAC TGGTACTTGC TGGGTGACTC GATGGAGATG TTACAAAGTA	ATTTCAGACC TGAGGTCCAA CATCCTGCCC TAAATCCAGG GTGGTGGTCA ACCTGCATAT	CTCAAGCTGG GTATTAAAAT TTTGACTTCT CAAGCTGACA CAGTGGTGTG GAAATAACTA	AGGCTGAGAA GCCCGAGACT ATATGGTGCC ATGAGAGTTA TGCGGGTTTG ATACTCTATC	ACCACACCTC TTTTGTGGGA CAGCTCATGG ATGATACCCA GAGGTAGGTG TAGACCAGTG	TAGGGTTGGT AGACATCTCA GAGGCCACCG TGGTCAGGGT GTTGCGGTCA ATTCTCAACC	GAGAGGCTTC TTCAAACCAC CCTGTGTGCT CACGATGATT TGGTGACACG TTCCTATGTT	TGAAGCCCTT CACAGCATGG GGTGGCTTTC TGGGAGGTAT GGCAACTCGA GTGGTGACCA	AGACCACCCC AAACATGAGG TTCCTGTCTG GGGGGGTGGG CAGAGGACTA TAAAATCATT	TAGTGACACA GATCTTGGAC TTAAAAACTT TAGAGAAACT TTTGGATCAC TTTGGTGCTA	CCTTCTCTAT ACATTGTATC CTGCAAAAAC GCAGTCTAGG AGCTGTGCCA CGTAATAACT	CAAGGCCAGA AGCAGCCTGG CCTCATAGAA ATTCGCCATC GCTATAGTGT GTAATTTGCT	CCTCCTAACC AAGCAGAGAG ACACCCAGAG GTGGTGTGAA GGTTAAGCTA ACTGTTATGA
6161 6301 6441 6581 6721 6861 7001	AGCAGTAGCT CTTCCCAAAC GGAGAAACGC TTGTGCTTCC TTGAGGCGCGT AGGCGTCACA ATCATAACAT	GAGAGCTCAC AAGCACCAAC TGGTACTTGC TGGGTGACTC GATGGAGATG TTACAAAGTA GAATATCTGA	ATTTCAGACC TGAGGTCCAA CATCCTGCCC TAAATCCAGG GTGGTGGTCA ACCTGCATAT TCTTTCCCAT	CTCAAGCTGG GTATTAAAAT TTTGACTTCT CAAGCTGACA CAGTGGTGTG GAAATAACTA GGTCTTAGGT	AGGCTGAGAA GCCCGAGACT ATATGGTGCC ATGAGAGTTA TGCGGGTTTG ATACTCTATC GACCCCTGTG	ACCACACCTC TTTTGTGGGA CAGCTCATGG ATGATACCCA GAGGTAGGTG TAGACCAGTG AGAAGGTTTT	TAGGGTTGGT AGACATCTCA GAGGCCACCG TGGTCAGGGT GTTGCGGTCA ATTCTCAACC TTTTTAACTC	GAGAGGCTTC TTCAAACCAC CCTGTGTGCT CACGATGATT TGGTGACACG TTCCTATGTT CCCCAAAGGG	TGAAGCCCTT CACAGCATGG GGTGGCTTTC TGGGAGGTAT GGCAACTCGA GTGGTGACCA CCATATGCAC	AGACCACCCC AAACATGAGG TTCCTGTCTG GGGGGGTGGG CAGAGGACTA TAAAATCATT AGGTTGAGAA	TAGTGACACA GATCTTGGAC TTAAAAACTT TAGAGAAACT TTTGGATCAC TTTGTTGCTA CTGCTGATCA	CCTTCTCTAT ACATTGTATC CTGCAAAAAC GCAGTCTAGG AGCTGTGCCA CGTAATAACT ATACTGTCAG	CAAGGCCAGA AGCAGCCTGG CCTCATAGAA ATTCGCCATC GCTATAGTGT GTAATTTGCT CTACACCGTT	CCTCCTAACC AAGCAGAGAG ACACCCAGAG GTGGTGTGAA GGTTAAGCTA ACTGTTAAGA AGTCTGTTAA
6161 6301 6441 6581 6721 6861 7001 7141 7281	AGCAGTAGCT CTTCCCAAAC GGAGAAACGC TTGTGCTTCC TTGAGGCGGT AGGCGTCACA ATCATAACAT TACCGTTAAC TTCCTTTAAA	GAGAGCTCAC AAGCACCAAC TGGTACTTGC TGGGTGACTC GATGGAGATG TTACAAAGTA GAATATCTGA CTACTGTTGA	ATTTCAGACC TGAGGTCCAA CATCCTGCCC TAAATCCAGG GTGGTGGTCA ACCTGCATAT TCTTTCCCAT ATCCCCAATA	CTCAAGCTGG GTATTAAAAT TTTGACTTCT CAAGCTGACA CAGTGGTGGTG GAAATAACTA GGTCTTAGGT GCAGTATGTG AACAAGGCCG	AGGCTGAGAA GCCCGAGACT ATATGGTGCC ATGAGAGTTA TGCGGGTTTG ATACTCTATC GACCCCTGTG TGGCCTGTAG GGAAGATGCT	ACCACACCTC TTTTGTGGGA CAGCTCATGG ATGATACCCA GAGGTAGGTG TAGACCAGTG AGAAGGTTTT CAGGGGCTCC CGTGGCCTCC	TAGGGTTGGT AGACATCTCA GAGGCCACCG TGGTCAGGGT ATTCTCAACC TTTTTAACTC CAAACTCACG CTDAGGTGAT	GAGAGGCTTC TTCAAACCAC CCTGTGTGCT CACGATGATT TGGTGACACG TTCCTATGTT CCCCAAAGGG CCGAGTGCAC	TGAAGCCCTT CACAGCATGG GGTGGCTTTC TGGGAGGTAT GGCAACTCGA GTGGTGACCA CCATATGCAC AAGAGAAGCT CAATGGGCAC	AGACCACCCC AAACATGAGG TTCCTGTCTG GGGGGGTGGG CAGAGGACTA TAAAATCATT AGGTTGAGAA GAGTCGCTTT GCACCACCAT	TAGTGACACA GATCTTGGAC TTAAAAACTT TAGAGAAACT TTTGGATCAC TTTGGTGATCA GCGATGAACA TCGCACTCAG	CCTTCTCTAT ACATTGTATC CTGCAAAAAC GCAGTCTAGG AGCTGTGCCA CGTAATAACT ATACTGTCAG CCGCCTTCTT	CAAGGCCAGA AGCAGCCTGG CCTCATAGAA ATTCGCCATC GCTATAGTGT GTAATTTGCT CTACACCGTT CTCTTTTGAT CCATABATGCA	CCTCCTAACC AAGCAGAGAG ACACCCAGAG GTGGTGTGAA GGTTAAGCTA ACTGTTATGA AGTCTGTTAG ACTGCTACC
6161 6301 6441 6581 6721 6861 7001 7141 7281 7421	AGCAGTAGCT CTTCCCAAAC GGAGAAACGC TTGTGCTTCC TTGAGGCGGT AGGCGTCACA ATCATAACAT TACCGTTAGT TTCCTTTAAA TTCTGCACCC	GAGAGCTCAC AAGCACCAAC TGGTACTTGC TGGGTGACTC GATGGAGATG TTACAAAGTA GAATATCTGA CTACTGTTGA GCCCCATCTT TTGCAGCCA	ATTICAGACC TGAGGTCCAA CATCCTGCCC TAAATCCAGG GTGGTGGTCA ACCTGCATAT TCTTTCCCAT ATCCCCAATA ATAGATATGA CACTCCCCGCC	CTCAAGCTGG GTATTAAAAT TTTGACTTCT CAAGCTGACA CAGTGGTGTG GAAATAACTA GGTCTTAGGT GCAGTATGTG AACAAGGCCA CAGCACCCGG	AGGCTGAGAA GCCCGAGACT ATATGGTGCC ATGAGAGTTA TGCGGGTTTG ATACTCTATC GACCCCTGTG GGAAGATGGT CAATGCATCT	ACCACACCTC TTTTGTGGGA CAGCTCATGG ATGATACCCA GAGGTAGGTG TAGACCAGTG AGAAGGTTTT CAGGGGCTCC CGTGGCCTCC CAGGCCCCCCG	TAGGGTTGGT AGACATCTCA GAGGCCACCG TGGTCAGGGT GTTGCGGTCA ATTCTCAACC TTTTTAACTC CAAACTCACG CTAAGGTGAT CTCAGGTTAA	GAGAGGCTTC TTCAAACCAC CCTGTGTGCT CACGATGATT TGGTGACACG TTCCTATGTT CCCCAAAGGG CCGAGTGCAC AAGGAAGAGG TCATAGAAAT	TGAAGCCCTT CACAGCATGG GGTGGCTTTC TGGGAGGTAT GGCAACTCGA GTGGTGACCA CCATATGCAC AAGAGAAGCT CAATGGCAG CCTGCTAATA	AGACCACCCC AAACATGAGG TTCCTGTCTG GGGGGGGGGG	TAGTGACACA GATCTTGGAC TTAAAAACTT TAGAGAAACT TTTGGATCAC TTTGTTGCTA CTGCTGATCA GCGATGAACA TCGCACTCAG TCGCTGTTTG	CCTTCTCTAT ACATTGTATC CTGCAAAAAC GCAGTCTAGG AGCTGTGCCA CGTAATAACT ATACTGTCAG CCGCCTTCTT GCCTGCCTCC TAATTGTTGG	CAAGGCCAGA AGCAGCCTGG CCTCATAGAA ATTCGCCATC GCTATAGTGT GTAATTGCT CTACACCGTT CCATAATGCA GGTAAGGCTT	CCTCCTAACC AAGCAGAGAG ACACCCAGAG GTGGTGTGAA GGTTAAGCTA ACTGTTATGA AGTCTGTTAG ACTCTGTTAC ACACTCCTTC ACACTCCTTC AAATGATCAA
6161 6301 6441 6581 6721 6861 7001 7141 7281 7421 7561	AGCAGTAGCT CTTCCCAAAC GGAGAAACGC TTGTGCTTCC TGAGGCGGC AGCGTCACA AGCGTCACA ATCATAACAT TACTGTTAGT TTCTGCACCC GACCATGGAA	GAGAGCTCAC TGGTACTTGC TGGTGACTTGC GATGGAGATG TTACAAAGTA GAATATCTGA CTACTGTTGA GCCCCATCTT TTGCAGCCA ATTATTAATA	ATTTCAGACC TGAGGTCCAA CATCCTGCCC TAAATCCAGG GTGGTGGTCA ACCTGCATAT TCTTTCCCAT ATCCCCAATA ATAGATATGA CACTCCCCGC ACCCAGGCCC	CTCAAGCTGG GTATTAAAAT TTTGACTTCT CAAGCTGACA CAGTGGTGTG GAAATAACTA GGTCTTAGGT GCAGTATGTG AACAAGGCCA CAGCACCCGG AGCCATGGTG	AGGCTGAGAA GCCCGAGACT ATATGGTGCC ATGAGAGTTA TGCGGGTTTG ATACTCTATC GACCCCTGTG GGAAGATGGT CAATGCATCT CATGCATCT	ACCACACCTC TTTTGTGGGA CAGCTCATGG ATGATACCCA GAGGTAGGTG TAGACCAGTG AGAAGGTTTT CAGGGGCTCC CGTGGCCTCC CAGGCCCCCCG TTTAAATTGT	TAGGGTTGGT AGACATCTCA GAGGCCACCG TGGTCAGGGT GTTGCGGTCA ATTCTCAACC TTTTTAACTC CAAACTCACG CTAAGGTGAT CTCAGCTTAA GTTGAGATGG	GAGAGGCTTC TTCAAACCAC CCTGTGTGCT CACGATGATT TGGTGACACG TTCCTATGTT CCCCAAAGGG CCGAGTGCAC AAGGAAGAGG TCATAGAAAT ATAACCTTGG	TGAAGCCCTT CACAGCATGG GGTGGCTTTC TGGGAGGTAT GGCAACTCGA GTGGTGACCA CCATATGCAC CAATGGCAG CCTGCTAATA CAATAATAGT	AGACCACCCC AAACATGAGG TTCCTGTCTG GGGGGGGGGG	TAGTGACACA GATCTTGGAC TTAAAAACTT TAGAGAAACT TTTGGATCAC TTTGTTGCTA CTGCTGATCA GCGATGAACA TCGCACTCAG ATGACTGTTTG ATAAATTAAT	CCTTCTCTAT ACATTGTATC CTGCAAAAAC GCAGTCTAGG AGCTGTGCCA CGTAATAACT ATACTGTCAG CCGCCTTCTT GCCTGCCTCC TAATTGTTGG AACGGGAGTA	CAAGGCCAGA AGCAGCCTGG CCTCATAGAA ATTCGCCATC GCTATAGTGT GTAATTGCT CTACACCGTT CCATAATGCA GGTAAGGCTT TTTAAATTAA	CCTCCTAACC AAGCAGAGAG ACACCCAGAG GTGGTGTGAA GGTTAAGCTA ACTGTTATGA AGTCTGTTAGA AGTCTGCTACC ACACTCCTTC AAATGATCAA TGCCACACTG
6161 6301 6441 6581 6721 6861 7001 7141 7281 7421 7561 7701	AGCAGTAGCT CTTCCCAAAC GGAGAACGC TTGTGCTTCC TTGAGGCGGT AGCCGTCACA ATCATAACAT TACTGTTAGT TTCTGCACCC GACCATGGAA TCCGTAGTCT	GAGAGCTCAC TAGTACTTGC TGGTACTTGC GATGGAGATG GATATCTGA CTACTGTTGA GCCCCATCTT TTTGCAGCCA ATTATAATA GGTAGTAAGC	ATTICAGACC TGAGGTCCAA CATCCTGCCC TAAATCCAGG GTGGTGGTCA ACCTGCATAT TCTTTCCCAT ATCCCCAATA ATAGATATGA CACTCCCCGC ACCCAGGCCC AGCTCAATGC	CTCAAGCTGG GTATTAAAT TTTGACTCT CAAGCTGACA CAGTGGTGTG GAAATAACTA GGTCTTAGGT GCAGTATGTG AACAAGGCCA CAGCACCCGG AGCCATGGTG TTCTGGAAGT	AGGCTGAGAA GCCCGAGACT ATATGGTGCC ATGAGAGTTA TGCGGGTTTG GACCCCTGTG GGACCCCTGTG GGAAGATGGT CAATGCATCT GTGTGGGTCA ACTAATGCTT	ACCACACCTC TTTTGTGGGA CAGCTCATGG ATGATACCCA GAGGTAGGTG TAGAACCAGTG AGAAGGTTTT CAGGGGCTCC CGTGGCCTCC CAGGCCCGCG TTTAAATTGT CTCCTTCCTG	TAGGGTTGGT AGACATCTCA GAGGCCACCG TGGTCAGGGT ATTCTCAAGGT ATTCTCAACC TTTTTAACTC CAAACTCACG CTAAGGTGAT CTCAGCTTAA GTTGAGATGG CCTCTCATGA	GAGAGGCTTC TTCAAACCAC CCTGTGTGCT CACGATGATAT TGGTGACACG TTCCTATGTT CCCCAAAGGG CCGAGTGCAC AAGGAAGAGG TCATAGAAAT ATAACCTTGG ATTCAGCAGA	TGAAGCCCTT CACAGCATGG GGTGGCTTTC TGGGAGGTAT GCCAACTCGA CCATATGCAC AAGAGAAGCT CAATAGGCAG CCTGCTAATA GAGTAAGGCA	AGACCACCCC AAACATGAGG TTCCTGTCTG GGGGGGTGGG CAGAGGACTA TAAAATCATT AGGTTGAGAA GAGTCGCTTT GGACGAGCAT ATAGTAGCAA AACTGGGATC GATCTGTAAA	TAGTGACACA GATCTTGGAC TTAAAAACTT TAGAGAAACT TTTGGTGCCA CTGCTGATCA GCGATGAACA TCGCCACTCAG CCGCTGTTG ATAAATTAAT AG <mark>CTTTGGGG</mark>	CCTTCTCTAT ACATTGTATC CTGCAAAAAC GCAGTCTAGG AGCTGTGCCA CGTAATAACT ATACTGTCAG CCGCCTTCTT GCCTGCCTCC TAATTGTTGG AACGGGAGTA GAGGGGACAT	CAAGGCCAGA AGCAGCCTGG CCTCATAGAA ATTCGCCATC GCTATAGTGT GTAATTTGCT CTACACCGTT CTCTTTTGAT CCATAATGCA GGTAAGGCTT TTTAAATTAA CTTAGAAGTA	CCTCCTAACC AAGCAGAGAG ACACCCAGAG GTGGTGTGAA GGTTAAGCTA ACTGTTATGA AGTCTGTTAA CCTTGCTACC ACACTCCTTC AAATGATCAA TGCCACACTG ATCTCCATCC
6161 6301 6441 6581 6721 6861 7001 7141 7281 7421 7561 7701 7841 7001	AGCAGTAGCT CTTCCCAAAC GGAGAAACGC TTGAGCGTTCC TTGAGGCGT AGCCGTCACA ATCATAACAT TACTGTAACAT TTCCTTTAAA TTCCGTAGTC GACCATGGAA TCCGTAGTCT AGGAGGAAGGC	GAGAGCTCAC AAGCACCAAC TGGTACTTGC TGGTACTTGC GATGGAGATG TTACAAAGTA CTACTGTTGA GCCCCATCTT TTTGCAGCCA ATTACTAATA GGTAGTAATG ACTCCCCAGG ACTCCCCCAGG	ATTECAGACC TGAGGTCCAA CATCCTGCCC TAAATCCAGG GTGGTGGTCA ACCTGCATAT TCTTTCCCAT ATCCCCAATA TATCCTCCCGG ACCCAGGCCC AGCTCAATGC GACTTCCCAGG	CTCAAGCTGG GTATTAAAT TTTGACTTCT CAAGCTGACA CAGTGGTGTG GAAATAACTA GGTCTTAGGT GCAGTATGTG AACAAGGCCA CAGCACCCGG AGCCATCGGG TTCTGGAAGT	AGCCTGAGAA GCCCGAGACT ATATGGTGCC ATGAGAGTTA TGCGGGTTTG ATACTCTATC GACCCTGTG GGAAGATGGT CAATGCATCT GTGTGGGTCA ACTAATGCTT CTGCTTAGACC	ACCACACCCC TTTTGGGGA CAGGTATGG ATGATACCCA GAGGTAGGTG TAGACCAGTG AGAAGGTTT CAGGGGCTCC CGTGGCCCCCG CAGGCCCCCG TTTAAATGT CTCCTTCCTG CCCTTCCTG	TAGGGTTGGT AGACATCTCA GAGGCCACCG TGGTCAGGGT GTTGCGGTCA ATTCTCAACC CAAACTCACG CTAAGGTGAT CTCAGCTTAA GTTGAGATGG CCTCCATGAT AGCCATGGTG	GAGAGGCTTC TTCAAACCAC CCTGTGTGCT CACGATGATAT TGGTGACACG TTCCTATGTT CCCCAAAGGG CCGAGTGCAC AAGGAAGAGG TCATAGAAAT ATAACCTTGG ATTCAGCAGA	TGAAGCCCTT CACAGCATGG GGTGGCTTTC TGGGAACTCGA GTGGTGACCA CCATATGCAC AAGAGAAGCT CCAATGGGCAG CCTGCTAATA CAATAATAGT GAGTAAGGCA GTGAATTCTC	AGACCACCCC AAACATGAGG TTCCTGTCTG GGGGGGTGGG CAGAGGACTA TAAAATCATT AAATCATG GAGTCGCATT GGACGCACGA AACTGGGATC GATCTGTAAA AAAGCCACAG	TAGTGACACA GATCTTGGAC TTAAAACTT TAGAGAAACT TTTGGATCAC TTTGTGCTA CGCGATGAACA GCGATGAACA TCGCCACTCAG TCGCCGTTTG ATAAATTAAT AGCTTTGGGG TGATGTCTAC	CCTTCTCTAT ACATTGTATC CTGCAAAAAC GCAGTCTAGG AGCTGTGCCA CGTAATAACT ATACTGTCAG CCGCCTTCTT GCCTGCCTCC TAATGTTGG AACGGGAGTA GAGGGGGACAT CCATCCTTCC	CAAGGCCAGA AGCAGCCTGG CCTCATAGAA ATTCGCCATC GCTATAGTGT GTAATTGCT CTACACCGTT CTCTTTGAT CCATAATGCA GGTAAGGCTT TTTAAATTAA CTTAGAAGTA TGGGGGCTGT	CCTCCTAACC AAGCAGAGAG ACACCCAGAG GTGGTGTGAA GGTTAAGCTA ACTGTTATGA ACTGCTATGA ACTGCTATGA ACACTCCTTC AAATGATCAA ACTCCCATCC CTGCCGGGACT
6161 6301 6441 6581 6721 6861 7001 7141 7281 7421 7561 7701 7841 7981 8121	AGGAGTAGCT CTTCCCAAAC GGAGAAACGC TTGGTCTCC TTGAGGCGGT AGGCGTCACA ATCATAACAT TACTGTTAGT TTCTGCACCC GACCATGGAA TCCTGTAGTA AGGAGGAAGG TTATTGGTTA	GAGAGCTACC AAGCACCAAC TGGATATTGC TGGATGTACT GGATGGAGATG GAATGGAGATG GAATATCTGA CTACTGTAGA GCCCCATCTT TTTGCAGCCA ATTATTAATA GGTAGTAAGC CATATGATAG CATATGATAG	ATTTCAGACC TGAGGTCCAA CATCCTGCCC TAAATCCAGG GTGGTGGTCA ACCTGCATAT TCTTTCCCAT ATCCCCCATA ATCCATATGA CACTCCCCGC ACCCCAGGCCC GACTTCCGAG GTCTTTTTT	CTCAAGCTGG GTATTAAAGT TITGACTTCT CAAGCTGACA CAGTGGTGTG GAAATAACTA GGTCTTAGGT GCACTAAGTG AACAAGGCCA AACAAGGCCA CAGCACCGG AGCCACGGTG TITTGGAAGT TICTGGAAGT	AGCCTGAGAA GCCCGAGACT ATATGGTGCC ATGAGAGTTA TGCGGGTTG GACCCTGTAC GGAAGATGGT CAATGCATCG GGAAGATGGT CAATGCATCT GTGTGGGTCA ACTAATGCTT CTGCTTAGAC GCTAATACCT	ACCACACCTC TITTGTGGGA CAGCTCATGG ATGATACCCA GAGGTAGGTG TAGACCAGTG AGAAGGTTTT CAGGGGCTCC CAGGCCCGCG TITAAATTG TCTTACATCC GGATTAGGT	TAGGGTTGGT AGACATCTCA GAGGCCACCG TGGTCAGGGT ATTCTCAACC TTTTTAACTC CAAACTCACC CTAAGGTGAT CTCAGCTTA GTGAGATGG CCTCTCATGA AGCCATGGTG TAAGTACCC	GAGAGGCTTC TTCANACCAC CCTGTGTGCT CACGATGATT TGGTGACACG TTCCTATGTT CCCCANAGGG CCGAGTGCAC CCGAGTGCAC TCATAGAAACACTTGG GCTCATGAAC AGGAAACCAC GCTCATGAAC AGGAAATCAC CACACTGTC	TGAAGCCCTT CACAGCATGG GGTGGCTTTC TGGGAGCTAT GGCAACTCGA CCATATGCAC AAGAGCAC CCATATGCAC CAATGGCAG CCTGCTAATA CAATAATAGCA GAGTAAGGCA GTGAATCTCC CTACTTGTGA	AGACCACCCC AAACATGAGG TTCCTGTGTG GGGGGGGGG CAGAGGGTGGG TAAAATCATT AGGTTGAGAA GAGTGGCTTC ATAGTAGCAA AACTGGGATC GATCTGTAAA AAAGCCACAG GCAGGCCTTC CCTTGGCTCT	TAGTGACACA GATCTTGGAC GATCTTGGACAC TTGAGAAACT TTTGGACAAC TTTGTGGTACA CGCATGATCA CGCATGATCA TCGCACGTCAG TCGCACGTCAC TCAACGACCA	CCTECTEAT ACATEGTATC CTGCAAAAC GCAGTCTAGG AGCTGTGCCA GCTAGTGCCA CCGTATTAACT ATACTGTCAG GCCTGCCTCC TAATTGTTGG AACGGAGACA CCATCCTTCC CCTTGGCCT CCALGGCCG	CAAGGCCAGA AGCAGCCTGG CCTCATAGAA ATTCGCCATC GCTATAGTGT CTATAGTGT CTACACCGTT CTATAGCGT CCATTATGCA GGTAAGGCTT TTTAAATTAA CTTAGAAGTA TGGGGGCTGT GCCCCTGGT GCCCCTGTT	CCTCCTAACC AAGCAGAGAG ACACCCAGAG GTGTGTGAA GGTTAAGCTA ACTGTTATGA AGTCTGTTAA CCTTGCTACC AAATGGTCAA TGCCACACTG ATGCTCATCC CTGCTGGACT TCGCTGGACT
6161 6301 6441 6581 6721 6861 7001 7141 7421 7421 7561 7701 7841 7981 8121 8261	AGCAGIAGCI TIGAGGCGCT AGGCGCTAAAC ATCATAACAT TACTGTTAGT TTCCTTAAA TTCTGCACCC GACCATGGA TCATGGAAGG TTATTGGTA GGGCCTAGA TTATTGGTA GGGACCTGTA	GAGAGCTCAC TGGTACTTGC TGGTACTTGC GATGGAGATG GATGGAGATG TTACAAAGTA GATATATTAG GCTACTGTTGA GCCCCATCTT TTTGCAGCCA ATTATTAATA GGTAGTAAGC CATATGATAG CATATGATAG CTTCCCCAGG CATATGATAG CTTGCAACCTT	ATTICAGACC TGAGGTCCAA CATCCTGCCC TAAATCCAGG GTGGTGGTCA ACCTGCATAT TCTTTCCCAT ATCCCCAATA ATCCCCAATA CACCCCGCC ACCTCCCGAG GACTCCCGAG GACTTCCCGAG GACTTCCCGAG GCCTTCTTTT GACACAGGAG CCCAGGTATA	CTCAAGCTGG GTATTAAAAT TTTGACTTCT CAAGCGTGCG GAAATAACTA GGTCTTAGGT GCAGTATGTG AACAAGGCCA AGCCATGGTG GTCCTGGTGTG GTCCTGGTGTG GTCTTGCTTCT TCCAGACATA AGGGTGCCAG	AGGCTGAGAA ATATGGTGCC ATATGGTGCC ATGAGAGTTA TGCGGGTTG ATACTCTATC GACCCCTGTG GGAAGATGGT CAATGCTT CAATGCTT CTGCTGGTAGAC CTGCTAGAAAT GCTATTGATG	ACCACACCTC TTTTGTGGGA CAGCTATGG ATGATACCCA GAGGTAGGTG TAGACCAGTG CAGGGCTCC CGTGGCCTCC CAGGCCCCCC CAGGCCCCCC TTTAAATTGT CTCTACATCC GGATTAAGTT GGCCAGGTTTT	TAGGGTTGGT AGACATCTAA GAGACCACCG TGTCCAGGGT ATTCTAAGCC TTTTTAACTC CTAAGGTGAT CTCAGCTTAA GTTGAGATGG CCTCCATGA AGCCATGGTG TAAGTGACCT TAGACATCAC	GAGAGGCTTC TTCAAACCAC CCTGTGTGCT CACCAATGAT TGGTGACACG TTCCTATGTT CCCCAATGGT CCCGAGTGCAC AAGAAAGAG ATTACACTTGG ATTACACTGAC AGGAAATCAC CACACTGTC CACACTGTG	TGAAGCCCTT GGCGACTGC GGCGACTTC TGGCAGCTGA GCGCACTGA GCGTGACCA CCATATGCAC CATATGGCCA CCTGCTAATGA CATTATGGCCA GTGAATCTC CTACTGTGA TGTAACCAGG CTCCGAAAGC	AGACCACCCC ANACATGAGG TTCCTGTCTG GGGGGGTGGG CAGAGGACTA TAAAATCATT AGGTTGAGAA GAGTCGCACTT GAACCGGACC AACTGGGATC GATCTGTAAA ANAGCCACAG GCAGGCCTTC CCTTGGCTCT	TAGTGACACA GATCTTGGAC TTAAAAACTT TAGAGAACT TTTGGATCAC TTTGTGTGCTA CTGCTGATCA GCGATGAACA TCGCACTGATG TCGCCTGTTG GATGTCTAC TGAGGACCA CTGAGGACCA	CCTETETAT ACATEGTATC CEGCAAAAC GCAGTETAGG AGCEGTGCCA CGTAATAACT ATACTGTCAG CCGCCTICTT GCEGCCTCC TAATEGTCTG AACGGGAGATA CCATCCTICG CATACTGGCTCC GAAAAGGCCG GAGTETGTA	CAAGGCCAGA AGCACCTGG CCTCATAGAA ATTCGCCATC GCTATAGTGT GTAATTTGCT CTACACCGTT CTCTTTGAT CCTTATGCA GGTAAGGCTT TTTAAATTAA CTTAGAAGTA GGCCGCTGTT GGCCCATGTT GGCCCATGTT GGCCGCATGTG	CCTCCTAACC ANGCAGAGAG GTGAGAGA GTGATGTAA ACTGTTATGA ACTGTTATGA ACTCTGTTAA CCTTGCTAAC ACACTCCTTC ANATGATCAA TGCCACACTG TGCCACACTG TCTATTACTC ACGTTTCTCC CCCTGTGGAT
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СТАБЭСКАКТОВЕТ САКЭБАСКАКТОВЕТ САКЭБАСКАКТОВЕТ САКЭБАСКАКТОВЕТ САКЭБАСКАКТОВЕТ САКЭБАСКАКТОВЕТ САКЭБАСКАКТОВЕТ САКЭБАСКАКТОВЕТ САКЭБАСКАКТОВЕТ САКЭБАСКАКТОВЕТ САКЭБАСКАКТОВЕТ САКЭБАСКАКТОВЕТ САКЭБАСКАКТОВЕТ САКЭБАСКАКТОВЕТ ССЕРЕСТВЕТ ССЕРЕСТВЕТ САКЭБАСКАКТОВЕТ САКЭБАСКАКТОВЕТ САКЭБАСКАКТОВЕТ ССЕРЕСТВЕ ССЕРЕСТВЕТ ССЕРЕСТВЕТ ССЕРЕСТВЕТ ССЕРЕСТВЕТ ССЕРЕСТВЕТ ССЕРЕСТВЕТ ССЕРЕСТВЕ СС	GAGAGGCTTC TICAAACCAC CCTGTGTGC CACGATGTT TGGTGACACG TITCCTATGT CCCCAAAGGA CCGAGTGCAC AAGGAAACAG GTCATGAAA ATTAACCTGG CACGAGTCGC CCCGAGTGCC CCCGAGGCGC CCCGAGGCGC CCCGAGGCGC CCCGAGGCGC TGTCAAGAG ATGTCACACG GGCAGAAGACA ATCCCTCCAC TAAGAAGAGC ACCCTCCACG GGCAGAGACA ATCCCTCCACCAC TAAGAAGAGC CACGAGGGGC ACCCTCCACACG CACGAGGAGCA ATCCCTCCACACG CACGAGGAGCA CACGAGGAGGAGCA CACGAGGAGGAGCA CACGAGGAGCA CACGAGGAGCA CACGAGGAGGAGCA CACGAGGAGGAGCA CACGAGGAGGAGCA CACGAGGAGGAGCA CACGAGGAGGAGCA CACGAGGAGGAGCA CACGAGGAGGAGCA CACGAGGAGGAGCA CACGAGGAGGAGGAGCA CACGAGGAGGAGGAGCA CACGAGGAGGAGGAGGAGGAGGAGGAGGAGGAGGAGGAGG	TGAAGCCCTT GGAGCTTC 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Figure 2

Fragmentation of the rat p75NTR genomic DNA. A 9,372 bp BamHI fragment derived from 5' region of p75NTR (positions from -9,645 to -274) cloned in pBS KS+ (sequence with lower case letters) was digested with BsuRI and Alul. Sequence derived from UCSC Genome Browser on Rat Nov. 2004 Assembly (contigs AABR03076992.1 and AABR03076383.1). Protein binding was detected for fragments marked with green (BsuRI digest) and yellow highlight or underlined (Alul digest). Fragments marked with grey highlight were derived from pBS KS+.







Figure 3

Digestion of a 9372 bp genomic DNA fragment of the rat *p***75NTR gene (cloned in pBS KS vector) with BsuRI and Alul restriction enzymes.** (A) Agarose gel electrophoresis of total digests (T) and gel-isolated fractions 30–300 bp (L) and 300–700 bp (H). M, I kb ladder (Stratagene). (B) The expected digestion pattern generated by sequence analysis with DNAMAN software.



Denaturing PAGE

Figure 4

Identification of the protein binding regions in DNA fragments by a combination of EMSA and denaturing **PAGE.** (A) L and H molecular fractions of corresponding *Bsu*Rl and *Alul* fragments were incubated with (lane +) and without (lane -) PC12 nuclear extract (NE) and analysed by EMSA. Direct phosphoimaging of the wet I mm-thick gel is shown. (B) Denaturing PAGE of the shifted fragments. Lanes - and + show the pool of fragments used in EMSA and shifted bands (smear), respectively. Connecting lines indicate the bands or smear analyzed on two different gels. M, ³²P-labeled 100 bp ladder (Gibco-BRL).

EMSA

proteins and thus may be shifted more frequently than smaller fragments (see also below, Fig. 6). Despite this fact, enrichment of certain fragments in the shifted zone clearly suggests that these may contain regions involved in sequence specific DNA-protein interactions. Consistent with this conclusion, the 737 bp *Alul* fragment overlapped with the EMSA-positive (or shifted) *Bsu*RI 200 bp fragment detected earlier (Fig. 2). To confirm that the fragments identified here contain binding sites for nuclear proteins, an EMSA was carried out using individual fragments that overlapped with the identified ones (Fig. 5). This experiment showed that all three fragments produced specific shifted products.

Practical considerations

Previously, two highly similar methods have been developed for the detection of protein binding sites in different DNAs derived from plasmid, bacteriophages (Mu and Lambda), *E. coli* chromosome or human genome [10,11]. These methods are based on two-dimensional PAGE and allow simultaneous analysis of a large collection of fragments (about 2000). However, some DNA-protein interactions may remain undetected because of low affinity or the low concentration of an individual fragment in a large population of fragments [11].

The strategy developed in this study may be suitable for the initial analysis of genomic (promoter) regions extending up to 10 kb in length, revealing protein binding regions that can be further analysed using DNase footprinting [17,18] and promoter activity tests. It is important to note that nonspecific interactions can frequently occur between proteins and longer (>200 bp) DNA fragments used in EMSA. Nonspecific binding may be reduced if higher concentrations of competitor poly (dIdC) are used (Fig. 6). Therefore, for fragments >200 bp, higher concentrations (up to 1 mg/ml) of competitor must be used. It is recommended that the sufficient concentration of competitor is determined experimentally for each fraction of fragments or individual fragment and nuclear extract.

One of the limitations of traditional EMSA is that some complexes do not withstand the conditions and may produce a smear during electrophoresis. However, as shown here, if the area of the smear is cut out from the gel and the fragments are analyzed, it is possible to identify the fragments undergoing dissociation from the "fragile" complexes (Fig. 4). Alternatively, if the EMSA gel is run at low temperature (+4 °C) or at low voltage, it may be possible to stabilize protein DNA interactions and increase the chance of getting shifted fragile complexes [3].

The strategy described here has several advantages over traditional EMSA. It can be performed with a mixture of

fragments, thus increasing the length of the DNA fragment that can be analysed in a single experiment. It is based on a simple identification of fragments on a denaturing gel and may be used for the detection of labile interactions (complexes that dissociate during electrophoresis). In principle, the method described by Chernov et al [11] may be also applied to smaller fragments (<10 kb) with an additional improvement, i.e without the need of ligation and PCR. However, it is uncertain whether DNA fragments dissociating from the complexes during electrophoresis can be detected with their method.

Nevertheless, our strategy has also some limitations. Firstly, the 3'-end labeling with 3'-5' exonuclease and polymerase activities of Klenow fragment, is relatively inefficient and produces labeled fragments with different specific activities [19]. Also, fragments with G-C-rich structures at their termini are somewhat resistant to 3'-5exonuclease of Klenow fragment and thus are difficult to label in some cases. Secondly, some protein binding sites may be digested with the selected restriction enzymes. Thirdly, gel-elution of fragments based on diffusion alone is time consuming. These limitations, however, can be overcome by end-labeling fragments with bacteriophage T4 DNA polymerase, using restriction enzymes with different recognition specificities (e.g., A/T or G/C rich palindromes) and applying quick gel-elution methods [19]. It is worth to mention that our previous experience with two commercial gel extraction kits [OIAquick® Gel Extraction Kit (QIAGEN, Hilden, Germany) and Invisorb Spin DNA Extraction Kit (InViTek, Berlin, Germany)] has shown that certain purified restriction fragments do not produce mobility shifts if isolated at high temperature (50°C), i. e. using a step necessary for dissolving the gel slice (Fig. 7). This is apparently because of the changes in fragment conformation/kinking introduced at high temperature (K. Kaer and M. Speek, unpublished results). Therefore, the diffusion of fragments may be preferred at least for some DNA fragments.

In summary, the strategy developed here may be easily applied to any genomic fragment with known sequence for which protein binding regions are searched. Finally, selection of restriction enzymes with different recognition sequences may be used to expand the fragment coverage and to narrow down the location of protein binding sites.

Conclusion

We have described a strategy for the detection of protein binding regions in long fragments of genomic DNA. Contrary to the previously described high throughput detection methods [10,11], which can be used to detect high affinity protein binding from the large population of DNA fragments, our strategy uses intermediate (<50) number of fragments and detects low as well as high affinity bind-



F202 F395 F514

Figure 5

Confirmation of the protein binding regions with individual DNA fragments. F202, a 202 bp *Bglll-Ndel* fragment derived from -1.8 kb region partially overlapping with a 359 bp *Alul* fragment; F395, a 395 bp Pstl fragment derived from -6.3 kb region partially overlapping with a 737 bp *Alul* fragment; F514, a 514 bp *Pstl* fragment derived from -6.8 kb region overlapping with a 200 bp *Bsu*Rl fragment (for exact nucleotide positions see Fig. 2). NE, PC12 nuclear extract. A ten-fold excess of the same, but unlabeled fragment was used as a competitor. Arrowheads point at bands resulting from sequence-specific protein-DNA interactions. Note the smearing in case of F514, which suggests dissociation of complex(es) during electrophoresis. The asterisk indicates a weak band, corresponding to a putative specific complex.



Figure 6

The effect of the poly (dl-dC) concentration on the mobility shift of restriction fragments. A poly (dl-dC) concentration range from 100 to 800 μ g/ml was tested with 2-fold differences. At each concentration, the incubation of labeled restriction fragment with PC12 nuclear extract (NE) was performed using two different poly (dl-dC) preparations with the average sizes 250 and 500 bp. C₁, a 202 bp *Bglll-Ndel* fragment and C₂, a 384 bp *Ndel-Mphl* fragment derived from -1.8 kb and -1.6 kb regions of the rat *p75NTR* promoter, respectively. Arrowheads point at the major specific DNA-protein complexes. M, ³²P-labeled 100 bp ladder (Gibco-BRL).

ing regions. Moreover, as shown here, DNA fragments undergoing dissociation from the DNA-protein complexes during electrophoresis can be identified by this strategy. Our results also stress the importance of testing different poly (dI-dC) concentrations to reduce nonspecific interactions between longer restriction fragments and proteins. We believe that the strategy described here is suitable for the initial analysis of genomic regions (e.g., for searching transcription factor binding sites in promoter regions of genes) and can be complemented by DNase footprinting and promoter activity tests in the later stages of study.

Authors' contributions

MS and KM designed the strategy, carried out EMSA and PAGE experiments and drafted the manuscript. KK participated in EMSA experiments. MM helped with coordination and revision. All authors read and approved the final manuscript.

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Figure 7

EMSA experiments with different preparations of DNA fragments. A 275 bp fragment (F275), derived from L1 antisense promoter [20], was gel isolated by using QIAquick[®] Gel Extraction Kit (panel A) or gel-diffusion method described here (panel B), radiolabeled and incubated with (+) or without (-) nuclear extract. The presence (+) or absence (-) of competitor, a 10-fold excess of the unlabeled fragment, is shown. Note that specific mobility shift, shown by arrowhead, is visible only in panel B.

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