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Upstream stimulatory factors, USF1 and USF2 are differentially expressed during *Xenopus* embryonic development

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ABSTRACT

Upstream stimulatory factors (USF) 1 and 2 are members of the basic helix-loop-helix leucine zipper transcription factor family. They are considered to play critical roles in cell-cycle regulation and chromatin remodeling. Their gene expression patterns are considered ubiquitous but have not been fully investigated in terms of embryogenesis. We examined the expression of the genes encoding USF1 and USF2 in Xenopus laevis during embryonic development. Expression of both genes was first detected as maternal transcripts and was observed continuously throughout development. However, in situ hybridization analysis revealed that the two genes were expressed differentially. In the late blastula, both genes were expressed in the blastocoel roof and marginal zone. At the gastrula stage, USF2 was strongly expressed in the sensorial layer of the ectoderm and in the mesoderm, whereas USF1 expression was hardly detectable. From the neurula stage onward, expression of both genes was markedly enhanced in the neural tissues, neural crest, eye and otic vesicle. However, spatial expression of the genes within the neural tube differed in that the strongest USF1 signals were observed in the lateral region of the basal plate and the strongest USF2 ones in the dorsal region of the neural tube. Expression of the two genes occurred in different mesoderm derivatives at the tailbud stage (USF1, somite; USF2, pronephros and lateral plate mesoderm of the tail region). USF1 was expressed in the notochord of the early neurula, but was lost at the stage.

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Upstream stimulatory factor (USF) family proteins are well known as ubiquitously expressed transcription factors (Gregor et al., 1990; Sirito et al., 1994; reviewed by Corre and Galibert, 2005). In vertebrates, there are two types of protein, USF1 and USF2, which share the conserved basic helix-loop-helix leucine zipper (b-HLH-LZ) domains. These two factors form a homo- or heterodimer via their HLH-LZ domains. They bind to the E-box consensus site (CANNTG) and pyrimidine-rich initiator (inr) element adjacent to the start site in the TATA-less promoter. USFs interact with various factors (tissue-specific or general transcription factors, chromatin remodeling enzymes, and preinitiation complexes of general transcription factors). Functional analysis in cultured mammalian cells has indicated that USFs are involved in the gene networks of stress responses, the cell-cycle, and cell proliferation (reviewed by Corre and Galibert, 2005).

Gene-targeting studies have revealed the roles of *USF* genes at an individual level. *USF1/USF2* compound mutant mice show embryonic lethality, and *USF2* null-mutant mice have a smaller than normal mice, and displayed proportionate body features (Sirito et al., 1998). *USF1* null mice lack obvious morphological abnormalities, but they occasionally have epileptic seizures and show enhanced barbering behavior (Sirito et al., 1998). These results indicate that the *USF* genes are important for embryonic development and brain function. However, there have been few in-depth analyses of their role in vertebrate embryonic development, and especially in neural development.

Although expression of the genes encoding USF1 and USF2 is ubiquitous, USF homodimers and heterodimers are found in different ratios in different cell types (Sirito et al., 1994; Viollet et al., 1996). It has been proposed that these factors may control differently target genes by specific interactions via their distinct N-terminal domains with different transcription factors (Corre and Galibert, 2005). Functional differences between USF1 and USF2 may partly underlie the phenotypic differences in the mutant mice. However, clarification of the comparative expression profiles of the two USF genes is necessary for us to understand their biological significances more clearly.

We examined the expression profiles of *Xenopus laevis USF1* and *USF2* in the context of embryonic development. We expected that the analysis of *Xenopus* embryos would give us a clear picture of early embryonic expression patterns. Kaulen et al. (1991) earlier reported the USF1 as a B1 factor, TFIIIA promoter binding protein. However, the expression profile of the gene encoding B1 has not been reported.





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HSUSF1 MKGOOKTAETEEGTVOIOEGAVATGEDPTSVAIASIOSAATFPDPNVKYVFRTENGG-OV 59 Δ MmUSF1 MKGOOKTAETEEGTVOIOEGAVATGEDPTSVAIASIOSAATFPDPNVKYVFRTENGG-OV 59 GgUSF1 MKGQQKAAETEEGTVQIQEGAVATGEDPTSVAIASIQSAATFPDPNIKYVFRTENGGTQV 60 XIUSF1 MKGQQKVADIEEGSVRVQEGAVATGEDPTSVAIASIQSAATFSDPNVKYVFRTENGGTQV 60 *** * ******** HSUSF1 MYRVIQVSEGQLDGQTEGTGAISGYPATQSMTQAVIQGAFTSDDAVDTEGTAAETHYTYF 119 MmUSF1 MYRVIQVSEGOLDGOTEGSGAISGYPATOSMTOAVIOGAFTSDDAVDTEGAAAETHYTYF 119 GQUSF1 MYRVIQVADGQLDGQTEGTSAISGYPAAQSMTQAVIQGAFTSDDAVETEATATETHYTYF 120 XIUSF1 MYRVIQVAEGQLDGQTEGTGAISGFPATQ**SMS----**QGAFT**S**DDAGETDASGPETHYTYF 116 ******* **** ** *** ******* HSUSF1 PSTAVGDGAGGTTSGSTA-AVVTTOGSEALLGOATPPGTGOFFVMMSPOEVLOGGSORSI 178 MmUSF1 PSTAVGDGSGGTTSGSTT-AVVTTQGSEALLGQATPPSTGQFFVMMSPQEVLQGGSQRSI GgUSF1 PTAAVADSSTSAGAGTTATAVVTTQNSEALLGQPTP--TGQFFVMMSPQEVLQGGTQRSI 178 XlusF1 P-TTVTD**s**STST------VVTTHTTDTLIGQAG**S**TAPGQFYVMM**S**PQDVLQGGSQR**S**I 167 **** + basic region Helix-Loop-Helix HSUSF1 APRTHPYSPKSEAPRTTRDEKRRAQHNEVERRRDKINNWIVQLSKIIPDCSMESTKSGQ MMUSF1 APRTHPYSPKSEAPRTTRDEKRRAQHNEVERRRDKINNWIVQLSKIIPDCSMESTKSGQ 238 238 GgUSF1 APRAHPYSPKAEAPRATRDEKRRAQHNEVERRRRDKINNWIVQLSKIIPDCSMENTKSGQ 238 APRTHPY**S**PK**S**DGPRTTRDDKRRAQHNEVERRRRDKINNWIVQLSKIIPDCSMESTKSGQ XlUSF1 227 Leucine-Zipper HSUSF1 SKGGILSKACDYIQELRQSNHRLSEELQGLDQLQLDNDVLRQQVEDLKNKNLLLRAQLRH 298 MMUSFI SKGGILSKACDYIQELRQSNHRLSEELQGLDQLQDDDVLRQQVEDLKNKNLFIRAQLRH 298 GgUSFI SKGGILSKACDYIQELRQSNHRLSEELQGLDQLQDDNVLRQQVEDLKNKNLFIRAQLRQ 298 X1USFI SKGGILSKACDYIQELRQSNLRLSEELQGLDQLQMDNELLRQQVEDLKNKNLIIRAQLRQ 298 X1USFI SKGGILSKACDYIQELRQSNLRLSEELQVDQLQMDNELLRQQVEDLKNKNLIIRAQLRQ 298 HsUSF1 HGLEVVIKNDSN 310 MmUSF1 HGLEVVIKNDSN 310 GqUSF1 HGVEIVIKNESH 310 XIUSE1 HOVETTIKSDGR 299 B HSUSF2 MDMLDPGLDPAASATAAAAASHDKGPEAEEGVELQEGGDGPGAEEQTAVAITSVQQAA-F 59 MMUSF2 MDMLDPGLDPASSATAAAAASHDKGPEAEEGVELQEGGDGPGAEEQTAVAIASVQQAA-F GqUSF2 MDMLDPGLDAAAAS---AAPSHEKSQDGEEGVELQEG--EGAPGEEAAVAIASVPVPGGF 59 55 XIUSF2 MDMLDQGLD-----S-ASHDKGQDTEEVVELHEG-DETSAEEHTAVAIATVQQAA-F 49 ** * ** *** ** HSUSF2 GDHNIQYQFRTETNGGQVTYRVVQVTDGQLDGQGDTAGAVSVVSTAAFAGGQQAVTQVGV 119 MmUSF2 GDHNIQYQFRTESNGGQVTYRVVQVTDGQLDGQGDAAGAVSVVSTAAFAGGQQAVTQVGV 119 GqUSF2 ADSALOYOFRTESNGGOVTYRVVOVSEAPIDGP--EGTAVSVVST--FAGAPOAVAO--- 108 X1USF2 ADHNIQYQFRTENNGGQVTYRVVQVTDGQLDGQGDATGAVSVVSTAAFSGTQQAVAQ--- 106 ****** HSUSF2 DGAAQRPGPAAASVPPGPAAPFPLAVIQNPFSNGGSPAAEAVSGEARFAYFPASSVGDTT 179 MmUSF2 DGAAQRPGPAAASVPTGPAAPFPLAVIQNPFSNGGSPAAEAVSGEARFAYFPASSVGDTT 179 GqUSF2 -----GDGT 138 XIUSE2 -----AVIQNPFSNGGSPTTDAVSGEARFAYFPASTVGDTT 142 HSUSF2 AVSVQTTDQSL-QAGGQFYVMMTPQDVLQTGTQRTIAPRTHPYSPKIDGTRTPRDERRRA 238 MmUSF2 AVSVQTTDQSL-QAGGQFYVMMTPQDVLQTGTQRTIAPRTHPYSPKIDGTRTPRDERRRA 238 GgUSF2 M-SVQ-ADPTLAQAGGQFYVMMTPQDVLQTGTQRSIAPRGHPYSPKVDGTRVPRDERRRA 196 202 basic region Helix-Loop-Helix HsUSF2 QHNEVERRRRDKINNWIVQLSKIIPDCNADNSKTGASKGGILSKACDYIRELRQTNQRMQ 298 OHNEVERRRRDKINNWIVQLSKIIPDCHADNSKTGASKGGILSKACDYIRELRQINQRMQ 298 OHNEVERRRRDKINNWIVQLSKIIPDCHADNSKTGASKGGILSKACDYVRELRQSNQRLQ 256 OHNEVERRRRDKINNWIVQLSKIIPDCNAESTKTAASKGGILSKACDYIRELRQTNQRVQ 262 MmUSF2 GqUSF2 XIUSF2 ********* ******** ******* Leucine-Zipper ${\small C}_{\rm Hs}{\small usf2}_{\rm GGO}{\small vtyrvvQvtdgQldgQgdtaGavsvvstaafagGQQavtQvGvdGaaQrPgPaaasvPPgPaapfPLaviQn}_{148}$ BŁUSFZ GGQVTYRVVQVTDGQLDGQGDTAGAVSVVSTAAFAGGQQAVTQVGVDGATQRPGPAAASVPPGPAAPFPLAVIQN 148 RnUSFZ GGQVTYRVVQVTDGQLDGQGDAAGAVSVVSTAAFAGGQQAVTQVGVDGAAQRPGPAAASVPTGPAAPFPLAVIQN 148 MmUSFZ GGQVTYRVVQVTDGQLDGQGDAAGAVSVVSTAAFAGGQQAVTQVGVDGAAQRPGPAAASVPTGPAAPFPLAVIQN 148 GaUSF2 GGQVTYRVVQVTDDQLEATADGTGAVSVVSTTAFAGAPQAVAQ------AVIQN GGQVTYRVVQVTEDHLEAAGDG-GAVSVVSTAAFAGAQQAVAQ-----AVIQN DrUSF2 GgUSF2 GGQVTYRVVQVSEAPIDGPEGT--AVSVVST--FAGAPQAVAQ------AVIQN

Fig. 1. Amino acid sequence comparisons of USF proteins. Sequence alignments of (A) USF1, entire region; (B) USF2, entire region and (C) a USF2 region including exon 4 of the human sequence. Amino acid sequences of USF proteins (Hs, human; Mm, mouse; Gg, chicken; XI, frog; Rn, rat; Bt, cow; Ol, medaka fish; Dr, zebrafish; Ga, stickleback fish) were aligned by CLUSTALX (1.8) with default parameters (Jeanmougin et al., 1998) and optimized manually. Highly conserved regions characteristic of USF proteins are indicated by boxes (as labeled on the sequences). Residues shown by bold letter in Xenopus laevis USF1 sequence are possible MAP kinase-phosphorylation targets, which are predicted by KinasePhos (2.0) (Wong et al., 2007). Bold rules above sequences in B and C indicate the region corresponding to the human USF2 fourth exon. Asterisks indicate amino acid residues conserved among all species. The position of T153 in human USF1 is indicated by +. USF1 sequences were derived from BAA76541 (human); CAA64627 (mouse); AAV91517 (chicken) and AAH97655 (frog). USF2 sequences were derived from CAA68942 (human); AAB60674 (mouse); AAT27442 (chicken); AAH87339 (frog); AAI28736 (rat); NP_001001162 (cow); ENSORLP00000011299 (medaka); CAK05404 (zebrafish). The amino acid sequence of stickleback USF2 was deduced from the nucleotide sequence data of BT028064 (Gasterosteus aculeatus clone CNB117-F09 mRNA sequence).

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