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(54) 发明名称

一种构建自闭症谱系障碍的小鼠模型的方法

(57) 摘要

本发明提供了一种构建自闭症谱系障碍的小鼠模型的方法,其特征在于,包括:在小鼠受精卵时期利用胚胎显微注射技术胞浆注射甲基化载体以及靶向MeCP2基因TSS区的gRNA载体,得到自闭症谱系障碍的小鼠模型;其中,所述的甲基化载体含有dCas9片段以及人源DNMT3L和DNMT3A催化功能域。本发明的定点甲基化载体,可以有效实现细胞中的位点特异的甲基化。

1. 一种构建自闭症谱系障碍的小鼠模型的方法,其特征在于,包括:在小鼠受精卵时期利用胚胎显微注射技术胞浆注射如SEQ ID NO:11所述核苷酸序列所示的甲基化载体以及靶向MeCP2基因TSS区的如SEQ ID NO:24所述的可表达gRNA载体,得到自闭症谱系障碍的小鼠模型;其中,所述的甲基化载体将人源DNMT3L和DNMT3A催化功能域融合到dCas9片段的N端。

2. 如权利要求1所述的构建自闭症谱系障碍的小鼠模型的方法,其特征在于,所述的甲基化载体通过将人源DNMT3L和DNMT3A的催化功能域连接至dCas9蛋白N端形成。

3. 如权利要求1所述的构建自闭症谱系障碍的小鼠模型的方法,其特征在于,所述的靶向MeCP2基因TSS区的gRNA载体含有至少一条靶向MeCP2基因特异位点的gRNA片段。

4. 如权利要求1所述的构建自闭症谱系障碍的小鼠模型的方法,其特征在于,所述的构建自闭症谱系障碍的小鼠模型的方法还包括:在小鼠受精卵时期利用胚胎显微注射技术胞浆注射如SEQ ID NO:14所述核苷酸序列所示的甲基化对照载体以及靶向MeCP2基因TSS区的如SEQ ID NO:24所述的可表达gRNA载体,得到自闭症谱系障碍的小鼠对照模型,其中,所述的甲基化对照载体通过突变甲基化载体的DNMT3A催化活性位点得到。

5. 如权利要求1至4中任一项所述的构建自闭症谱系障碍的小鼠模型的方法,其特征在于,所述的显微注射的条件为20-80ng/ $\mu$ l甲基化载体或甲基化对照载体,5-50ng/ $\mu$ l靶向MeCP2基因TSS区的gRNA载体。

6. 如权利要求1至4中任一项所述的构建自闭症谱系障碍的小鼠模型的方法在实现体外细胞中位点特异的甲基化进而研究基因特异位点甲基化后对功能的影响中的应用。

7. 如权利要求1至4中任一项所述的构建自闭症谱系障碍的小鼠模型的方法在用于构建MeCP2位点特异甲基化引起的ASD的小鼠模型中的应用。

## 一种构建自闭症谱系障碍的小鼠模型的方法

### 技术领域

[0001] 本发明涉及一种小鼠体内位点特异甲基化的技术,属于表观基因编辑领域,更具体的说涉及基于CRISPR系统与甲基转移酶融合,并结合胚胎显微注射技术进行在体MeCP2基因特异甲基化来构建自闭症谱系障碍的小鼠模型。该技术同时也可用于模拟和构建因其他基因发育过程中甲基化异常而引起生理状态变化的小鼠模型,和在体干预表观修饰异常引起的疾病。

### 背景技术

[0002] 自闭症谱系障碍(Autism spectrum disorders,ASD)是一类复杂的神经疾病,影响了1.5%的新生儿童。ASD患者有社交障碍,焦虑和重复刻板行为等症状。ASD有很强的遗传因素和临床异质性。超过400个基因被证明与ASD有关。然而,现在没有确定的基因突变能在大多数的ASD病人中被证明<sup>1</sup>,同时,越来越多的证据表明环境因素在ASD的发病进程中起到重要作用<sup>2</sup>。例如,同卵双生的两个个体拥有几乎完全相同的基因组序列信息,但在同卵双生患者的ASD病例中,两个个体是否发病和个体之间的发病进程有很大差异,这些结果都暗示了非遗传因素(环境因素)可能在ASD中起到重要作用<sup>3</sup>。环境因素对ASD影响的可能的作用机制是表观修饰的异常,例如,DNA甲基化和组蛋白甲基化的异常。事实上,ASD的相关基因,例如MeCP2,Fmr1和Shank3等,DNA甲基化异常已经在ASD病人中被报道<sup>4-10</sup>。

[0003] MeCP2编码的甲基化CpG结合蛋白2(methylated CpG-binding protein 2)是可以结合上甲基化的CpG位点的转录抑制因子。MeCP2蛋白的功能丧失或功能获得(Loss or gain of function)性突变都会导致RTT综合征或自闭症。ASD患者通常被诊断带有智力障碍,自闭,发育迟缓等症状。正如我们所说ASD有很强的遗传因素的同时,现在也有越来越多的证据说明表观修饰异常在ASD中具有重要作用。MeCP2启动子区的异常高甲基化和MeCP2蛋白的表达量降低已经在ASD患者的额叶皮层中被检测到<sup>7,8</sup>。同时,我们利用ASD病人的外周血在,病人中可以观察到MeCP2基因的转录起始位点(transcription start sites,TSS)区域的异常高甲基化。然而,MeCP2基因的甲基化和ASD表型之间的直接因果关系还未被证明和建立。为了达到这一目的和建立甲基化异常导致的自闭症小鼠模型就必须在实现体内位点特异的甲基化。

[0004] 自从2013年利用CRISPR/Cas9第一次对哺乳动物细胞进行基因编辑以来<sup>11,12</sup>,基因编辑这个领域被摆到了最显眼的位置。CRISPR/Cas系统是来源于细菌和古细菌免疫系统,由RNA介导的可靶向特异性核苷酸序列的核酸内切酶系统,其中来源为化脓性链球菌的Cas9蛋白(SpCas9)使用最为广泛。RNA介导的Cas9起作用主要依靠gRNA和Cas9蛋白所形成的复合物,Cas9与gRNA复合物首先识别2-4个碱基的protospacer临近模块(protospacer-adjacent motif,PAM)。PAM高度保守地存在于靶向序列的5'端或3'端。一旦复合物结合上PAM,DNA双链打开,与gRNA互补配对,随后发生切割。例如SpCas9就由RuvC和HNH功能域在PAM序列上游第三和第四个碱基之间造成基因组双链断裂。随着断裂基因组的修复,在双链断裂位点会随机丢失或插入碱基,造成开放阅读框移码突变,从而达到敲除基因的目的。失

去切割DNA活性的dCas9蛋白保留了与gRNA形成复合物和结合特异性核苷酸序列的能力，dCas9蛋白融合一系列表观修饰因子后可以做为有效操作特异位点表观修饰的工具。2016年陆续有实验室报道利用dCas9进行了体内和体外的定点甲基化和去甲基化<sup>13-16</sup>。这为我们的研究提供了理论基础。

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## 发明内容

[0023] 本发明的目的是开发新型定点甲基化工具,利用工具实现小鼠体内定点甲基化,并建立甲基化异常导致的ASD小鼠模型。

[0024] 为了达到上述目的,本发明提供了一种构建自闭症谱系障碍的小鼠模型的方法,其特征在于,包括:在小鼠受精卵时期利用胚胎显微注射技术胞浆注射甲基化载体以及靶向MeCP2基因TSS区(转录起始区域)的gRNA载体,得到自闭症谱系障碍的小鼠模型;其中,所述的甲基化载体含有dCas9片段以及人源DNMT3L和DNMT3A催化功能域。

[0025] 优选地,所述的甲基化载体通过将人源DNMT3L和DNMT3A的催化功能域连接至dCas9蛋白N端形成。

[0026] 优选地,所述的甲基化载体为DNMT3L-DNMT3A-dCas9质粒。

[0027] 优选地,所述的甲基化载体的序列为SEQ ID NO:11。

[0028] 优选地,所述的靶向MeCP2基因TSS区的gRNA载体含有至少一条靶向MeCP2基因特异位点的gRNA片段。

[0029] 优选地,所述的构建自闭症谱系障碍的小鼠模型的方法还包括:在小鼠受精卵时期利用胚胎显微注射技术胞浆注射甲基化对照载体以及靶向MeCP2基因TSS区的gRNA载体,得到自闭症谱系障碍的小鼠对照模型,其中,所述的甲基化对照载体通过突变甲基化载体的DNMT3A催化活性位点得到。

[0030] 更优选地,所述的甲基化对照载体为DNMT3L-DNMT3A<sub>mut</sub>-dCas9质粒。

[0031] 更优选地,所述的甲基化对照载体的序列为SEQ ID NO14。

[0032] 更优选地,所述的显微注射的条件为20-80ng/ $\mu$ l甲基化载体或甲基化对照载体,5-50ng/ $\mu$ l靶向MeCP2基因TSS区的gRNA载体。

[0033] 更优选地,所述的显微注射的条件为50ng/ $\mu$ l甲基化载体或甲基化对照载体,25ng/ $\mu$ l靶向MeCP2基因TSS区的gRNA载体。

[0034] 本发明还提供了一种甲基化载体,其特征在于,含有dCas9片段以及人源DNMT3L和DNMT3A催化功能域。

[0035] 优选地,所述的甲基化载体的序列为SEQ ID NO:11。

[0036] 本发明还提供了一种甲基化对照载体,其特征在于,通过突变甲基化载体的DNMT3A催化活性位点得到,所述的甲基化载体含有dCas9片段以及人源DNMT3L和DNMT3A催化功能域。

[0037] 优选地,所述的甲基化对照载体的序列为SEQ ID NO:14。

[0038] 本发明还提供了一种载体组合,其特征在于,包括上述的甲基化载体和gRNA载体。

[0039] 优选地,所述的gRNA载体为靶向MeCP2基因TSS区(转录起始区域)的gRNA载体。

[0040] 优选地,所述的靶向MeCP2基因TSS区(转录起始区域)的gRNA载体的序列为SEQ ID NO:24。

[0041] 优选地,所述的载体组合还包括上述的甲基化对照载体。

[0042] 本发明还提供了上述的甲基化载体或甲基化对照载体在用于构建位点特异甲基化的细胞系中的应用。

[0043] 本发明还提供了上述的甲基化载体或甲基化对照载体在实现体外细胞中位点特异的甲基化进而研究基因特异位点甲基化后对功能的影响中的应用。

[0044] 本发明还提供了一种细胞系,其特征在于,其转染了甲基化载体或甲基化对照载体,所述的甲基化载体含有dCas9片段以及人源DNMT3L和DNMT3A催化功能域,所述的甲基化对照载体通过突变甲基化载体的DNMT3A催化活性位点得到。

[0045] 本发明还提供了一种构建小鼠模型的方法,其特征在于,包括:在小鼠受精卵时期利用胚胎显微注射技术胞浆注射定点甲基化载体以及gRNA载体,得到小鼠模型;其中,所述的定点甲基化载体含有dCas9片段。

[0046] 优选地,所述的显微注射的条件为20-80ng/ $\mu$ l定点甲基化载体,5-50ng/ $\mu$ l gRNA载体。

[0047] 更优选地,所述的显微注射的条件为50ng/ $\mu$ l定点甲基化载体,25ng/ $\mu$ l gRNA载体。

[0048] 优选地,所述的gRNA载体为靶向MeCP2特异位点的gRNA。

[0049] 本发明还提供了上述的构建小鼠模型的方法在用于构建MeCP2位点特异甲基化引起的ASD的小鼠模型,用于构建其他基因甲基化异常引起的小鼠疾病模型,用于模拟其他基因发育过程中甲基化异常而引起的生理状态变化的小鼠模型中的应用。

[0050] 本发明还提供了一种实现在体定点甲基化的方法,其特征在于,包括:利用胚胎显微注射技术胞浆注射定点甲基化所用载体,用于在体干预因表观修饰异常引起的疾病。

[0051] 本发明提供了一种位点特异甲基化的工具及利用该工具建立了MeCP2启动子区甲基化引起自闭症的小鼠模型。

[0052] 本发明利用dCas9蛋白融合人源甲基转移酶DNMT3A及其配体DNMT3L蛋白,在小鼠受精卵时期通过利用胚胎显微注射技术胞浆注射DNMT3L-DNMT3A-dCas9载体和靶向MeCP2基因TSS区的gRNA,模拟ASD病人,构建了MeCP2甲基化特异性升高导致的ASD小鼠模型。

[0053] 与现有技术相比,本发明的有益效果是:

[0054] 1,本发明的定点甲基化载体,可以有效实现细胞中的位点特异的甲基化。

[0055] 2,本发明的定点甲基化载体,可以有效实现小鼠体内的位点特异的甲基化。

[0056] 3,本发明的定点甲基化载体具有高准确性,脱靶效应低。

[0057] 4,本发明的MeCP2甲基化异常引起的ASD小鼠模型,可以有效模拟ASD病人的症状。

[0058] 5,本发明的MeCP2甲基化异常引起的ASD小鼠模型可以有效提供DNA甲基化对ASD产生具有直接作用的证据。

## 附图说明

[0059] 图1为DNMT3L-DNMT3A-dCas9和5U6-gRNA的示意图;

[0060] 图2为DNMT3L-DNMT3A-dCas9在Neuro-2a细胞中的编辑结果;

- [0061] (a) 实时荧光定量PCR检测N2a细胞中MeCP2的表达量；
- [0062] (b) MeCP2定点甲基化亚硫酸氢盐测序结果；
- [0063] 图3为MeCP2TSS区附近的gRNA的位置示意图及基因编辑结果；
- [0064] (a) gRNA在TSS区所在位置；
- [0065] (b) T7EN1酶切结果；
- [0066] (c) Sanger测序结果；
- [0067] 图4为DNMT3L-DNMT3A-dCas9在Neuro-2a细胞中编辑后的脱靶效应的分析结果。
- [0068] (a) 简化重亚硫酸盐甲基化测序 (RRBS) 样本之间相关性分析结果；
- [0069] (b) 检测到的CpG位点甲基化水平图谱；
- [0070] (c) 差异甲基化区域平均甲基化水平结果；
- [0071] (d) 差异甲基化区域甲基化百分比结果；
- [0072] (e) 潜在脱靶位点甲基化水平；
- [0073] 图5为DNMT3L-DNMT3A-dCas9在小鼠体内甲基化结果。
- [0074] (a) 甲基化小鼠MeCP2甲基化比例；
- [0075] (b) MeCP2定点甲基化亚硫酸氢盐测序结果；
- [0076] 图6为MeCP2TSS区位点特异甲基化小鼠MeCP2表达量降低。
- [0077] 图7为MeCP2TSS区位点特异甲基化小鼠具有ASD行为表型。
- [0078] (a) 三箱实验(阶段二)结果；
- [0079] (b) 三箱实验(阶段三)结果；
- [0080] (c) 旷场实验结果；
- [0081] (d) 十字高架实验结果；
- [0082] (e) 梳毛实验结果；
- [0083] (f) 悬尾实验结果；
- [0084] (g) 新物体识别实验结果；
- [0085] (h) 食物偏好性社交传递实验结果；

## 具体实施方式

[0086] 如下通过实施例对本发明做进一步解释说明。所描述的实施例仅用于说明本发明的特征,不因此限制本发明。他人一些非本质替换或改进在本发明的保护范围内。实施例中未注明厂商的试剂或仪器均可通过市场购买获得。未详细注明的实验方法,按照常规条件或试剂厂商推荐的方法实施。

### [0087] 实施例1

#### [0088] 1. 定点甲基化系统质粒的构建

[0089] 设计正向引物带有NheI酶切位点及15bp骨架载体同源臂GGGAGACCCAAGCTGGCTAG CACCATGGGACCTAAGAAAAAGAGGAAGGTGGCGGCCGCTGGCGGCAGCATGTTCGAAACCGTGCCTGTG (SEQ ID NO:1),反向引物带有15bp同源臂CCTCTTCTCAGCTGGGTGGCTGCCGCGGGCACTAGTCCGCTGCTGAA GCTGCGCCCCTGCTTAAAAATACTTGAAATATTCT (SEQ ID NO:2),加水溶解至10 $\mu$ M。使用诺唯赞高保真酶试剂盒(Vazyme, p501-d2)扩增人源DNMT3L cDNA(来源为用反转录试剂盒(Takara, DRR036A)反转录获得,模板浓度:1ng/ $\mu$ l)。设计正向引物CCAGCTGAGAAGAGGAAGCCC

(SEQ ID NO:3), 反应引物带有15bp同源臂TAGAGTATTTCTTGTCGCTCTCGGGGGTGGCGCTCTCGCTGGTACCGGGGTCTCGCTGCCGCT (SEQ ID NO:4), 加水溶解至10 $\mu$ M。使用诺唯赞高保真酶试剂盒 (Vazyme, p501-d2) 扩增人源DNMT3A cDNA (来源为用反转录试剂盒 (Takara, DRR036A) 反转录获得, 模板浓度:1ng/ $\mu$ l)。反转录体系, 扩增体系和PCR反应条件如下示:

[0090] 反应体系 10 $\mu$ l

{	水	至 10 $\mu$ l
	试剂	2 $\mu$ l
	总 RNA	500 ng

[0091] PCR反应条件:37 $^{\circ}$ C 15min-----85 $^{\circ}$ C 5S-----4 $^{\circ}$ C hold。总RNA用Trizol提取HEK 293 细胞 (ATCC, CRL-12108) 得到。

[0092] 反应体系 50 $\mu$ l

{	水	20 $\mu$ l
	2xbuffer	25 $\mu$ l
	dNTP	1 $\mu$ l
	For 引物	1 $\mu$ l
	Rev 引物	1 $\mu$ l
	cDNA 模板	1 $\mu$ l
	高保真酶	1 $\mu$ l

[0093] PCR 程序

{	1 cycle {	95 $^{\circ}$ C	5min	
		} 30 cycles {		95 $^{\circ}$ C
	62 $^{\circ}$ C			30S
	72 $^{\circ}$ C			1min
	} 1 cycle {	72 $^{\circ}$ C	5min	

[0094] 4 $^{\circ}$ C  $\infty$

[0095] PCR扩增产物经通过AxyPrep PCR Clean-up试剂盒 (Axygen, AP-PCR-500G) 纯化回收。

[0096] 以1 $\mu$ g的pST1374-Cas9-N-NLS-flag-linker载体 (Addgene ID:44758) 为模板用NheI (NEB, R0131S), buffer为10xCutsmart buffer (NEB, B7200S) 作酶切37 $^{\circ}$ C 孵育1h。酶切体系如下:

[0097] 酶切体系

{	水补至	50 $\mu$ l
	目的片段/载体	1 $\mu$ g
	10xCutsmart buffer	5 $\mu$ l
	NheI 酶	1 $\mu$ l

[0098] 酶切产物用AxyPrep DNA凝胶回收试剂盒 (Axygen, AP-GX-250G) 纯化回收。

[0099] PCR回收产物和酶切回收产物混合后用重组试剂盒 (Vazyme, C215-02) 构建载体,



重组体系如下：

[0100]	重组体系	}	水补至	10 $\mu$ l
			目的片段 1 (DNMT3L)	50 ng
			目的片段 2 (DNMT3A)	50 ng
			载体	50 ng
			5xCE MultiS buffer	2 $\mu$ l
			Exnase MultiS	1 $\mu$ l

[0101] 重组反应即为将重组体系放于37℃孵育30-60min,转化涂板,经Sanger测序得到正确的pSt1374-N-NLS-DNMT3L-L-DNMT3A-L-cas9-NLS质粒。

[0102] 设计正向引物GGACTGGCTATCGGGACAACTCCGTTGGCTG (SEQ ID NO:5),反向引物CCCGATAGCCAGTCCAATAGAGTATTTCTTG (SEQ ID NO:6),加水溶解至10 $\mu$ M。使用诺唯赞点突变试剂盒 (Vazyme, C214-01) 突变D10A位点。设计正向引物CGTGGACGCTATTGTTCCACAGTCCTTCC TCAA (SEQ ID:7),反向引物ACAATAGCGTCCACGTCATAATCGGACAGCCG (SEQ ID:8),加水溶解至10 $\mu$ M。使用诺唯赞点突变试剂盒 (Vazyme, C214-01) 突变H840A位点。设计正向引物GATAAGG CCCGCGTAAGTCTGACAATGTTC (SEQ ID:9),反向引物CCGCGGGCCTTATCGGATCTGGTCAGCACCTT GTT (SEQ ID:10),加水溶解至10 $\mu$ M。使用诺唯赞点突变试剂盒 (Vazyme, C214-01) 突变H863A位点。反应体系如下：

[0103]	反应体系 50 $\mu$ l	}	水	至 20 $\mu$ l
			2xMax buffer	25 $\mu$ l
			dNTP	1 $\mu$ l
			For 引物	1 $\mu$ l
			Rev 引物	1 $\mu$ l
			模板 1 ng/ $\mu$ l	1 $\mu$ l
			高保真酶	1 $\mu$ l

[0104]	PCR 程序	}	1 cycle	{	95 $^{\circ}$ C	5min
			30 cycles	{	95 $^{\circ}$ C	30S
					60 $^{\circ}$ C	30S
					72 $^{\circ}$ C	4min
			1 cycle	{	72 $^{\circ}$ C	5min
				4 $^{\circ}$ C	$\infty$	

[0105] PCR完成后,进行扩增产物Dpn I (NEB, R0176S) 消化,去除甲基化模板质粒,反应体系如下：

[0106] 反应体系 50 $\mu$ l { 扩增产物 50  $\mu$ l  
Dpn I 1  $\mu$ l

[0107] 将反应体系置于37 $^{\circ}$ C孵育1-2h。之后进行重组反应 (Vazyme, C215-01/02), 反应体系如下:

[0108] 反应体系 50 $\mu$ l { 水 至 10  $\mu$ l  
5xCE II buffer 2  $\mu$ l  
Dpn I 消化产物 50-400 ng  
Exnase II 1  $\mu$ l

[0109] 重组反应即为将重组体系放于37 $^{\circ}$ C孵育30-60min, 转化涂板, 经Sanger测序得到正确的pSt1374-N-NLS-DNMT3L-L-DNMT3A-L-dcas9-NLS质粒 (又称DNMT3L-DNMT3A-dCas9质粒), 序列信息见附录序列列表SEQ ID NO:11。

[0110] 设计正向引物GCAGTCCCTCCAATGACCTCTCCATCGTCAACCCTGCTCG (SEQ ID NO:12), 反向引物TCATTGGAGGGACTGCCCCAATCACCAGATCGAAT (SEQ ID NO:13), 加水溶解至10 $\mu$ M。使用诺唯赞点突变试剂盒 (Vazyme, C214-01) 突变DNMT3A催化活性位点。反应体系如下:

[0111] 反应体系 50 $\mu$ l { 水 至 50  $\mu$ l  
2xMax buffer 25  $\mu$ l  
dNTP 1  $\mu$ l  
For 引物 1  $\mu$ l  
Rev 引物 1  $\mu$ l  
模板 1 ng/ $\mu$ l 1  $\mu$ l  
高保真酶 1  $\mu$ l

[0112] PCR 程序 { 1 cycle { 95 $^{\circ}$ C 5min  
30 cycles { 95 $^{\circ}$ C 30S  
60 $^{\circ}$ C 30S  
72 $^{\circ}$ C 4min  
1 cycle { 72 $^{\circ}$ C 5min  
4 $^{\circ}$ C  $\infty$

[0113] PCR完成后, 进行扩增产物Dpn I消化, 去除甲基化模板质粒, 反应体系如下:

[0114] 反应体系 50 $\mu$ l { 扩增产物 50  $\mu$ l  
Dpn I 1  $\mu$ l

[0115] 将反应体系置于37 $^{\circ}$ C孵育1-2h。之后进行重组反应, 反应体系如下:

[0116]	反应体系 50 $\mu$ l	水	至 10 $\mu$ l
		5xCE II buffer	2 $\mu$ l
		Dpn I 消化产物	50-400 ng
		Exnase II	1 $\mu$ l

[0117] 重组反应即为将重组体系放于37 $^{\circ}$ C孵育30-60min,转化涂板,经Sanger测序得到正确的pSt1374-N-NLS-DNMT3L-L-DNMT3Amut-L-dCas9-NLS质粒(又称DNMT3L-DNMT3Amut-dCas9质粒),序列信息见附录序列列表SEQ ID NO:14。

[0118] 设计构建5U6载体的引物,片段1正向引物:ATGCGTCTCAACCGCAGGAGTTCCTGTCTGTTTGTGTTTAGAGCTAGAAAATAGCAAG (SEQ ID NO:15),片段1反向引物ATGCGTCTCGTAAAACACCAGCCTGTGTGCTGCTGCGGTGTTTCGTCCTTTCCACAAG (SEQ ID NO:16),片段2正向引物ATGCGTCTCATTAGAGCTAGAAAATAGCAAGTAAAATAAG (SEQ ID NO:17),片段2反向引物:ATGCGTCTCGGCTCTAAAAC TCTCTCCGAGAGGAGGGAGCGGTGTTTCGTCCTTTCCACAAG (SEQ ID NO:18),片段3正向引物:ATGCGTCTCAGAGCTAGAAAATAGCAAGTAAAATAAGGC,片段3反向引物:ATGCGTCTCGTCTAGCTCTAAAACCGG CCTTGCGGTCCCACTCGGTGTTTCGTCCTTTCCACAAG (SEQ ID NO:19),片段4正向引物:ATGCGTCTCATAGAAAATAGCAAGTAAAATAAGGCTAG (SEQ ID NO:20),片段4反向引物:ATGCGTCTCGAAACCCG GTGGTGGCTTTCTCCACGGTGTTCGTCCTTTCCACAAG (SEQ ID NO:21)。使用诺唯赞高保真酶试剂盒 (Vazyme, p501-d2) 扩增载体pUC57kan-T7-gRNA-U6 (由华大基因按照常规方法合成,或者获得自Addgene, 115520)。载体pUC57kan-T7-gRNA-U6序列信息见附录序列列表SEQ ID NO: 23。扩增体系和PCR反应条件如下所示:

[0119]	反应体系 50 $\mu$ l	水	至 50 $\mu$ l
		2xMax buffer	25 $\mu$ l
		dNTP	1 $\mu$ l
		For 引物	1 $\mu$ l
[0120]	反应体系 50 $\mu$ l	Rev 引物	1 $\mu$ l
		模板 1 ng/ $\mu$ l	1 $\mu$ l
		高保真酶	1 $\mu$ l

[0121] PCR扩增产物经通过AxyPrep PCR Clean-up试剂盒 (Axygen, AP-PCR-500G) 纯化回收,共4个片段。以pGL3-U6-ccdB-EFla-Puromycin载体 (由华大基因按照常规方法合成,或者获得自Addgene, 115519) 为骨架,T4连接酶及其buffer (NEB, M0202L) 和ESP3I酶 (Life, ER0452) 配置切连体系,体系如下:

[0122]	反应体系 10 $\mu$ l	水	至 10 $\mu$ l
		DNA 片段	各 50 ng
		骨架	50 ng
		ESP3I 酶	0.5 $\mu$ l
		T4 连接酶	0.5 $\mu$ l
		T4 buffer	1 $\mu$ l

[0123] 反应程序：(37 $^{\circ}$ C 5min-----16 $^{\circ}$ C 10min)\*10cycle-----37 $^{\circ}$ C 15min-----80 $^{\circ}$ C 15min-----4 $^{\circ}$ C hold。得到的产物取1 $\mu$ l转化涂板，经Sanger测序得到正确的pGL3-5U6-gRNA质粒(又称5U6-gRNA质粒)序列信息见附录序列列表SEQ ID NO:24。pGL3-U6-ccdB-EF1a-Puromycin质粒序列信息见附录序列列表SEQ ID NO:25。DNMT3L-DNMT3A-dCas9和5U6-gRNA的示意图如图1所示。

[0124] 2. 细胞内定点甲基化MeCP2基因

[0125] 利用上述的甲基化系统转染Neuro-2a (N2a) 细胞，过程如下：

[0126] 1) Neuro-2a细胞(来自ATCC)复苏在10cm培养皿(Coming, 430167)中培养，培养基为含有10%胎牛血清(HyClone, SV30087)的DMEM(HyClone, SH30243.01)。放于37 $^{\circ}$ C恒温培养箱培养，培养箱内二氧化碳浓度为5%。当细胞密度达到50-80%时，细胞分盘至6孔板。

[0127] 2) 当每个孔中细胞密度为50%时，用含10%胎牛血清的DMEM培养基换液，培养2小时后，当细胞状态达到最佳时进行转染。每孔转染的质粒量分别是DNMT3L-DNMT3A-dCas9质粒和DNMT3L-DNMT3Amut-dCas9质粒2 $\mu$ g，5U6-gRNA质粒1 $\mu$ g。将质粒混入100 $\mu$ l的Opti-MEM(Gibco, 11058021)培养基中，静置待用。

[0128] 3) 将6 $\mu$ l的Lipofectamine 2000转染试剂(Thermo, 11668019)混入100 $\mu$ l的Opti-MEM培养基，静置5分钟。

[0129] 4) 将混有质粒的Opti-MEM加入混有Lipofectamine 2000的Opti-MEM，慢速吹打混匀，静置20分钟。

[0130] 5) 将混匀静置后的200 $\mu$ l液体加入6孔板中。

[0131] 6) 转染6小时后用含有10%胎牛血清的DMEM培养液换液。

[0132] 7) 转染24小时后，用终浓度为2 $\mu$ g/ml的Puromycin(InvivoGen, nt-pr-1)做药杀处理。

[0133] 8) 转染72小时后收细胞，部分细胞用酚氯仿法抽取基因组DNA，部分细胞用Trizol提取总RNA。

[0134] 抽取的总RNA(Takara, RR047A)按照试剂盒操作方法反转录为cDNA，cDNA做为qPCR模板来检测MeCP2的表达量，qPCR引物序列见附录序列列表SEQ ID:24-27所示(SEQ ID:26-27为GAPDH定量引物，SEQ ID:28-29为MeCP2定量引物)。用诺唯赞qPCR试剂盒(Q331-03)检测MeCP2的表达量。qPCR反应体系如下：

[0135]	反应体系 20 $\mu$ l	{	水	至 20 $\mu$ l
			Mix	10 $\mu$ l
			模板	2 $\mu$ l
			For 引物	1 $\mu$ l
			Rev 引物	1 $\mu$ l

[0136] 酚氯仿抽提得到的基因组DNA用亚硫酸氢盐转化试剂盒(QIAGEN,59104)进行转化。反应体系和反应程序如下:

[0137]	反应体系 140 $\mu$ l	{	水	至 140 $\mu$ l
			DNA	1 $\mu$ g
			Bisulfite Mix	85 $\mu$ l
			DNA Protect Buffer	1 $\mu$ l

[0138]	PCR 程序	{	变性	95 $^{\circ}$ C	5min
			孵育	60 $^{\circ}$ C	25min
			变性	95 $^{\circ}$ C	5min
			孵育	60 $^{\circ}$ C	85min
			变性	95 $^{\circ}$ C	5min
[0139]	PCR 程序	{	孵育	60 $^{\circ}$ C	175min
			Hold	20 $^{\circ}$ C	$\infty$

[0140] 转化后的DNA用亚硫酸氢盐转化试剂盒(QIAGEN,59104)回收,以回收后的产物为模板,进行亚硫酸氢盐PCR(BSP),PCR引物序列见附录序列表SEQ ID:28-32所示(SEQ ID NO:30为BSP上游引物1,SEQ ID NO:31为BSP下游引物1,SEQ ID NO:32为BSP上游引物2,SEQ ID NO:33为BSP上游引物2,SEQ ID NO:34为BSP下游引物2)。用Takara Taq酶和10xbuffer(Takara,R007B)PCR扩增位点特异甲基化靶位点。PCR反应体系和程序如下所示:

[0141]	反应体系 50 $\mu$ l	{	水	至 50 $\mu$ l
			10xbuffer	5 $\mu$ l
			dNTP	3 $\mu$ l
			For 引物	1 $\mu$ l
			Rev 引物	1 $\mu$ l
			模板	1 $\mu$ l
			酶	0.3 $\mu$ l

[0142]	PCR 程序	{	1 cycle	{	95 $^{\circ}$ C	5min
			35 cycles	{	95 $^{\circ}$ C	30S
					60 $^{\circ}$ C	30S
					72 $^{\circ}$ C	30S
			1 cycle	{	72 $^{\circ}$ C	5min
			4 $^{\circ}$ C	$\infty$		

[0143] PCR产物用AxyPrep DNA凝胶回收试剂盒(Axygen, AP-GX-250G)。回收后的产物接入pMD-19T载体(Takara, 6013)中,连接步骤为:将纯化后的PCR产物,与T载体混合,再与Solution 1(Takara, 6013)混合,冰上静置30min后转化。

[0144]	反应体系 5 $\mu$ l	{	T 载体	0.5 $\mu$ l
			PCR 产物	2 $\mu$ l
			Solution 1	2.5 $\mu$ l

[0145] 送至少10个以上阳性单克隆做Sanger测序,表达量结果和BSP结果如图2所示。

[0146] 3.MeCP2TSS区附近的gRNA的位置示意图及基因编辑结果

[0147] 为了获得本发明所使用的gRNA的基因编辑能力,设计了每条gRNA对应的20个碱基互补配对的上下游引物,加水溶解至100 $\mu$ M。用10x buffer 2 (NEB, B7002S), 引物和水配成退火体系。经退火后连接进入pGL3-U6-sgRNA (Addgene, 51133) 载体的BsaI (NEB, R0535S) 酶切位点上,以构建特异性gRNA表达载体。gRNA的引物序列及gRNA序列见附录序列表SEQ ID NO:33-47所示 (SEQ ID NO:35和36为MeCP2sgRNA1的正义链和反义链退火引物,SEQ ID NO:37和38为MeCP2sgRNA2的正义链和反义链退火引物,SEQ ID NO:39和40为MeCP2sgRNA3的正义链和反义链退火引物,SEQ ID NO:41和42为MeCP2sgRNA4的正义链和反义链退火引物,SEQ ID NO:43和44为MeCP2sgRNA5的正义链和反义链退火引物,SEQ ID NO:45和49分别为MeCP2sg1-5的序列)。退火体系和退火程序如下所示:

[0148] 退火体系

水补至	20 $\mu$ l
上游引物	9 $\mu$ l
下游引物	9 $\mu$ l
10x buffer 2	2 $\mu$ l

[0149] 退火程序

95 $^{\circ}$ C	5 min
95-85 $^{\circ}$ C	-2 $^{\circ}$ C/s
85-25 $^{\circ}$ C	-0.1 $^{\circ}$ C/s
4 $^{\circ}$ C	$\infty$

[0150] 利用限制性内切酶BsaI (NEB, R0535S) 对pGL3-U6-sgRNA (Addgene, 51133) 质粒进行酶切以得到线性化gRNA载体。酶切体系如下所示:

[0151] 酶切体系

水补至	50 $\mu$ l
载体	1 $\mu$ g
10xCutsmart buffer	5 $\mu$ l
BsaI 酶	1 $\mu$ l

[0152] 酶切产物用AxyPrep DNA凝胶回收试剂盒 (Axygen, AP-GX-250G)。回收后的产物连接入pMD-19T载体 (Takara, 6013) 中, 连接步骤如下:

[0153] 将纯化后的PCR产物, 同T载体混合, 再与Solution 1混合, 冰上静置30min后转化。

[0154] 反应体系 5 $\mu$ l

T 载体	0.5 $\mu$ l
PCR 产物	2 $\mu$ l
Solution 1	2.5 $\mu$ l

[0155] 送至少10个以上阳性单克隆做Sanger测序。

[0156] MeCP2TSS区所用gRNA切割效率如图3所示, 所用PCR引物序列见附录列表SEQ ID: 50-51所示 (SEQ ID: 50和51分别为PCR产物的上游和下游引物), 图3中对比所用的序列范围见附录列表SEQ ID: 52-56 (SEQ ID: 52-56分别为图3中MeCP2sg1-5对比时展示序列)。

[0157] 4. MeCP2小鼠体内甲基化编辑

[0158] 为了获得甲基化系统在MeCP2基因上编辑后的脱靶效应, 本发明利用限制性代表区域甲基化测序 (RRBS) 对所选的5条gRNA对应预测脱靶位点所在100bp范围的区域进行了甲基化水平分析。RRBS可以检测到131个预测脱靶位点序列, 其中有3个位点的甲基化水平略有上升 (99.7% vs 93.81%, 99.55% vs 96.13% 和 3.29% vs 0.16%)。图4中代表性结果序列信息见附录列表SEQ ID NO: 57-96 (SEQ ID NO: 57-64为MeCP2sg1的代表脱靶位点序列, SEQ ID NO: 65-72为MeCP2sg2的代表脱靶位点序列, 74-80为MeCP2sg3的代表脱靶位点序列, 81-88为MeCP2sg4的代表脱靶位点序列, 89-96为MeCP2sg4的代表脱靶位点序列)。因此, 本发明的甲基化系统脱靶效率低。

[0159] 5. MeCP2小鼠体内甲基化编辑

[0160] 利用“定点甲基化系统质粒的构建”所述系统进行胚胎显微注射,过程如下:

[0161] 1) 超排4周C57BL/6母鼠后与C57BL/6雄鼠合笼交配。0.5天后,取母鼠输卵管,收集受精的卵子。

[0162] 2) 将终浓度为50ng/u1的pSt1374-N-NLS-DNMT3L-L-DNMT3AL-dCas9-NLS载体(即pSt1374-N-NLS-DNMT3L-L-DNMT3A-L-dcas9-NLS质粒)和25ng/u1的pGL3-5U6-gRNA载体的混合液进行胞浆注射进入一细胞胚胎中。

[0163] 3) 注射后的胚胎培养于KSOM (Merck,MR-106-D) 中,能正常发育至二细胞期的胚胎移植如代孕ICR母鼠输卵管内。

[0164] 4) 小鼠出生后进行编号。

[0165] 酚氯仿抽提得到的鼠尾基因组DNA用亚硫酸氢盐转化试剂盒 (QIAGEN,59104) 进行转化。反应体系和反应程序如下:

[0166]	反应体系 140 $\mu$ l	}	水	至 140 $\mu$ l
			DNA	1 $\mu$ g
			Bisulfite Mix	85 $\mu$ l
			DNA Protect Buffer	1 $\mu$ l
[0167]	PCR 程序	}	变性	95 $^{\circ}$ C 5min
			孵育	60 $^{\circ}$ C 25min
			变性	95 $^{\circ}$ C 5min
			孵育	60 $^{\circ}$ C 85min
			变性	95 $^{\circ}$ C 5min
			孵育	60 $^{\circ}$ C 175min
			Hold	20 $^{\circ}$ C $\infty$

[0168] 转化后的DNA用亚硫酸氢盐转化试剂盒 (QIAGEN,59104) 回收,以回收后的产物为模板,进行亚硫酸氢盐PCR (BSP),PCR引物序列见附录序列列表SEQ ID:28-32所示 (SEQ ID NO:30为BSP上游引物1,SEQ ID NO:31为BSP下游引物1,SEQ ID NO:32为BSP上游引物2,SEQ ID NO:33为BSP上游引物2,SEQ ID NO:34为BSP下游引物2)。用TakaraTaq酶和10xbuffer (Takara,R007B) PCR扩增位点特异甲基化靶位点。PCR反应体系和程序如下所示:

[0169]	反应体系 50 $\mu$ l	}	水	至 50 $\mu$ l
			10xbuffer	5 $\mu$ l
			dNTP	3 $\mu$ l
			For 引物	1 $\mu$ l
			Rev 引物	1 $\mu$ l
			模板	1 $\mu$ l
			酶	0.3 $\mu$ l



[0170] PCR 程序

{	1 cycle	{	95°C	5min
	35 cycles	{	95°C	30S
			60°C	30S
			72°C	30S
1 cycle	{	72°C	5min	
			4°C	∞

[0171] PCR产物用AxyPrep DNA凝胶回收试剂盒(Axygen, AP-GX-250G)。回收后的产物接入pMD-19T载体(Takara, 6013)中,连接步骤为:将纯化后的PCR产物,与T载体混合,再与Solution 1(Takara, 6013)混合,冰上静置30min后转化。

[0172] 反应体系 5 $\mu$ l

{	T 载体	0.5 $\mu$ l
	PCR 产物	2 $\mu$ l
	Solution 1	2.5 $\mu$ l

[0173] 送至少10个以上阳性单克隆做Sanger测序,表达量结果和BSP结果如图5所示。图5. 胚胎显微注射小鼠甲基化测序分析。(a) 雄鼠鼠尾甲基化水平, Treatment为甲基化组, Control为对照组; (b) 代表性的MeCP2DNA甲基化小鼠的DNA甲基化模式, Treatment为甲基化组, Control为对照组。

[0174] 取出生后8周小鼠的海马组织,将组织取出,放在1.5ml EP管中,使用组织匀浆机使其均匀。预冷的PBS洗三次。按1ml裂解液加10 $\mu$ lPMSF(100mM),摇匀置于冰上。(PMSF要摇匀至无结晶时才可与裂解液混合)。一个样加400 $\mu$ l的混合裂解液,冰上30min,为使细胞充分裂解培养瓶要经常来回摇动。消化后12000 $\times$ g, 5min, 4°C,取上清, -80°C储存。用提取出蛋白跑SDS-PAGE胶, 80V电压30分钟,后120V电压60分钟。跑好的胶转膜到PDVF膜,条件为恒流250A, 90分钟。转膜完成后, 5%脱脂牛奶封闭1小时, TBST漂洗3次,每次5-10分钟, MeCP2(Cell Signaling, 3456T)一抗1:10004°C过夜,第二天TBST漂洗3次,每次5-10分钟,加(1:5000)稀释于5%脱脂奶粉中的二抗(ABclonal, AS014\_100 $\mu$ l)室温孵育2小时, TBST漂洗3次,每次5-10分钟。孵育好的PVDF膜用超敏显色液(Merck/Millipore, WBKLS0100)显色,检测蛋白表达程度。图6. 胚胎显微注射小鼠MeCP2表达量检测分析。13#和34#为甲基化小鼠, Control为对照小鼠。

[0175] 6. MeCP2甲基化小鼠具有ASD表型

[0176] MeCP2缺陷的小鼠具有明显的ASD症状,例如社交障碍,重复刻板行为和焦虑等。为了确认MeCP2甲基化的小鼠是否也有类似症状,从一系列行为学实验分析了MeCP2甲基化小鼠的表型。分析结果如图7所示, (a-b) 三箱实验结果结果, (a) 三箱实验phase 2行为结果, (b) 三箱实验phase 3行为结果; (c) 旷场行为结果; (d) 十字高架行为结果; (e) 梳毛实验结果; (f) 悬尾实验结果; (g) 新物体识别实验结果, 左边为新旧物体识别时间百分比, 右边为新旧物体识别时间; (h) 食物偏好性社交传递实验结果, 左边为食物摄入重量, 右边为不同食物摄入百分比。在三箱实验中, MeCP2甲基化小鼠对陌生小鼠显示较少的兴趣, 倾向于靠近熟悉的小鼠, P值小于0.01和P值小于0.001; 在梳毛实验中, MeCP2甲基化小鼠呈现出更多

的重复刻板行为,P值小于0.01;在高架十字迷宫实验中,MeCP2甲基化小鼠在开臂中时间比对照组小鼠少,提示实验组小鼠呈现焦虑行为,P值小于0.01;在旷场实验中,MeCP2甲基化小鼠总运动距离减少,运动能力降低,P值小于0.05;在新物体识别实验中,MeCP2甲基化小鼠显示记忆能力更强,P值小于0.01;在食物偏好性社会传递实验(STFP)中,MeCP2甲基化小鼠缺失对肉桂(Cin)和可可粉(Coc)的偏好性,提示社交能力降低,P值小于0.01和P值小于0.001。以上所有实验证明了MeCP2甲基化小鼠具有ASD表型。

[0177] 以上所述仅为本发明较佳实施例而已,并不用以限制本发明,凡在本发明的精神和原则之内,所作的任何修改、等同替换、改进等,均应包含在本发明的保护范围之内。

## 序列表

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<110> 上海科技大学

<120>一种构建自闭症谱系障碍的小鼠模型的方法

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<170>PatentIn version 3.5

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[0179]

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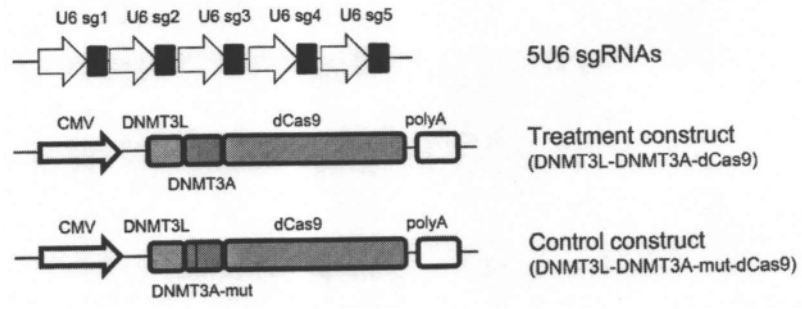


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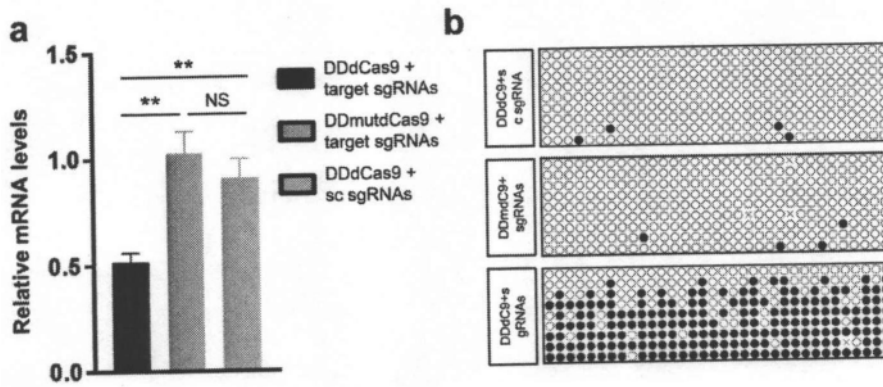


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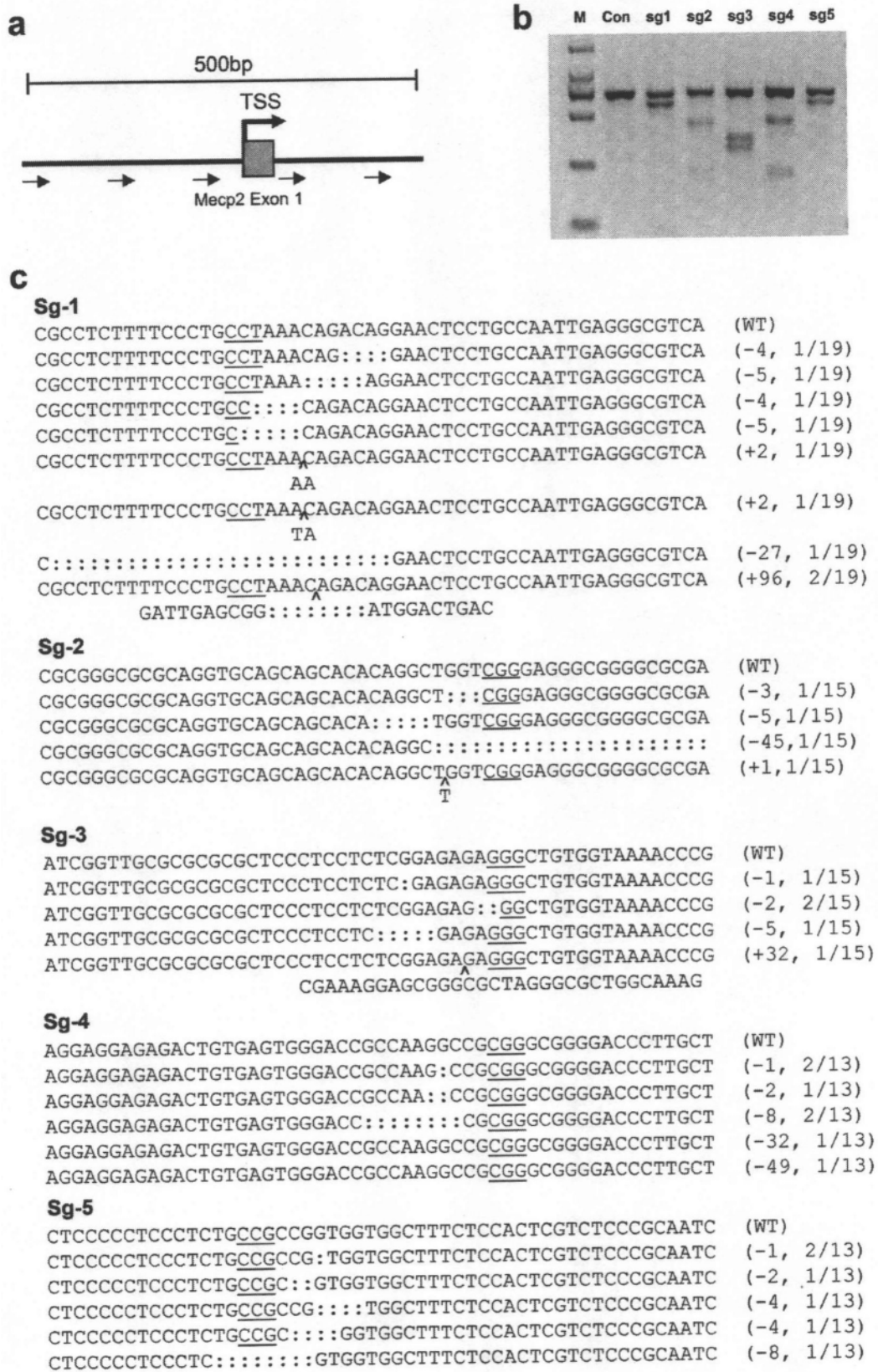


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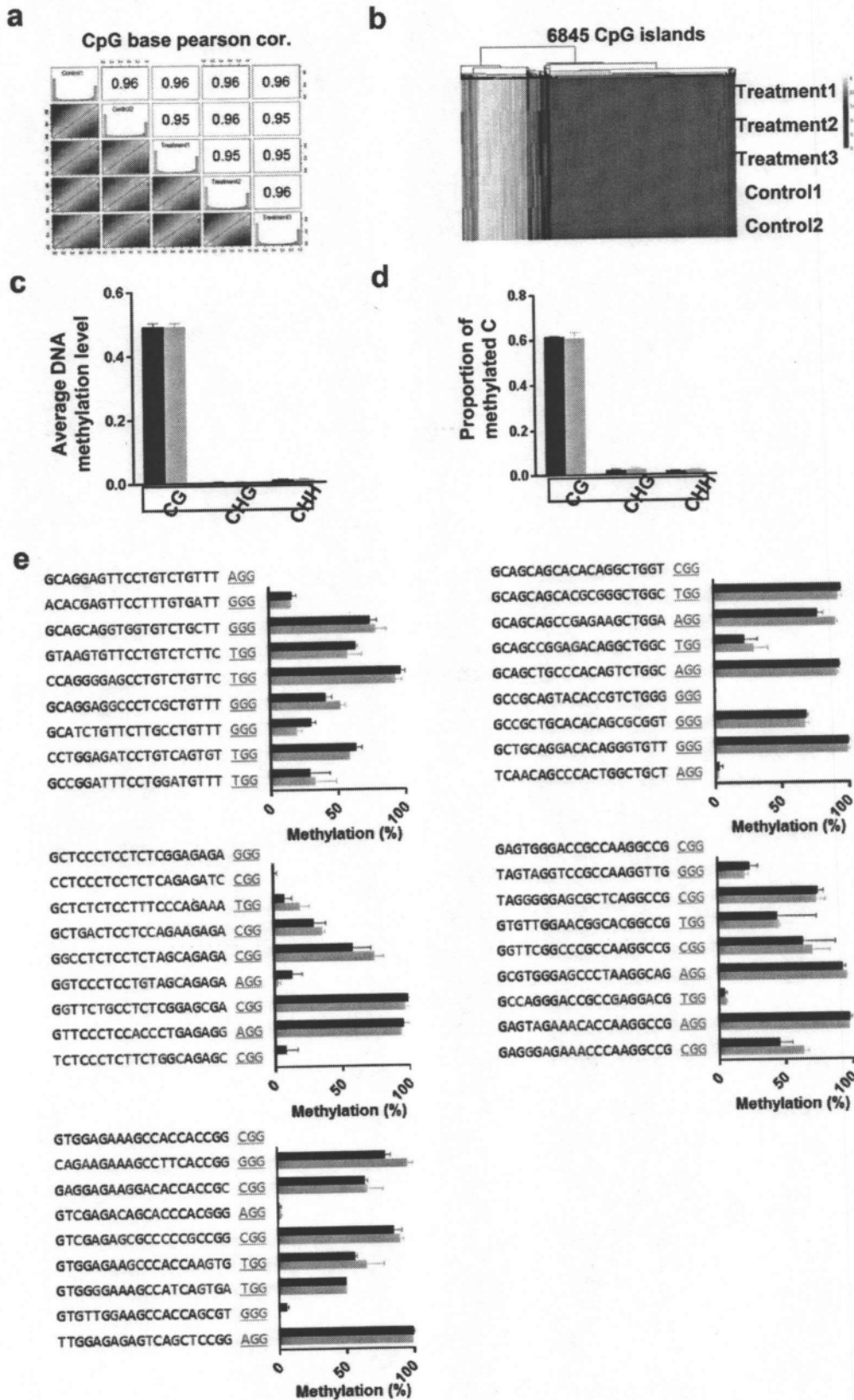


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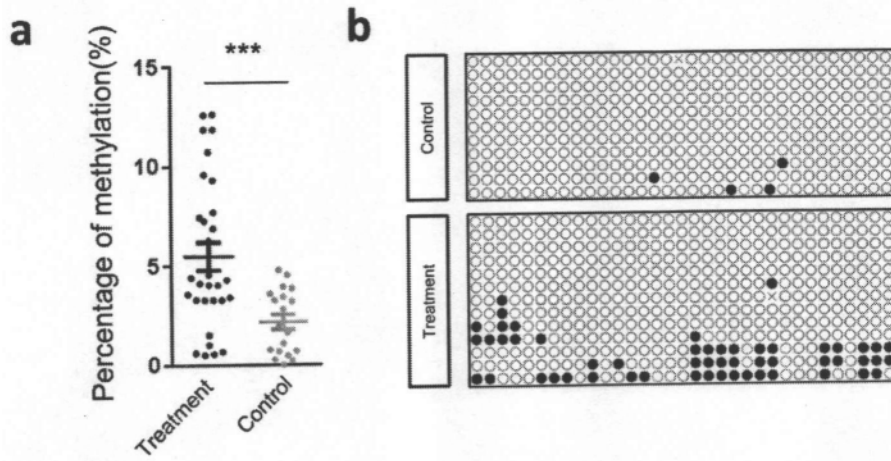


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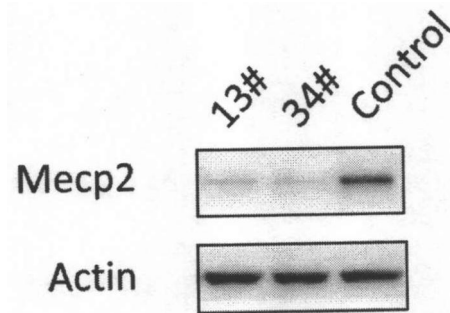


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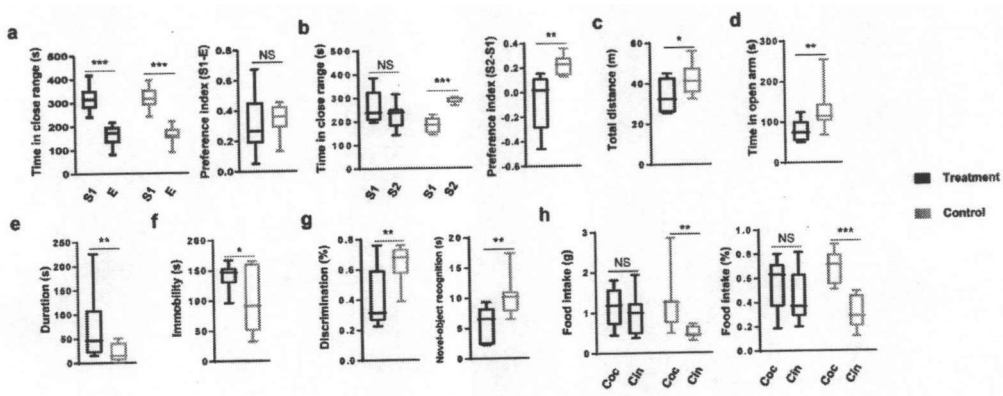


图7