11A　　脸识别

虽然人类认知非常有趣，对人类认知的分子研究却罕见。通常，先在动物研究某些基因，然后在人类研究它们。这种途径限制了研究在动物必需有的表型，而且常常是低等动物，因为在非人灵长类动物很难通过功能研究发现基因。因此，对于只在人类存在的认知、或在低等动物不存在的认知进行分子研究，远远落后于对于简单行为的分子研究。同种动物之间相互识别脸既是很高级的视觉认知，也是社会认知。对此，科学发掘了很多现象，也有一些机理研究，但理解有限。

11A1　脸识别能力

人识别脸的能力强于黑猩猩和猴（Rosenfeld and van Hoesen，1979；Parr，2011）。黑猩猩、猴、绵羊、鸟类（鸡和鸽）、狗等动物也有脸识别细胞（Kendrick and Baldwin，1987；Ryan and Lea，1994；Kendrick *et al.*,1996；Pascalis and Kelly，2009）。绵羊不仅有识别绵羊脸的细胞，还有识别人脸、狗脸的细胞（Kendrick and Baldwin，1987）。羊羔一到两个月认识母亲的脸（Kendrick *et al.*，1998）。雌绵羊还对雄绵羊的脸有偏好（Kendrick *et al.*, 1995）。低等动物一般依赖嗅觉，但有两种蜂（wasps，*Polistes fuscatus* 和 *Polistes metricus*），*P fuscatu* 是群居的、*P metricus* 是独居的，前者有识别个体脸的能力，后者没有（Sheehan and Tibbets, 2011）。

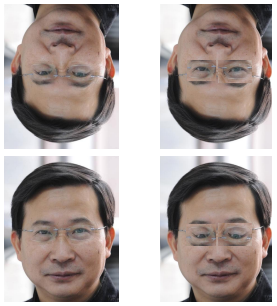

图 11-19　倒置效应

脸识别能力有倒置效应，对正立的脸敏感性远远大于倒置的脸（Yin，1969；Thompson，1980）。

用行为检测显示人对脸的关注在出生很早期就可能出现：9 分钟左右就对脸的反应大于其他（Goren，Sarty and Wu，1975），5 周就注视脸（Haith, Bergman and Moore, 1977），对脸是否好看也有不同的反应（Slater，1998，2000）。在 4 天区分不带围巾的母亲与其他人的脸、35 天区分带围巾的母亲和其他人的脸（Bushnell，Sai and Mullin，1989；Walton，Bower and Bower，1992；Pascalis *et al.*, 1995；Bruce *et al.*, 2000；Bartrip，Morton and De Schonen，2001）。3 个月识别熟悉的脸（De Haan *et al.*，2001）。用 fMRI 检测观察到，两个月的婴儿的对脸反应脑区被脸激活情况类似成人，但脸还激活婴儿的语言区域（Tzourio-Mazoyer *et al.*，2002）。脸激活与成人一样在 9 岁儿童（Gathers *et al.*，2004）、或 12 岁（Golarai *et al.*，2007）。黑猩猩在 4 周左右识别母亲的脸（Myowa-Yamakoshia，2005）。

11A2　对脸特异反应的神经细胞

1980 年代的一系列电生理实验证明猴的神经元对脸有特异反应（Bruce，Desimone and Gross,1981;Perret, Rolls and Caan,1982; Desimone *et al*., 1984; Perrett *et al*., 1984, 1985a, 1985, 1988b; Rolls, Baylis and Leonard, 1985; Saito *et al*., 1986; Perret, Mistlin and Chitty, 1987）。

初级视皮层 V1 继续投射到更高的区域，分为识别 where（物体空间位置）的背侧通路和识别 what（物体本征）的腹侧通路。

腹侧通路从 V1 到 V2、V4、及更远的区域，其可分辨的图像特征越来越复杂（Kobatake and Tanaka，1994）。颞下皮层（inferotemporal cortex，IT）可以识别更复杂的图形，如：圆、方块、多刺圆、手等（Gross, Bender and Rocha-Miranda，1969；Gross, Rocha-Miranda and Bender，1972）。

普林斯顿大学心理系科学家在猴的 IT（Gross, Rocha-Miranda and Bender，1972；Perret *et al.*, 1982；Desimone *et al.*, 1984）和颞上回（superior temporal sulcus，STS）（Bruce *et al.*, 1981）发现了识别脸的细胞，其中 IT 的脸识别细胞几乎都对脸特异反应，而对其他物体没有反应（Desimone *et al.*, 1984）。

STS 多感觉区域有只对脸反应的细胞（Bruce *et al.*, 1981）。例如，记录 497 个 STS 细胞，48 个只对脸反应，被脸持续激活，28 个细胞在脸有转向、或颜色、大小、距离变化后反应不变（Perret, Rolls and Caan，1982）。早期在 IT 一次记录中，41 个没有反应，110 个有反应的细胞中，66 个有选择性反应，其中 20 对形状反应、2 个对手反应、3 个对脸有选择性反应（Desimone *et al.*, 1984）。可以比较对脸和物体、脸和身体的反应，找到对这三种分别有选择性反应的细胞（Pinsk et al., 2005）。通过 fMRI 辅助确定电生理电极插入位置，可以找到特定区域内 97%的细胞都对脸有选择性反应（Tsao *et al*., 2006; Friewald, Tsao and Livingston, 2007），说明有脸特异区块（patch）。用脑表面光学成像观察，可以看到对脸呈现有选择性反应的脑区紧密相连（Wang, Tanaka and Tanifuji, 1996, 1998）。从而提出可能有脸朝向的功能柱（Tanaka，2003）。功能核磁共振实验也支持具有相似朝向选择性的面孔细胞在皮层上聚集（Dubois *et al*., 2015）。

脸识别细胞对于脸的要求是一个圆加两点一杠（大体相当于脸、眼和嘴）（Kobatake and

Tanaka，1994）。对脸有全面的识别和部件的敏感（Freiwald，Tsao and Livingston，2009）。在猴的脸识别细胞研究中，提出抑制性神经元可能对于脸识别很重要，去除 GABA 的抑制性作用后，原对脸（和其他物体）有特异反应的细胞失去反应特异性（Wang，Fujita and Murayama，2000）。用微电流刺激猴的面孔加工脑区 50-200 毫秒，可以增加其对脸的反应以及对个人面孔的识别（Afraz, Kiani and Esteky, 2006； Moelle *et al*., 2017）。

猕猴面孔脑区中较低级区域的神经元对面孔朝向非常敏感，而高级区域的神经元则可区分不同个体的面孔，且反应不依赖于面孔朝向，说明高级区域表征面孔个体这一抽象概念 (Freiwald and Tsao, 2010)。进一步的研究对面孔个体的具体编码方式进行了探索，用计算模型生成上千张参数化的面孔，给动物呈现面孔图片的同时记录猕猴的面孔脑区，发现面孔细胞的反应和面孔模型中的抽象特征呈简单的线性关系，从~200 个细胞的反应可相当准确地重构呈现给动物的原始面孔 （Chang and Tsao, 2017）。

人对脸反应的脑区类似于猴（Tsao *et al*., 2003; Tsao, Moellet and Freiwald, 2008；Pinsk *et al*., 2009；Srihasam *et al*., 2012）。在开颅手术的病人经过允许能用颅内记录事件相关电位改变（Allison *et al*., 1999; McCarthy *et al*., 1999, Puce, Allison and McCarthy, 1999），记录到脸特异反应。也直接记录到神经细胞对脸反应（Kreiman, Koch and Fried，2000）。更多的是用正电子扫描（PET）（Sergent，Ohta and MacDonald，1992；Haxby *et al*., 1994）和 fMRI（Malach *et al*., 1995；Puce *et al*., 1996; Clark *et al*., 1996; Kanwisher, McDermott and Chun，1997；McCarthy *et al*., 1997）。可以分别观察几个脑区（FFA、OFA 和 fSTS）对脸的部件和构型的敏感性（Liu, Harris and Kanwisher，2010）。跨颅磁刺激（TMS）是一种研究脑功能的方法（Walsh and Cowey，2000）。用 TMS 作用于特定脑区，可以观察到脸反应的变化（Pitcher *et al*., 2007, 2008, 2009）。FFA 对脸的部件和构型都敏感，OFA 和 fSTS 只对真的脸部件反应、对其构型不反应（Dzhelyova, Ellison and Atkinson, 2010）。

11A3 先天脸盲的遗传性

人类有不能识别脸的个体，诊断为脸盲（prosopagnosia，faceblind）（Bodamer，1947），分为先天型（发育型）和获得型。脸盲者可以识别其他物体，而不能识别脸（Farah, Levinson and Klein, 1995； Farah, 1996; Henke *et al*., 1998; Nunn, Postma and Pearson, 2001; Duchaine and Nakayama, 2005; Duchaine *et al*., 2006; Li and Song, 2007; Riddoch *et al*., 2008）。也有患者可以识别脸但不能识别其他物体（Feinberg *et al*., 1994; Moscovitch, Winocur and Behrmann，1997；McMullen，Fisk and Phillips，2000；Germine *et al*., 2011）。对于脸盲的机理，有多种解释，有些脸盲可能确实是脸识别能力的特异变化（Duchaine，2006）。

后天获得的脸识别异常，可以是病变或外伤（Yin, 1970; Meadow *et al*., 1974; Landis *et al*., 1986; Barton *et al*., 2002；Bouvier and Engel，2006；Schiltz *et al*., 2006； Steeves *et al*., 2006）。右脑单侧外伤就可以导致脸盲。如果可以在脑成像观察到病变部位，有助于了解参与脸识别的脑区（Riddoch *et al*.,2008）。这些可以与在正常人脑进行的核磁共振成像、外科手术人脑电生理记录相辅相成（Kanwisher, McDermott and Chun，1997；Tsao *et al*., 2003；Barraclouth and Perret，2011）。

双生子研究显示脸识别能力有高度遗传性（Polk *et al*., 2007；Wilmer *et al*.，2010；Zhu *et al*., 2010）。先天脸盲(congenital prosopagnosia, CP)，也称为发育性或遗传性脸盲(OMIM 610382)，最初在1976年被报道(McConachie, 1976) 是对脸的视觉学习和识别的选择性损害，缺乏任何可以检测到的神经损伤(Behrmann and Avidan, 2005; Damasio et al., 1990; Duchaine and Nakayama, 2006b; Gruter et al., 2008; Kress and Daum, 2003; McConachie, 1976; Nunn et al., 2001; Susilo and Duchaine, 2013)。问卷式的筛选方法(Kennerknecht, 2021; Kennerknecht et al., 2006; Kennerknecht et al., 2008a; Kennerknecht et al., 2007)与行为测试(Bowles et al., 2009) 都估计一般人群CP发病率在1.8 to 2.9%，全球估计数千万CP个体。家系研究(De Haan, 1999; Dobel et al., 2007; Duchaine et al., 2007; Galaburda and Duchaine, 2003; Grueter et al., 2007; Johnen et al., 2014; Kennerknecht et al., 2006; Kennerknecht et al., 2008b; Kennerknecht et al., 2007; Lee et al., 2010; McConachie, 1976; Schmalzl et al., 2008) 和双生子研究 (McKone and Palermo, 2010; Polk et al., 2007; Wilmer et al., 2010; Zhu et al., 2010) 提示CP与脸识别能力具有高度遗传性。家谱分析观察到简单的常染色体显性遗传模式(De Haan, 1999; Duchaine et al., 2007; Grueter et al., 2007; Kennerknecht et al., 2006; Lee et al., 2010; Schmalzl et al., 2008)，显示单个基因的突变可以导致脸识别缺陷。这些表明经典遗传学和基因组学可以用于研究脸识别。

11A4 脸识别的分子遗传学研究

对人类疾病的遗传研究非常成功(Gusella et al., 1983; Schrott et al., 1972; Tsui et al., 1985)。

对于用遗传学研究的可行性来说，没有必要假定人类认知与疾病有根本的差别。遗传学提供了可以研究人类认知的无创途径。近十年来，我们实验室进行了几次人类认知的全基因组相关研究(GWAS)，从记忆、社会从众性、到视觉认知的感知切换和下行控制(Chen et al., 2018a; Chen et al., 2018b; Zhu et al., 2019; Zhu et al., 2016; Zhu et al., 2018; Zhu et al., 2020)。虽然我们发现了相关的标记，但我们不知道涵盖标记的基因、或标记附近的基因与所研究的认知有没有因果关系。遗传学上，大家系的连锁分析成功地找到人类疾病的基因突变。因此，我们决定进行人类遗传分析，寻找影响脸盲的基因(Sun et al., 2024)。

我们从一个含18位日常生活中识别脸困难的大家系出发，发现了一个CP 罹患基因(*MCTP2*)，编码“多重 C2 区域跨膜 2”蛋白质。进一步研究获得更多证据：1) 连锁分析常染色体显性 CP 家庭 A 发现位于 15q26.1-q26.2 的 CP 位点；2) 一个 *MCTP2* 基因的特有突变 c.2147T>G (p.I716S) 是A家系中在MCR全基因组测序找到的唯一完全与CP共分离的可以改变蛋白质序列的突变；3) 从2904人组成的队列中找到的75位脸识别困难的个体中7位脸盲者中发现 *MCTP2* 基因5个罕见突变；4) 这7位脸盲者中，4位的家族成员愿被分析，皆显示基因型与表型的相关性；5) 1757受试者的另一队列有16位携带与第4点里面3位脸盲个体相同移码缺失突变c.239delG (p.S80fs)，其中14愿被进一步分析。14位携带者日常脸识别行为不同于来自同一队列的19位非携带者；6) 14位的4位有无疑的脸盲，其中两个家系愿被分析，结果都支持 c.239delG (p.S80fs) 与脸盲相关，进一步的支持来自更多家系，他们发展了明确的策略用非脸的线索克服其脸识别困难；7) 在1928位组成的队列基因相关分析也检测到了 *MCTP2* 基因罕见等位基因与脸识别能力的相关性；8) 在神经成像研究中，*MCTP2* 基因突变的家族成员脸识别缺陷与 rFFA 脑区对个体脸反应异常相关联。

MCTP2 基因编码的蛋白质有3个C2区域和两个跨膜区，类似参与突触传递的蛋白质(Shin et al., 2005)。其 C2 区域结合 Ca^{2+} (Shin et al., 2005)。很多有 Ca^{2+}结合 C2 区域的蛋白质参与膜和囊泡转运，在神经传递其关键作用(Cho and Stahelin, 2006; Shupliakov and Brodin, 2010)。从成千样本得到的基因表达微队列资料显示 *MCTP2* 基因表达于人脑，包括颞叶(McCall et al., 2011)。被脸选择性一致可靠地激活的脑区FFA，是颞叶皮层纺锤回的一个小区。人脑蛋白图谱显示了MTCP2蛋白质表达和分布概括，包括在纺锤回(Sjostedt et al., 2020)。

当然，高级认知需要很多细胞和分子。*MCTP2* 不会是唯一参与 CP 的基因。从 2904 人队列找到的 75 位 CP 患者中只有 7 位携带 *MCTP2* 基因突变。从 1928 人队列中女性脸识别能力与 *MCTP2* 罕见等位基因没有相关性。更多的连锁研究将有帮助。

我们发现更多家庭没有遗传基础，这需要更多分析。无假设的基因组分析可以考虑用下代基因组分析，包括常见和罕见遗传变异，需要大样本，超过百万人，找到更多遗传线索，也验证我们有关人脸识别的 *MCTP2* 结果。

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