大脑腹侧视觉通路知觉表征神经机制研究*

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摘 要 腹侧视觉通路知觉表征的神经机制是认知神经科学面临的基本问题。本文在介绍理论模型的基础上分析模型之间的分歧。文章指出探讨物体功能属性映射在大脑皮层表征的方式与自上而下的调控机制是该问题研究的重要维度;有效整合知觉表征模型与大脑调控机制的相关研究是深化知觉表征机制研究的关键。

关键词 知觉表征 知觉调控 模块化表征 分布式重叠表征

大脑表征外界刺激信息的方式是知觉研究的基本问题,涉及到两个方面:(1)大脑表征外界刺激信息的方式。存在争论的是表征不同范畴信息的脑区是否相同?(2)同一物体的不同维度信息如何映射到大脑皮层表征?

1 腹侧视觉通路知觉表征模型

大脑存在不同视觉信息加工通路:腹侧视觉通路(ventral visual pathway, VVP)与背侧视觉通路(dorsal visual pathway, DVP)。前者负责物体觉知与识别,后者专司物体的空间信息加工(Op de Beeck, Haushofer, & Kanwisher, 2008)。VVP 是指分布在枕叶皮层并延伸到颞叶腹侧与外侧的脑区。这些脑区之间缺乏明确界限,但在物体表征中发挥不同功能(Op de Beeck et al., 2008)。虽然研究证实 VVP 在物体知觉表征中发挥重要作用,但存在分歧:VVP 按照模块化方式表征(为模块化表征观点)(Grill - Spector, Kourtzi, & Kanwisher, 2001; Halgren et al., 1999);VVP 以体素的分布式模式表征刺激信息,同一体素表征不同刺激(分布式重叠表征观点)(Haxby et al., 2001)。

1.1 模块化表征 (Modular representation)

Fodor 提出认知操作是通过并行且相互分离的模块完成。模块只处理特定功能相适应的信息,模块内部的运作是独立进行(张烨,2011)。这种观点得到认知神经科学研究的证实。

单细胞记录技术对灵长类动物的研究证实颞叶单个细胞对不同类型刺激的反应存在差异(Kanwisher, McDermott, & Chun, 1997; Kanwisher & Yovel, 2006)。功能磁共振研究在更大空间尺度上证实 VVP 存在范畴特异性(Grill - Spector, 2003; Halgren et al., 1999; McCandliss, Cohen, & Dehaene, 2003)。目前,典型的范畴特异性脑区有 FFA 负责脸孔加工(Halgren et al., 1999; Kanwisher et al., 1997; Kanwisher & Yovel, 2006; McCandliss et al., 2003)与 PPA 负责场景加工(Ben - Shachar, Dougherty, Deutsch, & Wandell, 2007; Cohen et al., 2000; McCandliss et al., 2003)等。

1.2 分布式重叠表征(Distributed and overlapping representation)

根据模块化表征观点,范畴特异性的脑区只加工"偏爱刺激"。但研究证实范畴特异性脑区对"非偏爱范畴"刺激也反应(Tovee, Rolls, Treves, & Bellis, 1993)。

Haxby 等人(2001)以体素模式的相似性作为探讨不同刺激关系的指标研究了"非偏爱范畴"刺激的脑区激活是否包含该刺激的范畴信息问题。结果发现:范畴内刺激的激活模式具有非常高的相似性。把对该范畴反应强烈的体素排除后形成的激活模式仍然可以将该范畴与其他范畴区分开。当把对其他范畴反应显著的体素包含在激活模式内时,空间模式对该范畴区分仍然有效。据此,Haxby 提出分布式重叠表征观点。

1.3 部分分布式重叠表征(Partial distributed and overlapping representation)

Kanwisher 验证了 Haxby 等人的观点(Spiridon

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& Kanwisher, 2002) ,发现分布式模式可以区分范畴信息,但脑区对不同范畴刺激的表征不同质。

模块化表征与分布式重叠表征模型的根本分歧在于: 单个体素表征一个范畴信息还是表征多个范畴信息。部分分布式表征观点从“单个体素表征内容”的角度提出单个体素表征刺激不同属性的内容,范畴内的刺激之间共享属性越多,则这一范畴刺激激活的空间模式中共享的体素就会越多,从而导致范畴刺激激活的空间模式越相似; 反之,空间模式差别就越大 (O'Toole et al. , 2005) 。根据部分分布式表征的观点,大脑皮层对不同范畴刺激的表征是“连续体”(continuum) ,模块化表征和分布式重叠表征位于“连续体”的两端,如果范畴之间的属性差异较大,就体现为模块化表征; 与之完全相反,就表现为分布式重叠表征; 两者之间则表现为部分分布式重叠表征 (O'Toole et al. , 2005) 。

2 功能属性映射图(Functional properties mapping)

部分分布式表征并不能解决知觉表征的基本问题。如果单个体素表征物体的单个属性内容,即使我们可以找到某个脑区的激活随着物体刺激属性的改变模式,也很难推断这一脑区表征的 “基本”属性或“基本”维度信息(Op de Beeck et al. , 2008) 。传统观点认为大脑初级视觉皮层对物体不同特征组合的反应具有选择性 (Yu, Farley, Jin, & Sur, 2005) 。但这一结论是通过将其他特征平均后对单一特征进行探讨得出的,具有一定的局限性。研究者开始同时考查刺激的多个维度信息的表征模式,并发现物体表征模式并不是物体各个特征模式的简单组合(Basole, White, & Fitzpatrick, 2003) 。物体的激活模式是多个单一特征模式的合成物,任何特征的改变引起的物体表征激活模式的改变都是这一改变的特征模式与其他特征模式相互作用后的产物。

功能属性映射网络图的观点为从分布式重叠表征的角度解释范畴特异性现象提供新视角 (Op de Beeck et al. , 2008) 。VVP 可能存在表征物体属性的弱选择性的脑激活网络。单一网络只存在较弱的选择性。而刺激组合了几个功能属性,多个属性网络就会激活,多个功能属性网络的叠加表现出较强的选择性。这取决于属性网络是独立的,而且可以进行简单叠加。而且,不同属性网络之间的叠加可能并非简单的叠加,可能非线性的叠加。这一研究框架从刺激简单属性网络的角度有可能最终揭示 VVP 存在的范畴特异性现象。

3 腹侧视觉通路层级结构调控机制

大脑 VVP 形状特异性脑区在自上而下的调控过程中发挥重要作用 (Diekhof et al. , 2011; Friston, Henson, Phillips, & Mattout, 2006; Hsieh, Vul, & Kanwisher, 2010) 。高级视觉脑区对物体的表征可能反映了被试对物体的主观视觉经验。例如, VVP 内的形状特异性脑区(lateral occipital complex, LOC) 表征被试知觉到的物体形状而不是低水平的视觉特征 (Drucker & Aguirre, 2009; Haushofer, Livingstone, & Kanwisher, 2008; Kosslyn, Thompson, Kim, & Alpert, 1995; Stokes, Thompson, Cusack, & Duncan, 2009) 。近期的研究表明初级视觉皮层(例如,V1 / V2 / V3) 对物体的表征不仅反映了图像的感觉属性,也反映了中等水平的知觉处理加工的影响,如知觉到的图像的大小 (O'Craven & Kanwisher, 2000) 和图像的亮度 (Boyaci, Fang, Murray, & Kersten, 2007) 。研究者提出初级视觉区对刺激的表征受主观经验的影响可能反映了来自高级脑区(如,LOC) 的反馈信息 (Kosslyn, Ganis, & Thompson, 2001; Murray, Boyaci, & Kersten, 2006; Yoo, Freeman, McCarthy, & Jolesz, 2003) 。

4 结语

目前,以分布式重叠表征观点为基础的多变量模式分析方法 (Cox & Savoy, 2003; Haxby et al. , 2001; Naselaris, Kay, Nishimoto, & Gallant, 2011) 被广泛应用于大脑皮层神经表征问题的研究中。例如,Naselaris 等人发现借助编码模型可以描述大脑视觉皮层不同区域对物体不同维度的激活模式 (Naselaris, Prenger, Kay, Oliver, & Gallant, 2009) 。此外,Mitchell 等人通过类似途径也证实了大脑内部存在与抽象名词的语义信息对应的激活模式 (Mitchell et al. , 2008) 。这些研究表明我们有能力探讨物体的哪些“特征”足以完全描述视觉皮层在知觉加工过程中的神经活动 (Naselaris et al. , 2011) 。同时,由于多变量模式分析方法具有较高的敏感性 (Norman, Polyn, Detre, & Haxby, 2006) ,研究者探讨不同物体知觉表征模式之间的关系逐渐成为可能 (MacEvoy & Epstein, 2011) 。虽然大量研究证实大脑 VVP 存在调控机制 (Hsieh et al. , 2010) ,然而目前尚无研究从“信息内容”的角度揭示大脑

自上而下调控机制。随着多变量模式分析方法的发展，从脑激活模式的角度揭示大脑自上而下的调控机制，进而探讨 VVP 知觉表征机制将成为可能。

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Studies of the Neural Mechanism Underlying Perception Representation in the Ventral Visual Path of the Human Brain

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Abstract Over the past decade, neuroimaging studies have provided a detailed picture of the functional organization of the ventral visual pathway in object representation in the human brain. This study focused on the fundamental issue that lay in the neural representation in the cortex of the ventral visual pathway. The models in this field were for the first time introduced in this study including the core idea of each model and the limitations of the models based on the comparison with each other, which played important roles in understanding the essence of the neural event in mapping the sensory information to the cerebral cortex in the ventral object – pathway. In detail, the modular representation opinion was initially developed in this field, experimental evidence has been found to support the hypothesis of this model. For example, many studies have found that the existence of the category specific brain areas in the human brain including the fusiform face area (FFA), and the parahippocampal place area (PPA). However, other studies delivered some experimental findings which were not well interpreted from the perspective of the module representation model. Consequently, another model, the distributed and overlapping representation model, was developed, which proposed that the voxel information content should be shared or distributed as a function of the shared attributes of objects. So similar object categories shared more voxels than dissimilar categories due to the fact that the objects in these categories share more attributes. Although many study findings supported the hypothesis of the distributed and overlapping model, the decoding method was raised based on the distributed and overlapping method in terms of the machine learning method, which significantly influenced the studies of the functional brain in the neuroimaging field. It is still an important question of how to reconcile the opinions of the module representation and the distributed and overlapping representation. In fact, many researchers have considered this question and verified it in their research, in which the partial distributed representation model is one of them and tries to compensate the limitation of the distributed and overlapping representation. The partial distributed and overlapping model proposes that understanding partially distributed code is critical to linking neural responses with the physical world they represent. It should be further studied as to how the basic properties of the object are represented in the brain cortex, and how the neural network of the basic properties combine with the neural network of the whole object. The exploration of this issue may finally shed some light on the category specific feature in object representation observed in cerebral cortex. On the other hand, there is a hierarchical structure in ventral visual pathway, and the high level areas modulate the neural activity underlying the object representation of the low level cortex. We suggest that the research of the object representation in ventral visual pathway cortex should consider the top – down modulation mechanism of the human brain. Especially, the lateral occipital complex cortex may play an important role in the top – down modulation process. Based on the above considerations, this study suggested that further origin of the neural representation in ventral visual pathway.

Key words perception representation, perception modulation, fMRI, modular representation, distributed and overlapping representation.