

决策的神经动力学和回路机制

Neural dynamics and circuit mechanisms of decision-making

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摘要: 在这篇综述中,我简要地总结了目前有关决策的神经生物学研究,它们涉及两个主题。第一部分着重于决策回路中神经表现和动力学的本质。实验和计算结果表明,状态空间中种群活动的时间域和轨迹的渐近阈值代表了决策过程的双重性。此外,一个决策回路可以显示几个不同的动态状态,如斜坡模式(ramping mode)和跳跃模式(jumping mode),具有不同的定义性质。二是基于生物的力学模型与规范模型之间的关系。在不同的抽象层次上,实验与这些模型之间富有成效的相互作用,使研究人员能够提出越来越精细的问题,并对决策的神经基础有了新的认识。特别是,最近关于多选择决策的研究表明,偏离理性的选择行为模型可以用已建立的神经机制来解释。

引言

David Marr 是计算神经科学的先驱,他于 1980 年去世,年仅 35 岁,今天人们记住的主要是他的大脑建模[49]的三步法:首先,提出问题并确定其规范的解决方案(最佳的方式)。第二,寻找完成最优解的计算算法,第三,阐明算法在大脑中的实现。然而,如果忘记 Marr 在神经生物学方面的深厚根基(以及他关于小脑、海马体和新皮层理论的开创性论文三部曲),那就有失公允了。弗朗西斯克里克(Francis Crick)与 Marr 有过广泛的交流,他在 1991 年回忆道:“David Marr 的工作显然分为两个阶段:Marr I 关心的是神经回路及其可能的计算能力。Marr II (AI 阶段)功能更强。重点放在过程的理论和可能的算法上,很少关注实际的实现。我相信,如果他还活着,他会把这两种方法结合起来[19]。”大脑功能的“如何”(Marr I)问题与“为什么”(Marr II)问题之间的关系和相互作用在今天的神经科学杂志[11]上仍然是认识论讨论的主题。

随着神经科学的巨大进步,在 Marr 层次结构的不同层次之间来回转换的时机已经成熟:行为、计算算法和神经回路机制。最近关于决策神经基础的研究为这一观点提供了极好的例证。

规范理论与神经回路机制的相互作用

现代决策神经生物学研究大约在本世纪初开始起步。在知觉决策方面,先锋工作是使用随机点运动(random-dots motion,RDM)方向辨别任务完成的。在这项任务中,受试者被训练在一个接近阈值的随机点显示中对运动方向(如左或右)做出判断,并以眼跳运动报告感知到的方向。对猴的行为神经生理学研究显示,后顶叶皮层[67、68、65、13]和前额叶皮层[39]的单个神经元的随机活动与受试者的判断相关。另一方面,神经科学家开始研究基于奖励的选择行为的价值[57,63,71,3,24]。大约在同一时间,在一个看似无关的努力下,计算神经科学家正在开发越来越现实的神经持续活动模型,作为工作记忆(积极的短期记忆)的大脑机制。生物学上现实的突触回路模型显示,工作记忆系统不应该像快速开关那

样运作(在静止状态和记忆状态之间);相反,在自我持续的持续活动下,周期性突触兴奋需要是缓慢的[75]。人们很快认识到,这种缓慢的回响机制正是决策计算所需要的,因为深思熟虑的决策需要对不同选择选项的支持或反对证据的暂时积累(通过慢速瞬变),最终导致一个明确的选择(通过吸引子动力学)[76]。关于决策和工作记忆共同机制的提议得到了生理学观察的支持,生理学观察表明,与这两个过程相关的单个神经元活动信号存在于同一大脑区域,如前额和顶叶皮质[30,77],最近的一项人类研究表明,前额叶皮层(已知对工作记忆很重要)的破坏(使用经颅磁刺激)会对决策产生因果影响[62]。在过去的十年,复发性回路模型(recurrent circuit models,RNMs)阐述和广泛应用的计算和认知神经科学家感性决策[76,48,78,42,20,22,79,27••,41•,23,77,81,9,53,25•],选择动作[44]和价值取向的选择行为(70,36•,5••)。

在认知心理学中,决策过程中通过序列分析来临时积累证据的思想由来已久。根据漂移扩散模型(drift diffusion model,DDM)[47,69],一个“决策变量”整合了两个备选方案(A和B)的相关证据,当决策变量达到一个正值(备选方案A)或负值(备选方案B)阈值时,就做出了决策。DDM已经被证明是非常成功的,它可以解释行为数据[47,69],以及最近猴子在RDM任务中的准确性和反应时间[65,30]。DDM可以看作一种规范性理论,因为它是连续时间相当于序贯概率比检验(sequential probability-ratio test,SPRT),这是二进制下选择最优程序,它减少了不确定性意味着决定为一个给定的时间在所有测试误差率[10,6]。

RNM与DDM相比如何?首先,它们处于两个完全不同的抽象级别。DDM的积分时间为无穷大;而RNM则在很长但有限的整合时间内努力识别生物学机制。长整合时间的一个可能的神经基础是NMDA受体依赖的周期性突触兴奋。这一模型预测还有待实验验证。也有人提出,神经积分器可以用适当的网络结构来实现,而不需要重复连接[31]。其次,时间集成的功能好处在模型中得到了证明,它表明当系统允许在较长时间内集成输入时,性能会提高,但当系统达到表示分类选择的吸引子状态时,集成时间足够长的系统最终会停滞不前[76]。这一预测在最近的猴子实验[38]中得到了证实。第三,虽然在DDM中不同时间点显示的证据具有相同的权重,但RNM断言,早期获得的证据对最终选择的影响比稍后和立即做出决定之前提供的证据更大。这一RNM预测在一个实验中得到了支持,该实验在不同的时间点引入了一个简短的感官信息脉冲[35,79]。然而,在更一般的情况下,当感官证据或注意力随时间不断变化时,很久以前提供的信息可能被遗忘,面对新出现的证据,承诺可能被逆转[64]。决策过程中集成时间的生物学基础和可能的基本限制仍然是未来研究的一个突出课题。

在RNM中,分类形成是通过依赖于反馈抑制的吸引子动力学来实现的。这与DDM的实现不同,在DDM中,前馈抑制实现了对感觉输入[50]差异的显式神经计算。猴子实验为反馈抑制[32]和前馈抑制[8]提供了证据。请注意,在经验上,我们不知道证据的积累和分类选择的形成是否发生在一个单独的神经回路中。或者,这两个计算可以在不同的大脑区域顺序进行,或者通过协作和分布在多个大脑区域[17]的动态同时进行。

时间上的累积到阈值,状态空间上的群动态

可以从两种不同的角度看待RNM。可以将神经池的神经活动(每个神经池对

特定选择进行选择)绘制为时间的函数(图 1A-B), 可以为终止决策过程引入阈值(图 1A)。另一方面, 人们也可以在状态空间中描绘决策回路的动态, 其中对不同选项有选择性的神经池的触发率相互作用图(图 1C)。根据这一观点, 不同的选择由不同的“吸引子”状态来代表。数学术语“吸引子”仅仅意味着一个动态系统在小扰动下是稳定的。吸引子不一定是一个稳定的状态, 但可以是一个复杂的时空模式。此外, 系统的吸引景观不是刚性固定的;任何相对持续的输入(外部刺激或自上而下的认知控制信号)都能轻易地改变状态空间中的吸引体景观, 如图 1C(中、右面板)所示。

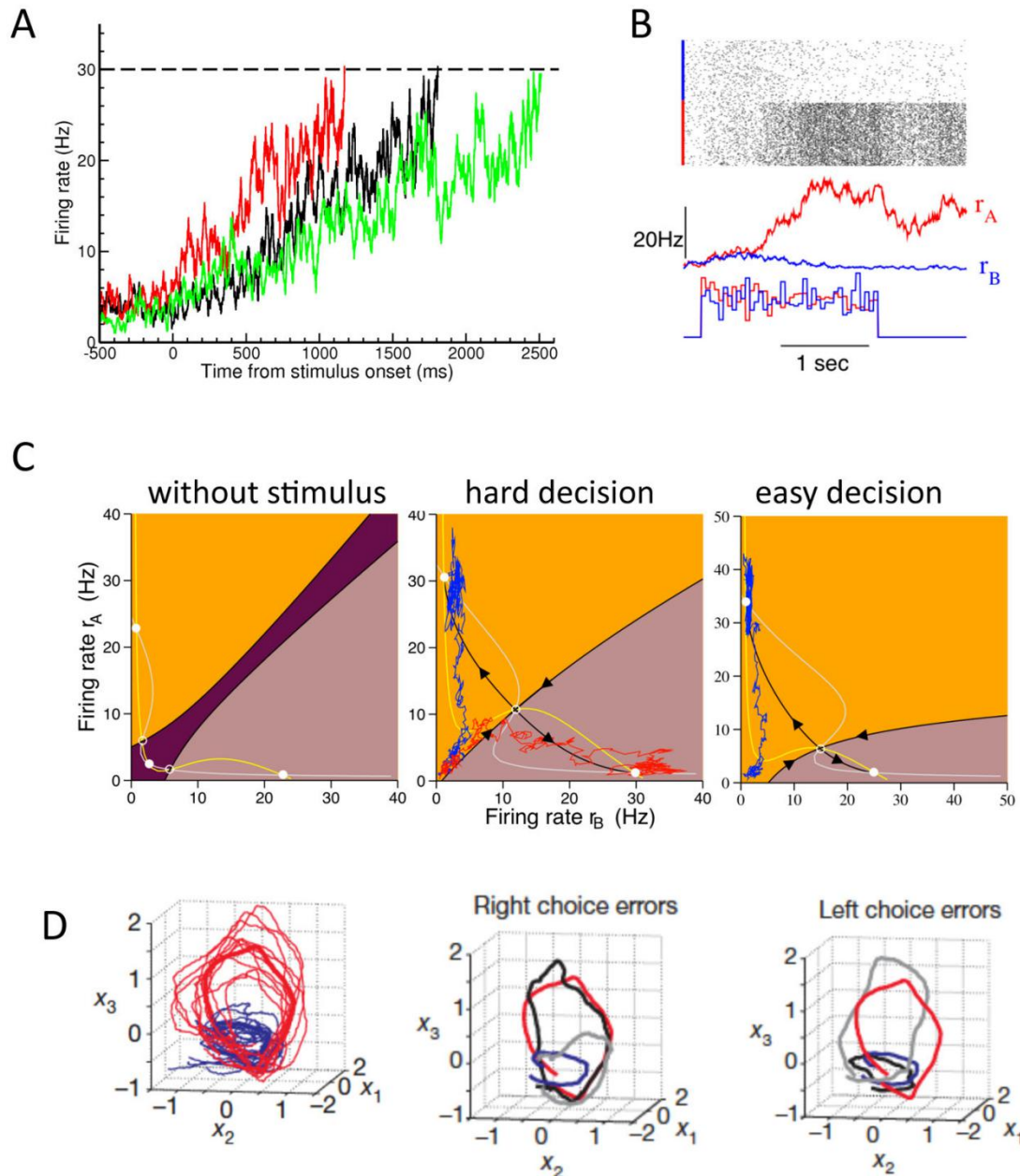


图 1: 决策的阈值斜坡和群动态。(A)在 RNM 中随机向阈值(虚线)斜坡的活动(显示了三个样本试验)。(B)在运动方向辨别任务的模拟中, 对不同选择进行选择的两个神经群显示了逐步倾斜, 然后是赢家通吃的竞争, 其中运动相干性 c' 量化了任务难度。(C) RNM 的群动态显示在发放率 r_A 和 r_B 的状态空间中。在没有外部输入(左面板)的情况下, 存在具有低(中)或高(右)相干性的运动刺激。注意, 吸引子景观敏感地依赖于输入(中间对右边)。(D)在执行虚拟导航决策任务的小鼠中,

从后顶叶皮层记录的约 65 个细胞的群动态。轨迹是特定于选择的(红色:右选择试验, 蓝色:左选择试验)。左:正确试验中的试验轨迹样本。中间和右边:错误的右选择和左选择试验的个别试验轨迹(灰色和黑色), 与正确的右(红色)和正确的左(蓝色)选择试验的平均轨迹作图。

状态空间框架强调种群动态而不是单个神经元。它为纯 DDM 无法解释的观测提供了自然解释: 时间积分有一个限制, 因为当斜坡停止时, 系统最终达到吸引子状态; 当系统还在选择吸引态盆地边界附近时(图 1C、中、右面板), 一个简短的证据脉冲在早期对最终选择有更强的影响; 在误差试验中, 反应时间更长, 因为一个错误的选择意味着系统必须经过一个鞍点, 在那里动力学速度显著减慢(图 1C, 中间的面板)。最后, 根据这个种群动力学观点, 即使神经放电率可能还没有达到阈值水平, 只要系统已经进入选择吸引子状态的盆地足够远, 就可以做出决策。从生物学上讲, 决策阈值的概念应该被理解为触发下游前运动神经元[42]中类似开关反应所需的决策神经元的激活水平。符合这个角度看是常见的观察, 在视觉搜索任务中, 行为反应时间这种时间竞争的视觉反应神经元的发射率显著偏离对方, 而不是到一个固定的阈值水平, 在 FEF[66, 80, 18, 34], SC[52]和 LIP[37, 73, 2]。

最近的一篇文章对群动态观点提供了显著的支持。Harvey 等[33••]记录了行为小鼠顶叶皮层(使用钙成像)中约 65 个(范围 37-94 个)单个神经元。在一项虚拟导航决策任务中, 在一段延迟时间后, 动物们会看到一个提示, 提示它们在两个回合(左或右)中哪个选择是正确的, 并在给定的试验中产生奖励。据报道, 记录群状态空间的动态轨迹在两种选择下是完全分离的(图 1D, 左面板)。此外, 在误差实验中, 从种群活动中解码出来的动物的选择通常是沿着正确选择的路径开始的, 但后来不知怎么地转向了与错误选择的路径一致(图 1D, 中间和右边的灰色轨迹)。最近的另一项研究使用了多个单个神经元的同步电记录, 表明种群动力学框架也适用于运动系统[15,16]。

斜坡模式和跳跃模式

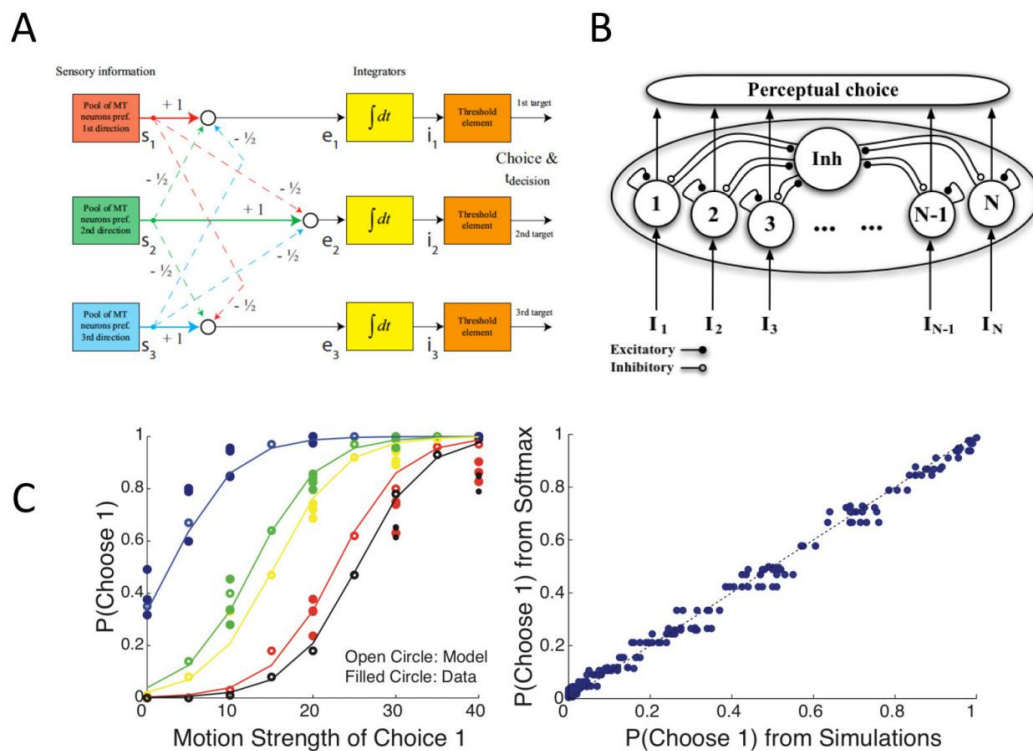
在大多数的实验中, 单个神经元的脉冲序列一次被记录下来, 这通常太不规律了, 以至于研究者无法确定它的潜在的放电率是否会随着时间的推移而平稳而准线性地上升(即渐变模式)。另一种方法是, 一个神经元可以在不同的试验时间显示离散的放电率跳跃, 因此试验平均的放电率显示一个分级的时间过程(跳跃模式)。在一种跳跃模式的实现中, 单个神经元被赋予了双稳定性, 例如由于钙激活的内向电流的存在[75,72,26,61]。如果神经元从一个状态随机切换到另一个状态, 大约以恒定的速率, 那么单个神经元的试验平均值(或单个试验中的群平均值)将呈现渐变率变化[61,60•]。另一种情况不需要单个神经元是双稳态的, 但是一个周期性网络可能从低自发状态切换到高选择状态[21,23,28,43,53]。换句话说, 在刺激下, RNM(图 1C 左侧)的静息状态可能仍然存在(图 1C、中、右侧)。系统在一段时间内保持这种状态, 直到噪声最终导致从它过渡到一个选择吸引状态, 这反映在时域作为一个跳跃的决策神经元的放电率。这种噪声诱导的随机事件发生在不同试验的随机时间, 导致试验平均值可能出现在一个渐变的斜坡时间过程中[55,61,53•]。值得注意的是, 在跳跃模式下, 如果没有噪声, 系统将保持在静止状态, 因此决策需要波动。决策过程中的噪声或随机性是一个人们知之甚少的问题。感知决策(识别、辨别等)通常是困难的, 因为感觉信息是有噪声的, 而且随着时间的推移, 感觉数据的集成是需要计算的, 因为它提高了信噪比

[47,30]。然而，决策电路也有内在的随机性，而且神经积分器的 Fano 因子（方差与尖峰计数平均值之比）可能会随着时间的推移而增加[54,14•]。这对于同时涉及感知决策和基于价值的选择的神经回路来说可能是普遍正确的，而决策系统的随机神经动力学可能在决策行为的不确定性中起着关键作用[29,77]。

区分对比模型的一种可能方法是，不仅要分析平均发放率，还要分析发放率变化的时间过程[14•];需要进一步的理论工作来定量评估斜坡模式和跳跃模式的神经变化的差异动力学。此外，同时记录多个神经元的新方法[15,33••]将使研究人员能够评估多个细胞是否如 RNM 的跳跃模式所预测的那样显示任何同步开关。在理论方面，跳跃时间的分布是如何由网络特性决定的还有待进一步阐明。

对偏离理性行为的神经机制解释

通常，对于给定的决策任务，什么构成了最优性是不清楚的。虽然 SPRT 对于两种强制选择任务是最优的，但是对于三种或更多选择的最优测试是未知的。已经提出了几种方法将 DDM 推广到多个备选方案[51、58、13•、40•]，其中一种方法如图 2A 所示。RNM 推广到多选择决策[74,27••, 1]，通常假设具有共同抑制的神经池之间存在竞争(图 2B)。该模型与人在 3-先择 RDM 方向辨别实验[58]中的性能数据吻合良好(图 1C, 左侧)。3-选择吸引子网络模型的决策行为可以用一个 softmax 函数很好地描述， $P(1) = \frac{\exp(\sigma V_1)}{\exp(\sigma V_1) + \exp(\sigma V_2) + \exp(\sigma V_3)}$ ， V_1 、 V_2 和 V_3 是三个选项优势的值或强度， σ 是一个量化随机度的一个参数(图 1C, 左和右面板)。



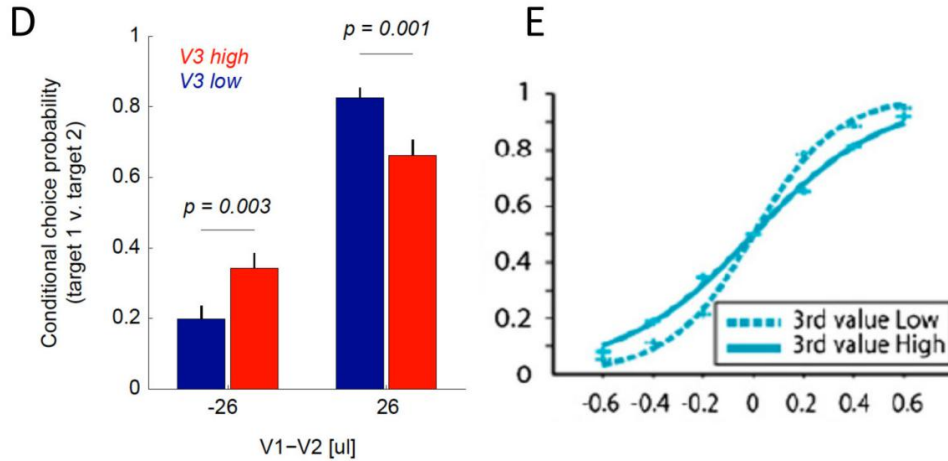


图2: 3-选择决策。(A)将DDM推广为3-选择。经许可改编自[58]。(B)多选的RNM。(C)左:选择选项1作为方向1运动相干性的函数的概率。实心圆:三个实验对象[58]的数据(填充圆);开环:3选择RNM的simulation结果(B);实体曲线:与softmax函数最适合的模型模拟。选项2和选项3的不同颜色对应不同的运动相干度对(蓝色:0和0,绿色:10/10,黄色:15/5,红色:20/20,黑色:25/15)。右侧面板:来自RNM仿真的性能数据与softmax函数预测的性能数据进行了对比。由Nathaniel Smith进行了模型模拟。这些结果需要在未来的研究中得到证实。(D)在一个基于价值的选择任务[45]中,按价值的顺序提供了3个选项(1:最佳,2:次优,3:最差)。根据规范决策理论,选项3应该是不相关的,其值的改变不应该影响前两个选项中选择选项1的相对概率 $P(1)/(P(1)+P(2))$ 。与这种理想的最优性相反,在猴子实验中,选项3的值越高,选择两个更好的选项中最好的一个的相对概率就越低,这与softmax决策准则不一致。数据由K. Louie和P. Glimcher提供。(E)与另一个猴子实验中(D)相似的发现,当内侧眶额皮质受损时。经允许改编自【59】。

softmax决策标准的一个预测是,从两个选项(比如1和2)中选择一个的相对概率 $P(1 | 1+2) = P(1)/(P(1)+P(2))$ 与第三个选项 V_3 的强度无关。这一预测在经济选择行为中以令人惊讶的方式被证明是矛盾的。在一项猴子和人类的实验中,三种选择与不同的奖励值相关(1:最好,2:次好,3:最差)[45,K Louie和P Glimcher,个人交流]。第三个选项的值比第一个和第二个选项的值都低,因此是不相关的,应该忽略。然而,当最坏的选项3的值增加时(同时仍然低于选项1和2),受试者在两个更好的选项中选择最好的相对概率降低,这与理性行为的规范模型相反(图2D)。在另一项猴子实验中也有类似的发现,但只是在内侧眶额皮质受损的情况下(图2E)[59]。这些发现强调了[46]值的神经表示的背景依赖性。

有趣的是,[45,K Louie和P Glimcher,个人交流]猴子实验中对理性行为的偏离可以简单地解释为假设神经回路被赋予了分裂规范化(divisive normalization),即神经元的活动除以回路中所有神经元的活动之和;通过标准化,神经发放率与相对而非绝对的动作值动作值相关[45,K Louie和P Glimcher,个人交流]。[45,K Louie和P Glimcher,个人交流]。分裂性归一化在许多脑皮层回路[12]中被广泛观察到,最近被认为在决策过程中发挥了有益的作用[4,46,56]。因此,这种结合猴子行为、生理和模型的方法证明了神经回路机制是如何预测稳健的行为趋势的,而这些趋势是不能被基于最优化的规范理论预测到的,也不容易被解释。

进一步的研究将澄清几个重要的问题。首先,为什么在一个实验中,正常的实验对象会出现这种偏离理性行为的情况,而在另一个实验中,只有大脑受损的动物才会出现这种情况,原因还有待观察。其次,当第三个选项是不同的值时,上述推理假设参数 σ 控制特性转化是相同的。然而, σ 可能不是固定的,因为增加价值以外的选择最好的呈现情况不确定,因此,决策过程可能会变得更加随机(以一个更大的 σ)。设计新的实验操作来直接测试这两个对比鲜明的场景是很有趣的。第三,虽然 RNM 模拟与 3 个选择感知决策实验的行为数据一致(图 2C),但是需要额外的数据来评估具有最低运动一致性的第三个选择是否像 softmax 决策规则预测的那样,不影响其他两个选择之间的相对决策。新的实验将探索这样一种可能性,即感性决策符合理性决策理论(至少在训练有素的动物中是这样),而基于价值的选择更容易产生看似非理性的行为效应,尽管如此,这些行为效应可以通过标准化等已建立的神经计算来解释。

结论

在这篇简短的综述中,我着重于最近决策的神经生物学研究的两个主题。一个是神经决策动力学的本质。决策过程有两种互补的观点:时域的渐近阈值和状态空间的种群动态。此外,根据 RNM,同一模型(参数变化不大)可以显示几种不同的动态状态,如斜坡模式和跳跃模式,这表明它们可能发生在大脑的不同局部回路中,或在单一大脑区域的不同条件下。新的实验方法,如测量和分析同时记录的单个神经元,将在未来几年为这些问题带来新的见解。第二个主题是规范理论和神经回路机制之间的关系。RNM 和 DDM 之间卓有成效的相互作用表明,该领域的研究将极大地受益于不同抽象层次的模型理论之间的交叉讨论,并与实验密切交互。在认识论上,神经回路机制不应该仅仅被看作是规范原则的实现,而应该是对人类和非人类动物非理性选择效应的原则性解释。未来的研究将在认知、计算和回路层面上进行整合,这将对我们理解决策行为的神经生物学有很大的帮助。

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