

The developmental origins of spatial navigation: Are we headed in the right direction?

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Navigation depends upon neural systems that monitor spatial location and head orientation. Recent developmental findings have led some to conclude that these systems are innate. Such claims are premature. But also, there are more meaningful ways to arrive at answers about developmental origins than by invoking the outdated nature-nurture dichotomy.

Spatial navigation in mammals is made possible by specialized neural systems that track the direction in which the head is pointing and the location of the body in space. Among the components that contribute to these processes are distinct classes of neurons—head direction cells, place cells, and grid cells—localized to specific brain areas. In a recent report [1], Bjercknes and colleagues found functional head direction cells in infant rats several days before their eyes open and before the developmental emergence of place cells and grid cells [2,3]. Recording from the pre- and parasubiculum and medial entorhinal cortex of freely moving rats as they explored an open arena, Bjercknes and colleagues found neurons with clear directional tuning on the first day of recording at 11 days of age. Although this tuning drifted within—and substantially changed between—recording sessions, the relative tuning of neighboring pairs of neurons was stable (i.e., their tuning drifted coherently). Directional tuning stabilized upon eye opening around 15 days of age. The authors conclude that the directional map develops ‘independently of both vision and outbound navigational experience’ and that visual input is required to anchor the map to the outside world.

Developmental analyses can be highly valuable for revealing processes governing the construction of complex skills like spatial navigation, and I applaud Bjercknes and colleagues for their elegant efforts in performing this difficult work. However, I take issue with the claim that their findings ‘point to a hardwired attractor network for representation of head direction’ and to ‘strong innate components in the mechanism for directional tuning in the brain.’ Similarly, another group addressing the same basic questions suggested the presence of a system that is ‘partly or wholly formed genetically,’ perhaps dependent upon ‘preconfigured, possibly innate, constructs’ [3]. Such claims of innateness—rooted in and fueled by the nature-nurture debate—are problematic for several reasons.

First, claims of innateness are routinely contradicted by subsequent empirical studies that reveal critical developmental events at younger—sometimes even prenatal—ages [4]. For example, Hubel and Wiesel famously reported in 1974 [5] that macaque monkeys whose eyelids were surgically shut around the time of birth exhibited fully formed ocular dominance columns several weeks later. Based on this, they concluded that the column system is ‘innately determined and not the result of early visual experience’. However, the subsequent discovery of spontaneous activity in the fetal retina revealed an alternative route to the development of ocular dominance columns. In response to these findings, Hubel and Wiesel wrote 24 years later [6] that ‘we were probably wrong in supposing that the wiring, because present at birth, must necessarily be the direct consequence of genetic instructions: we underestimated the importance of prenatal neural activity on connections’. In light of such examples, we might wonder whether head direction cells are innate based on experiments in rat pups at 11 days of age.

A second problem with claims of innateness is their nebulous nature. Rhetorically, there is no consistent and agreed-upon definition of innate or its sister term instinct. These terms are variously and inconsistently used to describe traits that are present at birth, genetically determined, developed prior to use, not learned, and so on [7]. This lack of linguistic precision reflects an underlying conceptual confusion about the kinds of experiences that we expect to play a role in the development of a specific behavior. For example, the claim that head direction cells are innate because they are detected at 11 days of age rests, in part, on the assumption that a rat pup, four days before its eyes open, has no relevant experiences within the nest that can account for the developmental emergence of head direction cells. Contrary to this assumption, however, suckling pups raised in experimental conditions that required them to shift more often among the dam’s nipples exhibited enhanced spatial memory as juveniles [8]. To make sense of this curious and unexpected finding, visualize the suckling pups navigating among a spatial array of nipples on the mother’s ventrum.

Developmental scientists have learned that both expected and unexpected processes cascade through developmental time to produce complex behavior [4]. Accordingly, we need a broad definition of experience that is not beholden to *a priori* expectations of what is ‘relevant’ to a developing animal. Construed in this way, relevant experience comprises the full diversity of developmental factors that shape, guide, and modulate neural activity and

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organization. For example, from the perspective of a neuron located in visual cortex, it hardly matters whether the ultimate source of its activation is light impinging on retinal photoreceptors or spontaneously active retinal ganglion cells. For that neuron, both sources of activity provide critically relevant experience. This perspective is hardly new: On the contrary, it has been championed for decades by proponents of what is now called developmental systems theory [9,10].

Therefore, having demonstrated the functionality of head direction cells by 11 days of age, subsequent research should address the factors that contribute to their development. Suckling experiences may contribute. But, as with retinal waves for the visual system, spontaneous activity might also contribute to the development and refinement of the head direction system and its associated sensorimotor neural circuits. In particular, newborn mammals, including rats, exhibit spontaneous motor activity—called myoclonic twitches—during active (or REM) sleep. These jerky movements of the limbs generate sensory feedback that, in turn, provides substantial activation to the developing nervous system. This twitch-related activity is ideally suited to participate in the self-organization of sensorimotor neural circuits [11,12]. Twitch-related feedback from skeletal muscles—including the nuchal muscle, which controls movements of the head—is conveyed successively to the spinal cord, medulla, thalamus, and sensorimotor cortex. From cortex, this feedback is further conveyed to hippocampus, almost certainly via the entorhinal cortex and subiculum [13,14]. Critically, the hippocampus, entorhinal cortex, and subiculum contain place cells, grid cells, and/or head direction cells. Thus, just as retinal waves provide spatially organized activation of the developing visual system [15], sleep-related twitches provide spatially organized activation of the major structures implicated in navigation, with obvious consequences for the topographic organization of the associated neural elements, including head direction cells.

I am not suggesting that we have identified the developmental origins of head direction cells. Rather, I am

suggesting that at this early juncture in the developmental analysis of spatial navigation we should resist the temptation to make claims about innateness: Such claims are misleading and only serve to delay the search for origins within the moment-to-moment mechanisms of development [4]. I believe that if we embrace a broad view of relevant experience, we will make more rapid progress toward understanding the full range of factors that shape our incredible ability to navigate the world.

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