Cortical Evolution 2015: Discussion of Neural Progenitor Cell Nomenclature

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Work over the past two decades has identified and characterized the neural progenitor cells (NPCs) that produce neurons in the cortex and other brain regions in the developing mammalian forebrain. Initial discoveries in the 19th century were made in embryonic human brain and can be traced back to the classical anatomists including His, Retzius, Schaper, Lenhossek, Magini, Kolliker and Ramón y Cajal (for a detailed history, see Rakic, 2003; Bystron et al., 2008). Most present-day researchers agree that NPCs are located in two proliferative zones that surround the ventricular lumen of the developing brain: the ventricular zone (VZ), which is adjacent to the ventricle, and the subventricular zone (SVZ), which is superficial to the VZ (Boulder Committee: Angevine et al., 1970). Initial work investigating cellular morphology surmised that VZ cells were neither neuronal nor mature glial cells. Hence the initial terms for VZ cells included names such as spongioblasts and fetal glia. Morphology and protein expression properties of VZ cells in human and non-human primates were more fully characterized after the introduction of electron microscopy and immunohistochemistry (Rakic, 1972; Levitt et al., 1981). Because the VZ cells in many species exist beyond the time of birth, and have a radial orientation not only in the telencephalon but also in the diencephalon and spinal cord, the combined term "radial glia" (RG) was introduced by Pasko Rakic (1971). The term radial glia has stuck for over half a century and is now generally used, often with some attributes.

RG cells located in the VZ are now considered to be the primary NPCs in many, if not all, brain regions. In the dorsal forebrain they can be identified by expression of the Pax6 transcription factor (Gotz et al., 1998; Englund et al., 2005). RG cells exhibit several patterns of division and generate multiple cell types during the course of cortical histogenesis. RG cells initially undergo symmetric divisions that produce additional RG cells and expand the proliferative population in the VZ (Takahashi et al., 1996). At the onset of cortical neurogenesis, RG cells begin undergoing asymmetric divisions (Takahashi et al., 1996), which produce one radial glial cell and a neuronal daughter cell (Malatesta et al., 2000; Hartfuss et al., 2001; Miyata et al., 2001; Noctor et al., 2001; Tamamaki et al., 2001). Later work demonstrated that RG cells produce many neuronal daughter cells indirectly, by generating NPC daughter cells that migrate to the SVZ, where they divide symmetrically to produce pairs of daughter neurons (Haubensak et al., 2004; Miyata et al., 2004; Noctor et al., 2004, 2008). The NPC daughter cells that divide in the SVZ to produce neurons have been given various names, including intermediate progenitor (IP) cells (Noctor et al., 2004), non-surface progenitor cells (Miyata et al., 2004), and basal progenitor cells (Haubensak et al., 2004). The NPC daughter cells in the SVZ can be distinguished from RG cells by their morphological characteristics and location of division, and in the cortex by expression of the Tbr2 transcription factor (Englund et al., 2005). Evidence gathered in rodents to date suggests that cortical neurogenesis involves a two-step process by which RG cells divide in the VZ to produce IP cells, and IP cells then divide in the SVZ to produce neurons (Kriegstein et al., 2006; Martínez-Cerdeño et al., 2006). Similar IP progenitor cells have been identified in the ventral forebrain (Lim and Álvarez-Buylla, 2014) and in the adult germinal niches: the V-SVZ and the subgranular zone of the dentate gyrus (Seri et al., 2004).

Over several decades it has been noted in several species that toward the end of the neurogenic period, RG cells detach from the ventricle and translocate toward the pial surface. This has been shown in fixed fetal tissue from humans (Choi and Lapham, 1978; deAzevedo et al., 2003), macaque (Schmechel and Rakic, 1979), and ferret (Voigt, 1989). In vivo and in vitro

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experiments in embryonic rat neocortex showed that the translocating cells expressed glial fibrillary acidic protein (GFAP) (Noctor et al., 2004), were mitotic, and generated glial cells (Noctor et al., 2008). More recent evidence showed that Pax6+ cells were located in the primate outer SVZ (Fish et al., 2008), and that the translocating cells in the cortex retain expression of the RG cell marker Pax6 (Fietz et al., 2010; Hansen et al., 2010; Reillo et al., 2011; Wang et al., 2011; Martínez-Cerdeño et al., 2012; Betizeau et al., 2013; Gertz et al., 2014; Poluch and Juliano, 2015); in addition, there may be a difference between translocating RG cells that transform into astrocytes, and those that exhibit "mitotic somal translocation" (Wang et al., 2011).

Many research groups are contributing important information to increase our understanding of NPC type, morphology, function, and diversity in the developing brain. In some cases distinct names have been assigned to each of the NPC types, always with the goal of proper description. For example, cells that divide away from the ventricular surface have been called extraventricular cells (Hamilton, 1901), subependymal cells (Allen, 1912; Smart, 1961), "cells that divide away from the ventricle near blood vessels" (Sauer, 1935), subventricular zone cells (Boulder Committee: Angevine et al., 1970), type C or transit-amplifying cells (Doetsch et al., 2002), IP cells (Noctor et al., 2004), non-surface progenitor cells (Miyata et al., 2004), and basal progenitor cells (Haubensak et al., 2004). Terms that have been used to describe translocating RG cells include: transitional RG (Choi and Lapham, 1978; deAzevedo et al., 2003), transitional astroglial cells (Schmechel and Rakic, 1979), transforming astroglial cells (Voigt, 1989), transforming radial glia (Noctor et al., 2002), translocating cells (Noctor et al., 2004), outer RG cells (Hansen et al., 2010), basal RG cells (Fietz et al., 2010), intermediate RG cells (Reillo et al., 2011; Reillo and Borrell, 2012), and translocating RG cells (Martínez-Cerdeño et al., 2012). The number of terms may reflect our increasing appreciation for precursor cell diversity, or simply changing perspectives on cellular function prompted by new data. Questions we ask include: Do the NPCs that have been given different names truly represent different cell types that perform distinct cellular functions? Are they species specific? Or do they represent basic building blocks of vertebrate brains that share key features across species? We felt that the Cortical Evolution 2015 conference (18–20 May, 2015, Toledo, Spain), at which colleagues discussed and compared the cerebral cortex of different species including rodents, reptiles, carnivores, non-human primates, and humans, would be the proper place to begin a discussion on cellular identity, classification, and nomenclature.

Although the use of different terms to describe a single cell type (which remains to be determined) may present challenges, alternatively, it could help to bring about a fuller understanding of cellular function. The well-known Boulder Committee recommended revised terminology for the embryonic vertebrate brain in 1970 (Boulder Committee: Angevine et al., 1970). We agree whole-heartedly with the perspective of the Boulder Committee as illustrated by their statement: "The recommendations are offered with the awareness that such terminological problems are among the inevitable (and perhaps desirable) consequences of scientific advance and with the hope that the pace of further progress will render these recommendations obsolete" (Boulder Committee: Angevine et al., 1970).

With these thoughts in mind, a roundtable event was held at the Cortical Evolution 2015 conference for participants to discuss how to build consensus on the terms used for NPC types. The roundtable was chaired by Dr. Pasko Rakic and was formed by Arturo Álvarez-Buylla, Wieland Huttner, Arnold Kriegstein, and Stephen Noctor. All attendants at the conference had the opportunity to participate in this discussion. Participants who shared their point of view were Andre Goffinet, Robert Hevner, Milos Judas, Verónica Martínez-Cerdeño, Zoltán Molnár, and John Rubenstein. The rest of this article summarizes key points brought up during the discussion.

Topics discussed can be summarized as two main points:

1. Should terms assigned to specific NPC types change according to their newly discovered properties? Or should these terms remain as novel properties arise?
2. What terms are more appropriate to be assigned to newly discovered NPC types and subtypes? Should these terms be based on the cytoarchitectonic or on functional cell properties?

There was general agreement among attendees that, at this point, it is perhaps too early to reach a consensus on the terminology that should be assigned to each of the NPCs. For example, RG cell function and characteristics change over the course of development, and there are also significant genetic, molecular, and morphological differences in RG cells between species (Rakic, 2003; Zecevic, 2004; Clinton et al., 2014; Liu et al., 2014). In addition, it was considered likely that the diversity of NPC types is not yet fully known. However, it was further suggested that once the genomic identity of these cells is known, it would be easier to assign terms for each of the NPC types. On this point, Dr. Arnold Kriegstein offered the suggestion that when more is known about the nature of each NPC type, we

would probably discover that different NPC types are currently lumped into a single term.

CHANGING TERMS?

It was suggested by Dr. Milos Judas that until we fully identify and understand the types of NPCs that exist in the cortex, we should not change their current name. Until that time, he suggested that, to avoid functional implications and remain topographic, we should use the term RG cell to define NPCs in the VZ. He proposed assigning a number to each subtype of RG cell identified (1, 2, 3, etc.). In general, members of the panel and audience agreed that the "RG cell" term should be maintained. Dr. Pasko Rakic added that maintaining the first name given to a cell gives a sense of history to science. Historically, there are many terms in science that with time may no longer be appropriate, but he thought that as long scientists know what the term refers to, names should be maintained. Dr. Judas mentioned Cajal-Retzius cells as an example. He explained that nobody changed the original term assigned to Cajal-Retzius cells, even though we now know that these cells have five different embryonic origins.

Dr. Stephen Noctor stated that to avoid confusion, it would be best to use previously published terms. He advised caution when using new terms, and acknowledging in publications the terms for each NPC that have been used previously. Also, if authors feel a new name is justified, they should describe how and why this cell type differs from previously described cells.

Dr. Álvarez-Buylla reminded attendees of the discussion on terminology at the Cortical Development meeting in Delphi in 2002. A central question at that meeting was whether the term "glia" was appropriate for RG cells, or whether that term should be changed. Dr. Álvarez-Buylla explained that with time, the term "glia" in reference to RG cells was maintained, but the meaning associated with it changed. Although originally the term glia was used to describe differentiated cells, currently it is widely used to describe NPCs. Similarly, the term "astrocyte," or astroglial, is currently used by many biologists to refer to terminal differentiated mature cells. However, in the adult brain a subpopulation of cells with astroglial properties also functions as NPCs. Dr. Álvarez-Buylla explained how the meaning associated with the term astrocyte will probably change over time as happened with the term "RG cell." However, he pointed out that there are important lineage links among the NPCs at different stages of development terms tend to separate them; this could be very confusing for newcomers in the field.

Dr. John Rubenstein added that terms referring to a single essential feature of the morphology or structure of a cell are not appropriate, because this feature can transform over time. He proposed using many different cell traits and clustering them. In these multiclusters, some features may be added or deleted over time as new discoveries arise, but the main concept should persist.

RADIAL GLIAL CELLS/APICAL PROGENITOR CELLS

One topic of interest for the panel was the use of the terms "RG cell" and "apical progenitor cell" in reference to NPCs in the VZ. Dr. Kriegstein offered the opinion that whereas the terms "apical" and "basal" refer to cell location in a biologically correct manner, the term "RG cell" should be preserved, as it has already been in use for a long time. Dr. Wieland Huttner agreed that during neurogenic stages RG cells are the primary stem cells. However, he proposed introducing the term "apical progenitor" as a collective term for a population of NPCs. He explained that he introduced this term to make the definition simple in terms of cell biology and tissue/epithelial polarity. In his scheme, apical progenitor cells undergoing mitosis at the ventricular surface would include neuroepithelial progenitor cells, RG cells, and IP cells that divide in the VZ. Overall, there was general agreement on the principal cell types that divide in the VZ. For this reason some participants thought that a new or additional term may not be necessary. This was considered a good example of how more information on NPC characteristics is needed before assigning a term to each type of NPC.

A discussion on Tbr2+ cells located in the cortical VZ followed. It was pointed out that some Tbr2+ cells are found near the lumen of the ventricle in the VZ, but are not considered to be neuroepithelial cells, or apical NPCs. Dr. Noctor pointed out that in the prenatal rat, some Tbr2+ cells are found at the surface of the ventricle, but only before the SVZ has formed, and that by the time the SVZ has formed, the Tbr2+ cells are no longer found dividing at the ventricle. He explained that Tbr2+ cells do not exhibit the characteristic interkinetic nuclear migration throughout the cell cycle that is a hallmark of neuroepithelial/VZ/RG cells. Dr. Huttner said that, based on work by the Haydar lab showing that "short neural precursor cells" (currently referred to as "apical IP cells" by Haydar, Tyler et al., 2015) are embedded in the adhesion belt and are not delaminated, these cells should be classified as apical progenitor cells. Dr. Huttner proposed that cell classification should be based on the M-phase status of each NPC.

Dr. Álvarez-Buylla pointed out that whether prenatal, postnatal, or adult germinal regions are referred to, ideally there should be unifying terms to help explain the continuity in progenitor progression from one stage to the next. As it is now, multiple terms are used to describe NPCs located next to the ventricle at different stages of development, in the juvenile or adult brain. For example, when does a neuroepithelial cell stop being a neuroepithelial cell and become an RG cell? Or when does an RG cell stop being an RG cell to become an adult astroglial cell with NPC properties? (For example, V-SVZ B1 cells; Lim and Álvarez-Buylla, 2014.) To make things more confusing, the term "ependyma" has previously been used to refer to neuroepithelial cells or any cell bordering the ventricles. However, "ependyma" has more recently been used to describe the postnatal ventricular epithelium comprised of differentiated multiciliated ependymal cells and tanycytes. He proposed that the term neuroepithelium and VZ should be used more generally to refer to NPCs with epithelial properties in the VZ (ventricle-contacting cells), with the VZ RG cell being a type of neuroepithelial cell with a long pial basal fiber. Dr. Álvarez-Buylla emphasized the need to revise terminology to link terms used in development to those used in juvenile and adult stages that would reflect the continuity of germinal activity.

OUTER RG CELLS/BASAL RG CELLS

Next followed a discussion on terms used to describe RG cells that lose contact with the ventricle and translocate out of the VZ toward the overlying cortical plate via somal translocation within the existing RG fiber. Multiple opinions were offered concerning the terms assigned to this type of RG cell. Initially the terms used to label cells were based on the key features identified, particularly the transitional nature of these cells as they transformed from RG cells into GFAP-expressing astrocytes, as shown in human (Choi and Lapham, 1978; deAzevedo et al., 2003), macaque (Schmechel and Rakic, 1979), and ferret (Voigt, 1989). Later these translocating cells were also identified in prenatal rat and shown to be mitotic (Noctor et al., 2004, 2008). Dr. Verónica Martínez-Cerdeño suggested that the term "translocating RG cell" should be conserved for those RG cells that lose contact with the ventricle.

Live imaging work on fetal human neocortex in Dr. Kriegstein's lab introduced the new term "outer RG" cells (oRGs) to reflect different characteristics between ventricular and nonventricular RG cells, and to indicate that in fetal human neocortex most of the translocating cells are found in the outer SVZ (Hansen et al., 2010). Dr. Kriegstein doubted that there are meaningful differences between oRG cells located in the iSVZ and oSVZ that had originally been identified by Smart and colleagues in 2002 (Smart et al., 2002). Therefore, he proposed to use the term "oRG cells" for detached RG cells within both the iSVZ and the oSVZ. He also proposed that the names of the cells should be modified if distinct functional properties were discovered (oSVZ and iSVZ RG cells). Dr. Huttner felt that the term "basal RG" cell introduced by his lab would be appropriate as a collective term for RG cells in the iSVZ and oSVZ, as this would distinguish them from RG cells in the VZ, which he would call apical RG cells. He stated that maintaining the terms "apical" and "basal" would acknowledge apical–basal polarity and that use of the term "basal RG cell" would provide flexibility if differences between RG cells in the iSVZ and oSVZ should be discovered later. He suggested that if it should turn out that these cells are different in the iSVZ and oSVZ, we could call them "outer basal RG cells" and "inner basal RG cells." Dr. Kriegstein replied that he would prefer not substituting one clear and accessible anatomical term for the term "basal RG cell" that lacks priority and could be associated with IP cells. He thought that the term "basal RG cell" could potentially be confusing and make the research less accessible to those outside the field of cortical development.

Dr. Noctor stated that in his opinion the terms basal and apical, when applied to cortical VZ and SVZ cells, are counterintuitive because in the rest of the cerebral cortex basal refers to a ventral location (i.e., basal dendrites, basal forebrain, basal ganglia) and that apical signified closer to the pial surface as in apical dendrite. He felt that adopting the proposed terms basal and apical for development required essentially an anatomical inversion. He recognized the cell biological concept that cells facing a lumen are identified as apical, but noted that these terms were better used for organs or glands that lack the clear anatomical orientation present in the cerebral cortex.

Dr. Robert Hevner was in favor of using the functional terms "RG and IP cells" rather than adopting a term that refers to location. He suggested that location could be assigned to each term afterward.

INTERMEDIATE PROGENITOR CELLS/ BASAL PROGENITOR CELLS

Dr. Kriegstein explained that when IP cells were discovered in the cortical SVZ, he and Stephen Noctor coined the term "IP cells" because these NPCs were in an intermediate stage between RG cells and neurons. He thought that terms assigned to NPCs should be logical and intuitive. Not all IP cells are basal; some are

apical and divide in the VZ, as he and Dr. Noctor showed in 2008 (Noctor et al., 2008). He felt that using the term "IP cell" reflects lineage rather than location and is more intuitive than including these cells in a group of cells labeled "basal progenitor cells."

Dr. Huttner was a proponent of the term "basal progenitor cells." He proposed the term "basal progenitor cell" to identify NPC populations that have delaminated from the ventricle, including basal IP and basal RG cells. If it should be determined that IP cells are not integrated into the apical junction belt but are always delaminated (even if they are one nuclei distance away from the ventricular surface), then he would agree the term "basal" would be correct. But if there are a subset of IP cells that undergo mitosis while integrated into the apical junction (as shown by the Haydar lab in Tyler et al., 2015) and a separate subset that are positioned away from the ventricle, then he stated he would propose to divide these cells into two groups: basal and apical IP cells (Florio and Huttner, 2014).

Dr. Kriegstein pointed out that NPCs located in different niches may generate neurons at the same time, but these neurons may acquire different cell fates. Based on these niches, it would be logical to give NPCs a name that reflects their niche, as IP cells in the iSVZ may be lineage-related to the ventricular RG, whereas the IP cells in the oSVZ may be related to the oRG.

Dr. Álvarez-Buylla thought that to call IP cells basal or apical would not be appropriate, at least for the SVZ. His reasoning was that that many cells migrate tangentially, and these are not fully defined by their location. If, however, the development of the cortex were strictly radial, he thought that the terms apical and basal would be appropriate. He added that in addition, the word "progenitor" carries a meaning. Therefore, he favored the term "IP cell." He also pointed out that some people in the stem cell field are using the term "transit-amplifying progenitor cell" for NPCs between the first progenitor cell and the final stage cell.

In an attempt to reach a consensus, Dr. Hevner expanded on Dr. Huttner's proposal by suggesting that we could combine the terms apical and basal with IP cells and RG cells, and label NPCs as apical IP cells, basal IP cells, apical RG cells, and basal RG cells.

ISVZ AND OSVZ

All participants agreed that in the case of the cerebral cortex the terms used for the iSVZ and oSVZ are ideal for the structures they describe. Dr. Martínez-Cerdeño asked what is the consensus about using these terms in those species in which these structures can be delineated in some regions of the cortex, for example, in the case of macaque in the occipital cortex, but not in others, as in the frontal macaque cortex (Martínez-Cerdeño et al., 2012). Dr. Molnár stated that the cell composition is similar between the inner and outer subventricular zones (iSVZ and oSVZ), and because of these similarities these terms should not be used in those cortical regions in which there is no clear-cut cytoarchitectural separation by an inner fiber layer between these two compartments. He added that although the origin of the inner fiber layer is still not clear, the separation of the SVZ into the iSVZ and oSVZ does not seem to be primate specific (Garcia-Moreno et al., 2012). Participants agreed on this concept.

In summary, over one and a half hours of discussion, many important and interesting points were raised. The conversation informed us about past and current nomenclature, and how our shared understanding will impact future nomenclature used in reference to different NPC types. The discussion began a dialogue among members of the field with the aim of seeking common ground on terminology for developmental neuroscientists, and raised important questions on the anatomical and functional characteristics of a variety of NPCs in human and other species. This discussion should be resumed as new properties of NSCs are elucidated.

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