

Review

Fate map of the chick embryo neural tube

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Fate-map studies have provided important information in relation to the regional topology of brain areas in different vertebrate species. Moreover, these studies have demonstrated that the distribution of presumptive territories in neural plate and neural tube are highly conserved in vertebrates. The aim of this review is to re-examine and correlate the distribution of presumptive neuroepithelial domains in the chick neural tube with molecular information and discuss recent data. First, we review descriptive fate map studies of neural plate in different vertebrate species that have been studied using diverse fate-mapping methods. Then, we summarize the available data on the localization of neuroepithelial progenitors for the brain subregions in the chick neural tube at stage HH10–11, the most used stage for experimental embryology. This analysis is mainly focused on experimental fate mapping results using quail-chick chimeras.

Key words: brain, chicken, fate-map, neural plate, neural tube.

Fate maps of the central nervous system at the neural plate stage

By comparing patterns of molecular expression in many vertebrate species, it was possible to identify the main components of the central nervous system (Rubenstein *et al.* 1994; Shimamura *et al.* 1997; Puelles *et al.* 2000; Puelles and Rubenstein 2003). These studies provided evidence that the patterns of gene expression can be related to primary morphogenetic processes that organize the histological primordia of the embryonic central nervous system into distinct domains. Neural plate and neural tube are subdivided into longitudinal domains: floor plate, basal plate, alar plate and roof plate. Signals produced by the axial mesendoderm and non-neural ectoderm are able to generate consecutive longitudinal domains of cell fate specification in the progenitors of the embryonic central nervous system (Rubenstein *et al.* 1994, 1998; Shimamura *et al.* 1995; Tanabe and Jessel 1996; Dessaud *et al.* 2007). On the other hand, transverse domains (proneuromeres and neuromeres) expressing distinct combinations of genes

are present in the neural plate and neural tube (Rubenstein *et al.* 1994; Shimamura *et al.* 1997). These domains were first observed by classic authors at the beginning of the last century and this idea was later recovered in the prosomeric model (revised in Puelles *et al.* 1987 and Puelles 1995). The prosomeric model proposes that the brain is subdivided into longitudinal and transversal segments (Bulfone *et al.* 1993; Puelles and Rubenstein 1993, 2003; Rubenstein *et al.* 1994; Puelles 1995, 2001a). These studies were mainly based on gene expression patterns, but lacked information concerning the cell lineage relationships between molecular domains in the neuroepithelium and the neural formations in the mantle layer of the central nervous system.

Fate-map studies contributed to solve this problem providing important information in relation to the organization of the brain in different vertebrate species (see Table 1; axolotl: Jacobson 1959; *Xenopus laevis*: Eagleson and Harris 1990; zebrafish: Woo *et al.* 1995; Staudt and Houart 2007; mouse: Inoue *et al.* 2000; chicken: Couly and Le Douarin 1985, 1987; Smith-Fernandez *et al.* 1998; Cobos *et al.* 2001b; Fernandez-Garre *et al.* 2002; Garcia-Lopez *et al.* 2004; Pombero and Martinez 2009). The fate-map technique consists of marking neuroepithelial fields in order to detect them during the subsequent development, which allows us to relate gene expression to the neuroepithelial origin of the neural formations. Fate-map studies carried out in different species have demonstrated that neural plate organization is a highly conserved structure in vertebrates (Fig. 1).

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Received 15 January 2009; revised 19 January 2009; accepted 20 January 2009.

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Abbreviations

A, amygdale; a, nucleus angularis; ABa, antero-basal nucleus of the hypothalamus; ac, anterior commissure; AEP, entopeduncular area; amb, ambiguous motor nucleus; AP, alar plate; ap, area postrema; APT, anterior pretectal nucleus; ar, alar reticular nucleus arc, arcuate nucleus; Avc, arcuate nucleus of the hypothalamus; aVI, accessory abducens motor nucleus; B, vestibular cell group B; br, basal reticular nucleus; cb, cerebellum; ce, external cuneate nucleus; ch, choroid plexus; cha, choclear nucleus angularis; chas, coclear nucleus angularis shell; chd, choclear nucleus lemnaris; chmc, choclear nucleus magnocellularis; cho, nucleus olivary superior; cp, commissural plate, pallial commissure; d, descending vestibular nucleus; dcn, dorsal column nuclei; Dd, nucleus Deiters dorsalis; DF, dorsofrontal nucleus; dh, dorsal horn; Di, diencephalon; DL, dorsolateral anterior nucleus of the thalamus; DLL, dorsal nucleus of the lateral lemniscus; DM, dorsomedial anterior nucleus of the thalamus; DMH, dorsomedial hypothalamic nucleus; DP, dorsal pallium; DPT, diffuse pretectal area; DR, dorsal raphe nucleus; dV, dorsal trigeminal motor nucleus; Dv, nucleus Deiters ventralis; dVr, rostral part of dorsal trigeminal motor nucleus; Eth, thalamic eminence; FB, forebrain; Hb, habenular nucleus; HB, hindbrain; ICl, intercalated nucleus; ICo, intercollicular area; IGL, intergeniculate leaflet; Illm, oculomotor nerve; Illv, third ventricle; InC, interstitial nucleus of Cajal; InR, rostral interstitial nucleus; IP, interpeduncular nucleus; IPT, intermediate pretectal nucleus; Is, isthmus; IsO, isthmooptic nucleus; IsPC, isthmic parvocellular nucleus; isRt, isthmic reticular formation; IsV, ventral isthmic nucleus; IvM, pathetic nucleus; IX, glossopharyngeal motor nucleus; la, nucleus laminaris; lld, nucleus lemnisci lateralis, pars dorsalis; lli, nucleus lemnisci lateralis, pars intermedia; llv, nucleus lemnisci lateralis, pars ventralis; LoC, locus ceruleus; LP, lateral pallium; lt, lamina terminalis; m, medial vestibular nucleus; MB, midbrain; MCPi, magnocellular preisthmic nucleus; ME, medial eminence; Mes, mesencephalon; MG, medial geniculate nucleus; MM, mammillary/retromammillary region; MP, medial pallium; mRt, mesencephalic reticular formation; OB, olfactory bulb; och, optic chiasm; oid, inferior olivary nucleus pars dorsalis; oiv, inferior olivary nucleus pars ventralis; Op, optopeduncular area; os, optic stalk; OvPG, oval pregeniculate nucleus; p, principal sensory nucleus of the trigeminal column; pA, pallial amygdala; PA, pallidum; Pa, paraventricular area; Pal, pallium; pc, posterior commissure; PG, pregeniculate nucleus; PH, posterior hypothalamic area; Pi, pineal gland; Pit, infundibulum/posterior pituitary; pl, lateral pontine nucleus; pm, medial pontine nucleus; pM, mesencephalic profundus nucleus; POA, preoptic area; PRT, prerubral tegmentum; Prels, preisthmic region of the midbrain; PRot, perirotundic area; PrPT, principal pretectal nucleus of the commissural pretectum; pSe, pallial septum; psp, pallial-subpallial boundary; PT, pretectum; PTh, prethalamus; PThE, prethalamic eminence; p1Rt, reticular formation of p1; p1Tg, pretectal tegmentum; p2Rt, reticular formation of p2; p2Tg, thalamic tegmentum; p3, reticular formation of p3; R, retina; rc, central reticular nucleus; rgc, gigantocellular reticular nucleus; Rh, rhombencephalon; rIX, retrofacialglossopharyngeal motor nucleus; rl, lateral reticular nucleus; rhI, rhombic lip; rhI(oi), inferior olivary nucleus; rhI(pl), lateral pontine nucleus; rhI(pm), medial pontine nucleus; rhI(egl), external granular layer; RM, retromammillary nucleus; RMC, red nucleus, magnocellular part; RMM, retromammillary tegmentum; ro, nucleus raphe obscurus; Rot, rotundus nucleus; rp, nucleus raphe pallidus; RP, roof plate; rpc, parvicellular reticular nucleus; RPC, red nucleus, parvicellular part; rpgc, nucleus reticularis ponti/gigantocellularis; Rt, reticular nucleus; s, nucleus of the tractus solitarius; Se, septum; SLu, nucleus semilunaris; SNC, substantia nigra, compact part; SNR, substantia nigra, reticular part; sOp, suboptopeduncular area; SP, secondary prosencephalon; spA, subpallial amygdala; spPa, subparaventricular area; sPal, subpallium; spd, dorsal supraespal motor nucleus; SpL, lateral spiriform nucleus; SpM, medial spiriform nucleus; spSe, subpallial septum; spv, ventral supraespal motor nucleus; SRot, subrotundus nucleus of the thalamus; ST, striatum; STh, subthalamic nucleus; SubG, subgeniculate nucleus of the prethalamus; sVII, superficial facial motor nucleus; Tect, optic tectum; TG, tectal gray formation; Th, thalamus; ToS, torus semicircularis; TPP, tegmento pedunculo-pontine nucleus; TTh, nucleus of the tectothalamic tract; V, trigeminal motor nucleus; vA, vestibular cell group A; Vd, descending trigeminal nucleus; vh, ventral horn of spinal cord; VMH, ventromedial hypothalamic nucleus; vn, vestibular nuclei; vn(i), inferior vestibular nucleus; vnA, nucleus A of Wold; vnB, vestibular cell group B; vnd, vestibular descendens nucleus; vnDd, Deiters dorsalis nucleus; vnDv, Deiters ventralis nucleus; vnm, vestibular medial nucleus; vntg, nucleus tangentialis; vnVs, vestibular superior nucleus; Vp, principal trigeminal nucleus; Vd, descendent trigeminal nucleus; VI, abducens motor nucleus; VII, medial facial motor nucleus; VP, ventral pallium; Vs, superior vestibular nucleus; VTA, ventral tegmental area; X, vagal motor nucleus; XI, spinal accessory nerve nucleus; XIIl, hypoglossal motor nucleus, pars lingualis; XIIts, hypoglossal motor nucleus, pars tracheosyringalis; xa, anterior commissure; xcb, cerebellar commissure; xhb, habenular commissure; xIV, pathetic commissure; xp, pallial commissure; xrm, retromammillary commissure; xs, spinal commissure; xtect, tectal commissure; zi, zona intermedia.