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Dispersing movement of tangential neuronal migration in superficial layers of the developing chick optic tectum

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ABSTRACT

During embryonic brain development, groups of particular neuronal cells migrate tangentially to participate in the formation of a laminated structure. Two distinct types of tangential migration in the middle and superficial layers have been reported in the development of the avian optic tectum. Here we show the dynamics of tangential cell movement in superficial layers of developing chick optic tectum. Confocal time-lapse microscopy in organotypic slice cultures and flat-mount cultures revealed that vigorous cell migration continued during E6.5–E13.5, where horizontally elongated superficial cells spread out tangentially. Motile cells exhibited exploratory behavior in reforming the branched leading processes to determine their pathway, and intersected with each other for dispersion. At the tectal peripheral border, the cells retraced or turned around to avoid protruding over the border. The tangentially migrating cells were eventually distributed in the outer *stratum griseum et fibrosum superficiale* and differentiated into neurons of various morphologies. These results revealed the cellular dynamics for widespread neuronal distribution in the superficial layers of the developing optic tectum, which underline a mode of novel tangential neuronal migration in the developing brain.

1. Introduction

The optic tectum in non-mammalian vertebrates and the superior colliculus in mammals have multi-layered structures. The superficial layers receive visual inputs through retinal ganglion cell axons, and the deeper layers perform integration of multiple sensory modalities and output function (King, 2004; Butler and Hodos, 2005). The avian optic tectum is composed of 15 layers subdivided by distinct neuronal cell types (Ramón y Cajal, 1911; LaVail and Cowan, 1971a; Senut and Alvarado-Mallart, 1986). Tectal layers are formed primarily by radial migration of post-mitotic neuronal cells from the ventricular layer to their destination, depending on their time of birth (LaVail and Cowan, 1971b; Gray et al., 1988; Gray and Sanes, 1991; Sugiyama and Nakamura, 2003).

During brain development, groups of particular neuronal cells migrate tangentially. It has been extensively studied in the mammalian cerebral cortex that cells originating from ganglionic eminences migrate tangentially towards the cortex in order to give rise to GABAergic interneurons (Anderson et al., 1997; Parnavelas, 2000; Corbin et al., 2001; Lambert de Rouvroit and Goffinet, 2001; Marín and Rubenstein, 2001; Nadarajah and Parnavelas, 2002). Cajal-Retzius cells derived from the discrete regions of the pallium migrate superficially in tangential directions to colonize the entire cortex (Bielle et al., 2005; Meyer et al., 2002; Takiguchi-Hayashi et al., 2004). Additionally, in the developing hindbrain, precerebellar neurons generated in the rhombic lip migrate circumferentially around the medulla to form the inferior olive, the lateral reticular and the external cuneate nuclei (Harkmark, 1954; Altman and Bayer, 1987a, 1987b; Bourrat and Sotelo, 1988, 1990; Tan and Le Douarin, 1991; Ambrosiani et al., 1996; Ono and Kawamura, 1989; Kawauchi et al., 2006).

In the avian optic tectum, two streams of tangential migrations in the middle and superficial layers have been reported using Golgi staining, retrovirus-mediated cell labeling, and quail-chick chimeric transplants (Domesick and Morest, 1977; Puelles and Bendala, 1978; Gray and Sanes, 1991; Martínez et al., 1992). Recently, the movement of the tangentially migrating cells in the middle layers (prospectively in the deep layers) has been visualized by time-lapse recording of fluorescent-labeled cells in tectal tissue culture (Watanabe et al., 2014; Watanabe and Yaginuma, 2015). During E6–E8, tangential migrants with a bipolar cell shape move in an axophilic way, clinging to the fasciculus of tectal efferent axons in the prospective stratum album centrale (SAC). After E8, they translocate toward the upper layers to differentiate into multipolar neurons in the stratum griseum centrale (SGC) (Domesick and Morest, 1977; Puelles and Bendala, 1978; Watanabe et al., 2014). On the other hand, the mode of tangential migration in the superficial layers remains elusive; this

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includes cell behavior, range, duration, direction of migration, and cell fate.

In the current study, we show the dynamics of tangential cell migration in superficial layers of the developing chick optic tectum. Time-lapse analysis revealed dispersing movement of individual cells with branched leading processes, which were reforming to find out the pathway to proceed for spreading. Motile cells exhibited exploratory behavior to avoid protruding over the tectal peripheral border. These results reveal cellular dynamics for the widespread distribution of neurons in the superficial layers in the developing optic tectum, which underline a mode of novel tangential neuronal migration in the developing brain.

2. Results

2.1. Tangential migration in superficial layers in tectal slice culture

In our previous study, we noticed horizontally elongating cells in sections of the superficial layers of the chick optic tectum during E7.5–E10.5, which were supposed to migrate tangentially (Watanabe et al., 2014). To outline the tangential movement in the layered structure, we first monitored tangential migration of fluorescently-labeled cells in a tectal slice culture. Using Tol2-mediated gene transfer for stable transgene expression (Sato et al., 2007), the expression vectors encoding EGFP and mCherry with nuclear localizing signal (mCherry-Nuc) were co-electroporated into E1.5 mesencephalon for overall labeling of the neuroepithelial cells in the prospective tectal wall. Slice culture of the labeled tectal tissue was conducted at E7.5 to monitor cell behavior under confocal time-lapse microscopy.

Video 1 shows time-lapse images taken every 10 min over a period of 20 h (among N = 6 specimens visualized). Horizontal cell movement was remarkable in the upper layers, especially in the marginal cell sparse zone above prospective layer VI (layer nomenclature after LaVail and Cowan, 1971a). There were few cells that left from the superficial tangential stream, indicating that the passable layers for tangential migration were confined. Individual migrating cells had a long and motile leading process extending toward the proceeding direction, and exhibited saltatory movements intermitted by short periods of slow movement. Nuclear movement (mCherry-Nuc) indicated that overall cell speed was not decreased over time, and was sustained throughout the whole observation period. Migration occurred all over the tectal surface in the cultured slice. Video 2 follows the movement of an arrow select cells from Video 1 in higher magnification. While some cells procceded unidirectionally along the dorso-ventral axis (red or blue arrow directed dorsoventrally; light blue arrow directed ventrodorsally), another cell seemed to wander by turning back several times (yellow arrow). These observations suggest that the tangential migration of the labeled cells was active in the superficial layers, where the cells might be moving horizontally in non-linear manner.

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.ydbio.2018.03.010.

2.2. Tangentially migrating cells spread in superficial layers

While the slice culture system recapitulated the tangential movement specific to the superficial layers, it did not reveal cell behavior or the directionality of migration on the horizontal plane. Therefore, we set up focal fluorescent labeling on the tangential migrants and performed a flat-mount culture to observe cell movement on the horizontal plane in the superficial layers.

In a previous study, we reported that electroporation at E4.5 enabled labeling of neuroepithelial cells in the ventricular layer, which migrated radially and eventually turned to join both the middle and superficial streams as tangentially migrating cells (Watanabe et al., 2014). After adjusting the timing of electroporation, we found that superficial migrating cells were predominantly labeled when the electroporation was performed at E5.5 (Fig. 1). Two days after focal labeling by electroporation, dorsal and ventral streams of superficial migrants had been emigrating from the radially arranged columns of GFP-positive cells (Fig. 1A; open and closed arrow, respectively; N = 3). In a case when a large area was labeled by electroporation, the superficial migrants were scattered broadly on the tectal surface at E10.5 (Fig. 1B–F; N = 3), suggesting that the migrating cells spread ubiquitously throughout the superficial layers.

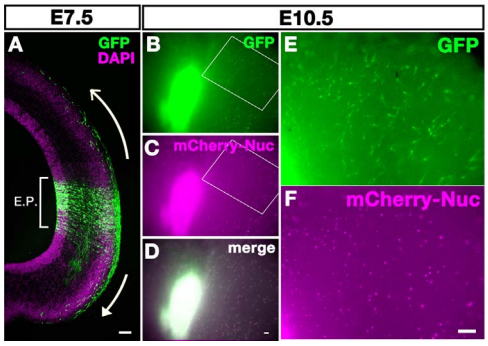

Fig. 1. Labeling of tangentially migrating cells, which spread over the tectal surface. Electroporation was performed at E5.5 into a portion of the tectal wall to transfect the pCAGGS vectors expressing EGFP and mCherry-Nuc. (A) The dorsal and ventral stream of superficial migrants emigrated from the radially arranged columns of GFP-positive cells at E7.5 (open and closed arrow, respectively). (B–D) When a large area was labeled by electroporation, the superficial migrants from the labeled columns were scattered broadly on the tectal surface at E10.5. (E, F) A higher magnification view of the area enclosed by a white box (B, C). Scale bars; (A) (B–D) (E, F) 100 μm.

2.3. Dispersing movement of superficial migration

It is noteworthy that the labeled cells stayed superficial during the thickening of the tectal layers, because these layers develop extensively under the tangential stream. We speculated that this superficial disposition of the migrating cells should facilitate our observation on the superficial migration from the pial side within the focal length. Therefore, we applied a flat-mount culture of labeled tectal tissue on the culture insert and traced the cell movement on the horizontal plane from the pial side. The expression vectors encoding EGFP and mCherry-Nuc were focally electroporated at E5.5. Tectal tissue was cut at E7.0 and laid pia-side down on the culture insert in a glass-bottom dish to monitor cell behavior by confocal time-lapse imaging under an inverted microscope.

Overall movement of tangential migration was captured as time-lapse images taken every 10 min over a period of three days from E7.0 (E7-E9, Video 3; N = 4). At the onset of culture, fluorescent labeling was focused on an electroporated area (approximately 300 × 400 μm) as revealed in the nuclear distribution of mCherry-Nuc (Video 3, right panel).

At the initial phase (0–24 h), the labeled emigrating cells left from the labeled area, and proceeded preferentially in dorsal and ventral directions. After the initial phase (24–48 h), the following cells left the labeled area and spread in various directions. In the latter phase (48–72 h), the migrating cells had broadly scattered to the surrounding region of the spot. The migration was multi-directional but not simple linear radial dispersion because the migrating cells occasionally changed direction. Each cell had a long leading process, which stretched over 100 μm at the maximum and changed length during migration. The leading process sometimes sprouted a new branch, which might have triggered the steering of the migration direction. The cells intermittently paused during migration before directional change, and subsequently migrated steadily again. As a result, the migration was neither radial nor erratic, but multi-directional, in that the migrating cells from the labeled area were dispersing out in various directions.

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