Chapter 12
Patterning the Posterior Lateral Line in Teleosts: Evolution of Development

Alain Ghysen, Hironori Wada and Christine Dambly-Chaudière

Abstract The lateral line system of teleost fishes presents large variations of patterns and forms, usually thought of as adaptive. This raises the question of how divergent adult patterns are achieved, and how selective pressures have contributed to this divergence. Our understanding of the development of this sensory system has much improved over the past 10 years, mostly through work on the zebrafish. Because this progress is restricted to a single species, we cannot yet answer questions about the determinism of lateral line evolution, but we can at least propose plausible and testable hypotheses. Here we review the mechanisms that mediate the transition from embryonic to adult pattern in the zebrafish posterior lateral line system (PLL), and we show that the adult pattern is largely determined by developmental events that take place during early larval life. We also show that simple variations in the use of the same mechanisms account for the very different patterns observed in juvenile zebrafish and blue-fin tuna, and could potentially account for many or all of the patterns observed in other adult teleosts. We conclude that, in the case of the lateral line at least, large variations in pattern depend on minor changes in the deployment of conserved developmental programs, with uncertain adaptive value. We propose that organisms neurally adapt to whatever tools they are provided with by their own development, and use them as best as they can, thereby giving the impression that such tools were actually selected for.

Il n'est mouvement qui ne parle.(*There is no such thing as a movement that does not speak*).Michel de Montaigne, Livre II, Chap. XII.

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12.1 Introduction

12.1.1 Structure of the Lateral Line System

Many reviews have dealt with the basic organization of this sensory system (e.g., Coombs et al. 1989, 2014; and this book), and this aspect will only be briefly summarized here. The lateral line system comprises a number of discrete peripheral sensory organs, which may be either mechanosensory or electrosensory. The distribution of organs over the fish body is not exactly reproducible from individual to individual, but the overall pattern (number and location of the various lines, density of organs along each line, etc.) is constant within a species.

In most teleost fishes, the lateral line system comprises only mechanosensory organs, and the present chapter is restricted to a discussion of the mechanosensory lateral line system. The elementary unit of this system, the neuromast, comprises a core of mechanosensory cells that resemble very much the hair cells of the vertebrate inner ear. Neuromast hair cells are surrounded by non-sensory support cells, which secrete a gelatinous cupula in which the sensory hair cell apical processes (kinocilium, stereocilia) are embedded, and by an outermost rind of mantle cells.

In many species, a subset of neuromasts sink in the underlying dermal bones of the head and scales, and become enclosed in canals that communicate with the outside world through pores. Different sensory stimuli are most effective for superficial and canal neuromasts, and it is thought that the former measure flow velocity, whereas the latter measure pressure gradients and flow acceleration, an aspect of lateral line physiology that has attracted much attention (see e.g., Coombs and Montgomery 1999, and this book).

12.1.2 Early Work on Lateral Line Development

The original work on lateral line development was carried on in amphibians, most notably by Harrison and Stone. Working on the frog *Rana*, Harrison was to our knowledge the first to suggest that the posterior lateral line system (PLL), which extends on the trunk and tail, is set up by a cranial primordium that migrates all the way from the otic region to the tip of the tail (Harrison 1904). During this

migration, the primordium deposits groups of cells, the prospective neuromasts, in its wake. Harrison (1904) also noted that a fiber always connects the primordium to its associated cranial ganglion, and proposed that sensory axons are actually towed by their migrating target cells.

In a number of excellent papers, Stone (1922, 1933, 1937) followed up this pioneering work. He observed migrating primordia in living salamanders (*Ambystoma*), and used grafts of pigmented cells in unpigmented background to demonstrate that both sensory and support cells of the trunk lateral line originate from the primordium. He also observed that a trail of deposited cells extends between neuromasts, and that sheath cells from the grafted placode migrate along the lateral line nerve (1933). Stone further showed that the path followed by the primordium must be defined by some extrinsic cue, but neuromast deposition must be intrinsic to the migrating primordium, as it does not depend on the host tissue. He discovered that each neuromast deposited by the primordium can bud off new neuromasts (which he called accessory neuromasts, or bud-neuromasts) during later development (1937).

Following G. Streisinger's choice of the zebrafish *Danio rerio* as a new "model" system to study the genetics of development, a number of aspects of zebrafish embryology have been described in great detail, including the development of its lateral line system. Metcalfe (1985) showed that, as in amphibians, the zebrafish PLL is laid down by a migrating primordium derived from a postotic placode, and that sensory axons extend into this primordium and accompany it during its migration, as proposed by Harrison (1904) in frogs. He further demonstrated that the sensory neurons that innervate the neuromasts are derived from the same postotic placode as the migrating primordium, and become postmitotic at the very early time of 10 h postfertilization (hpf), during gastrulation (Metcalfe 1983).

12.1.3 Early Work on Lateral Line Evolution

Previous analyses of lateral line evolution have mostly relied (1) on comparative descriptions of adult patterns, or more rarely of larval patterns, with the aim of inferring a putative ancestral pattern, and (2) on the mapping of morphological patterns on independently derived phylogenetic trees, with the aim of revealing evolutionary trends (see e.g., Webb 1989a; Northcutt 1990). Whereas this approach has provided us with a useful catalog of pattern variations, its strictly descriptive nature yields no information on the underlying developmental processes.

Recent progress in our understanding of PLL development has begun to reveal the mechanisms involved in this development, and their molecular bases. Although this progress is mostly limited to zebrafish so far, it paves the way to a re-analysis of the evolution of lateral line development in other species—an analysis looking for changes in the generative mechanisms that cause variation in the final patterns, rather than for pattern variation on its own sake.

In this chapter we summarize the various processes that lead from embryonic to adult PLL patterns in zebrafish, and we examine the implication of similar processes in a few other teleost species, mostly in the blue-fin tuna, *Thunnus thynnus*, where early larval development has been directly compared to that in zebrafish. This comparison is particularly interesting as *Danio* and *Thunnus* belong, respectively, to the Ostariophysi and the Acanthopterygii superorders of teleost fishes, which diverged around 290Myrs ago (Steinke et al. 2006; Hurley et al. 2007), and are therefore as distantly related as any two teleosts can be.

12.1.4 Terminology

Because the same words have been used with different meanings in different contexts (e.g., secondary neuromasts, accessory neuromasts, etc.), we will define the different names used throughout this chapter, mostly based on the recent work in zebrafish, which will be summarized in the next section.

The PLL includes all neuromasts on the body, except those on the head (anterior lateral line system). The neuromasts on the caudal fin are usually considered part of the PLL. Here we retained the name of caudal lateral lines (CLL, Wada et al. 2008) for these neuromasts, as they are a special subset produced by budding from the terminal PLL neuromasts.

Primary PLL neuromasts are those derived from the embryonic primordium, primI, whereas *secondary* neuromasts are those derived from the larval primordia, primII and primD. The distinction between primary and secondary neuromasts is an important one, since it appears that in both the zebrafish, *Danio rerio*, and the blue-fin tuna, *Thunnus thynnus*, hair cells in primary neuromasts are plane-polarized along the anteroposterior axis, whereas those of the secondary neuromasts are polarized along the dorsoventral axis.

Within each group (primary and secondary) some neuromasts are directly deposited by the migrating primordium, but other neuromasts develop later, through the proliferation of interneuromast cells laid down by the migrating primordia. Because those late neuromasts are intercalated between the pre-existing neuromasts deposited by the migrating primordia, they are called *intercalary* neuromasts. Primary (primI-derived) intercalary neuromasts may develop much after secondary neuromasts have been deposited by primII- or primD, and the difference between primary and secondary neuromasts has thus nothing to do with time of appearance.

Neuromasts of all types (primary or secondary, deposited or intercalary) can bud off additional neuromasts during adulthood. Those additional neuromasts are called *accessory*, or *bud-neuromasts*, as originally defined in amphibians by Stone (1937). The words “accessory neuromasts” have unfortunately been given more recently a different meaning in fishes (Coombs et al. 1988), where they are used to name superficial neuromasts associated to canals, although nothing is known of the origin of such superficial neuromasts, and it seems likely that they may actually

have different origins in different species (see Sect. 12.3.2.6 below). To avoid unnecessary confusion, therefore, we used "bud-neuromasts" throughout this chapter. Bud-neuromasts remain closely associated to the founder neuromast and end up forming rows of neuromasts that are called *stitches*. The founder neuromast of a stitch is usually impossible to distinguish from its bud-neuromasts, which can themselves bud off new bud-neuromasts (Ledent 2002; Wada et al. 2010).

Pattern will be used throughout with the meaning of spatial distribution of sensory organs on the body surface.

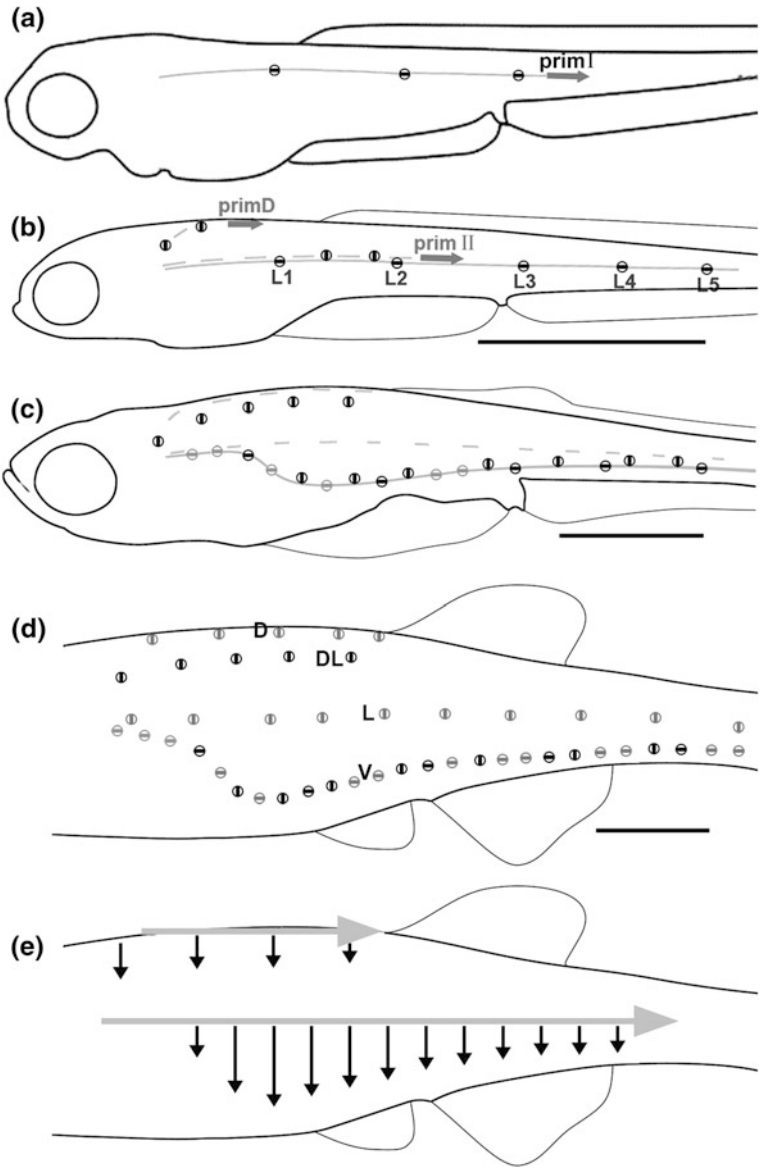
12.2 Development of the Posterior Lateral Line System in zebrafish

12.2.1 Embryonic Development of the Zebrafish PLL

A number of laboratories have joined forces over the past 10 years to get mechanistic insights into the embryonic and early larval development of the zebrafish PLL. As a result, we now have a fairly comprehensive understanding of the embryonic development of the system. This part of lateral line development will be summarized here, to the extent that it contributes to an understanding of evolutionary variation, but only briefly, as there are many reviews published over the past few years that have discussed this process (Ghysen and Dambly-Chaudière 2004, 2007; Lecaudey and Gilmour 2006; Ma and Raible 2009; Aman and Piotrowski 2010; Chitnis et al. 2012).

The embryonic primordium arises as part of the PLL placode, which extends posterior to the otic placode. There is evidence that the PLL placode enters a phase of mitotic quiescence around gastrulation, suggesting a very early determination step (Metcalfe 1983; Laguerre et al. 2005). It seems likely that the placode is determined by interactions between ectoderm and the underlying hindbrain rhombomeres (reviewed in Baker and Bronner-Fraser 2001; Schlosser 2006), but this has not yet been fully elucidated.

Once formed, the embryonic primordium migrates along the horizontal myoseptum to the posterior tip of the body (Fig. 12.1a). This oriented migration is mediated by SDF1/CXCR4 signaling, where the signal (SDF1) is produced by cells along the myoseptum, whereas the receptor (CXCR4) is present in the leading cells of the migrating primordium (David et al. 2002; Knaut et al. 2003; Li et al. 2004). Migration also requires the presence of another SDF1 receptor, CXCR7, in the trailing region of the primordium (Dambly-Chaudière et al. 2007; Valentin et al. 2007). It has been proposed that CXCR7 sequesters SDF1, making it unavailable for CXCR4 signaling (Boldajipour et al. 2008) and thereby producing a gradient of SDF1/CXCR4 signaling within the primordium (Dambly-Chaudière et al. 2007). This gradient was proposed to explain directional migration toward the tail, as has now been demonstrated by Donà et al. (2013).


(a)
prim I
(b)
primD
prim II
L1
L2
L3
L4
L5
(c)
(d)
D
DL
L
V
(e)

◀ **Fig. 12.1** Development of the PLL in zebrafish. **a** The embryonic primordium primI migrates from the postotic region to the tip of the tail during the second day of life, and deposits five anteroposteriorly polarized neuromasts, L1–L5, as well as a trail of interneuromast cells (*gray line*). **b** Two additional primordia, primII and primD, migrate during larval life and deposit dorsoventrally polarized neuromasts, as well as a discontinuous trail of interneuromast cells *(dashed gray lines)*. **c** Over the first half of larval life, primI-derived interneuromast cells proliferate and form intercalary neuromasts (*light gray circles*) with anteroposterior polarity. **d** During larval life, neuromasts of the early lateral line migrate ventrally and end up forming a ventral line (*V line*), whereas the neuromasts of the early dorsal line also migrate ventrally and end up forming a dorsolateral line (*DL line*). At late larval stages, primII- and primD-derived interneuromast cells proliferate in turn, and form two new lines of intercalary neuromasts (*light gray*) with dorsoventral polarity. These new lines are aligned, respectively, along the lateral myoseptum (*L line*) and dorsal midline (*D line*). **e** Scheme to outline the fact that all primordia migrate along the rostrocaudal axis, whereas all neuromasts migrate along the dorsal axis. Scale bar: 1 mm

The anisotropy revealed by the complementary distribution of the two SDF1 receptors in the migrating primordium is mediated by Wnt signaling in the leading region (Aman and Piotrowski 2008), and FGF signaling in the trailing region (Lecaudey et al. 2008; Nechiporuk and Raible 2008). Wnt signaling is responsible for cell proliferation in the PLL placode and primordium (Gamba et al. 2010; Aman et al. 2011; Valdivia et al. 2011), thereby compensating for the loss of cells concomitant to neuromast deposition (Laguerre et al. 2005). FGF signaling is responsible for the mesenchymo-epithelial transition that leads to neuromast deposition (Lecaudey et al. 2008; Nechiporuk and Raible 2008).

Neuromast deposition seems to be an intrinsic property of the PLL primordium (Gompel et al. 2001). It has been proposed that deposition is a simple function of primordium size: proliferation would bring the primordium to some threshold size and trigger the next event of deposition, as suggested by the observation that the rate of deposition is decreased following gain-of-function interference with Wnt signaling (Aman et al. 2011). Although this mechanism is appealingly simple, the control of deposition is likely to be more complicated, however, as a decrease in cell proliferation due to inactivation of the Wnt target, *lef1*, results in a truncation of the line due to eventual lack of cells, rather than to larger spacing between neuromasts (Gamba et al. 2010; Valdivia et al. 2011; McGraw et al. 2011). Our present understanding (and its limitations) of neuromast deposition, self-organization, and differentiation has been excellently covered in Chitnis et al. (2012).

The primordium deposits five clusters of about 25 cells each, at regular intervals, and fragments into 3 terminal clusters upon reaching the tip of the tail. Each cluster differentiates as a neuromast within a few hours after deposition. Besides the periodic deposition of neuromasts, the primordium also deposits a trail of interneuromast cells, which will later form additional (intercalary) neuromasts (see below). Interneuromast cell deposition may be due to strong adhesion between primordium cells, making it almost impossible to break cell continuity. The exact factors, or cell adhesion molecules, involved in the continuity of proneuromasts and interneuromast cells have not been determined.

12.2.2 Postembryonic Development of the Zebrafish PLL

The transformation of the embryonic pattern of five lateral and 2–3 terminal neuromasts into the adult pattern is mediated by five independent mechanisms.

1. Shortly after the embryonic primordium, primI, has begun its journey, a second primordium originates from the same postotic placode that generated primI (Sarrazin et al. 2010) and splits in two groups: primII, which migrates and deposits neuromasts along the horizontal myoseptum as primI did, and primD, which migrates and deposits neuromasts along the dorsal midline until the base of the dorsal fin (Fig. 12.1b; Sapède et al. 2002). Whereas primI-derived neuromasts are polarized along the anteroposterior axis (Fig. 12.2a, b; López-Schier et al. 2004), however, primII- and primD-derived neuromasts are polarized along the dorsoventral axis (Fig. 12.2c, d).

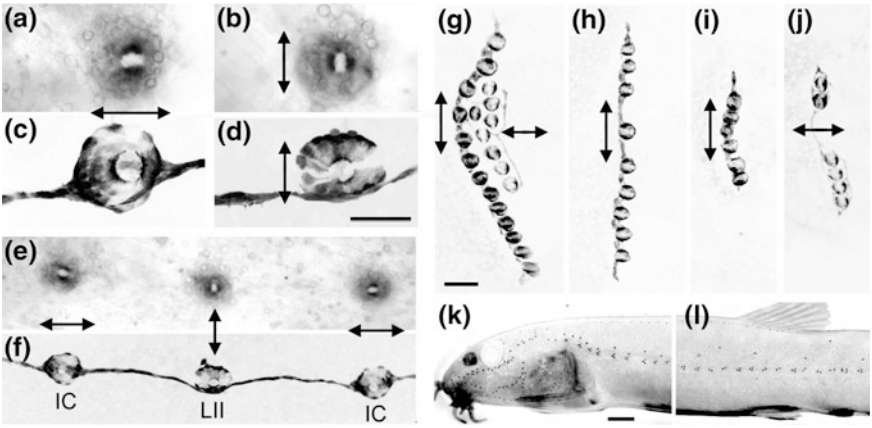


Fig. 12.2 Neuromast polarity and stitches. Anisotropy of a primI-deposited neuromast as revealed by alkaline phosphatase labeling (**a**) or by fluorescence of GFP in the ET20 (Parinov et al. 2004) transgenic line (**c**) parallels the anteroposterior polarization of its hair cells (*double headed arrow*). **b**, **d** A primII-derived neuromast shows dorsoventral anisotropy, as do its hair cells (*double headed arrow*). Fluorescence displayed in *black*. Scale bars: 20 μm. **e**, **f** Intercalary neuromasts (*IC*) flanking a primII-derived neuromast (*LII*) retain the anteroposterior anisotropy characteristic of the embryonic neuromasts deposited by primI, as revealed by alkaline phosphatase labeling (**e**) or in the ET20 line (**f**). **g–j** Neuromast polarity is retained by all neuromasts of a stitch. All stitches shown are from the same fish. **g** primII-derived stitch on somite 10, with 13 neuromasts, **h** primII-derived stitch on somite 17, with 9 neuromasts, **i** primII-derived stitch on somite 26 of the same fish, with 6 neuromasts, **j** primI-derived stitch on somite 24 with 6 neuromasts. In **g**, a primI-derived intercalary neuromast was present next to the founder LII neuromast, and has formed a smaller stitch with anteroposterior polarity. Stitches include less and less neuromasts from about somite 10 to the tip of the tail. Scale bar: 200 μ. **k**, **l** PLL stitches in the adult loach *Misgurnus anguillicaudatus* (Cypriniform) in the anterior region (**k**), and at the level of the anal fin (**l**), the size of stitches is similar all along the fish length, as is the fish thickness. Scale bar: 1 mm, size of fish: 36 mm

2. Once neuromasts are deposited, they undergo further migration. In contrast to the primordia, which migrate in anteroposteriorly, differentiated neuromasts migrate dorsoventrally (Fig. 12.1c, d). Due to this migration, the line formed by primI and completed by primII, which is initially located along the horizontal myoseptum, ends up at a much more ventral position (V line, Fig. 12.1d), whereas the line formed by primD, initially located along the dorsal midline, ends up in a more lateral position (DL line, Fig. 12.1d). It has been speculated that the independent control of the anteroposterior dimension through primordium migration, and of the dorsoventral dimension through neuromast migration, could facilitate large changes in the overall PLL pattern among species (Fig. 12.1e; Ghysen and Dambly-Chaudière 2003).
3. During larval development, interneuromast cells proliferate to form additional, "intercalary" neuromasts (Fig. 12.1c, light gray). The delay between deposition and cell proliferation is imposed by the glial cells that accompany the growing neurites and become apposed to the interneuromast cells (Grant et al. 2005; Lopez-Schier and Hudspeth 2005). primI-derived intercalary neuromasts begin to appear at about 8dpf (light gray, Fig. 12.1c), whereas primII- and primD-derived intercalary neuromasts appear around 3 weeks, near the end of larval life. Interestingly, intercalary neuromasts derived from primI-deposited interneuromast cells have hair cells polarized along the anteroposterior axis, as in primI-deposited neuromasts (Fig. 12.2e, f), whereas intercalary neuromasts derived from primII- or primD-derived interneuromast cells have hair cells that are polarized along the dorsoventral axis, as in primII- and primD-deposited neuromasts (Nuñez et al. 2009).
4. Once the juvenile pattern is completed (Fig. 12.1d), an amplification process begins where each juvenile neuromast produces a number of bud-neuromasts (also called "accessory" neuromasts by Stone, who was the first to study the process of budding, in amphibians). In fishes, this process has only been studied to date in the opercular line on the zebrafish head (Wada et al. 2010). All bud-neuromasts of a zebrafish stitch have the same polarity as the founder neuromast (Fig. 12.2g–j), with the exception of the stitches formed by primII-derived intercalary neuromats (Fig. 12.1d, L line). In this case, the founder neuromasts are polarized dorsoventrally, as is fit for primII-derived neuromasts, but some of the bud-neuromasts are polarized along the anteroposterior axis (Ghysen and Dambly-Chaudière 2007). The mechanism underlying this change in polarity is not known, nor is the mechanism whereby neuromast polarity is transmitted from the founder neuromast to its budded progeny. This is most unfortunate, as overall stitch polarity may be a major factor in shaping the information that the brain receives from peripheral sense organs and uses to form sensory perception, and understanding how polarity is determined may help us understand the interplay between developmental constraints and functional selection.
5. A second process that takes place after the juvenile pattern is established, is that some neuromasts sink into the underlying scales on the body, or dermal bones on the head, and become enclosed in "canals." This process is minimal in the PLL of zebrafish, as only the anterior-most three or four primI-derived

intercalary neuromasts become enclosed in a canal (Webb and Shirey 2003; Wada unpublished observations). Formation of a trunk canal is a major PLL feature in many teleost species, however, and the scales that enclose a canal often become morphologically distinct from the other body scales, resulting in the presence of a "lateral line" which is visible to the naked eye, and gave its name to the entire system.

12.3 Evolution of PLL Patterns

12.3.1 Origin of Variations in the Embryonic PLL Pattern

Embryonic PLL patterns are remarkably conserved among those teleost fishes that have been studied, as they always comprise a number of regularly spaced neuromasts aligned along the horizontal myoseptum, and one or a few terminal neuromasts near the tip of the tail (Pichon and Ghysen 2004). There is some variation in the total number of embryonic neuromasts, however. It appears from the small sample of species that we have examined, that neuromast number is correlated with embryo size. For example, blue-fin tuna embryos, in spite of being quite distantly related to zebrafish and living in a totally different environment, are of almost the same size, and have the same number of PLL neuromasts (Ghysen et al. 2012). In contrast, some fishes lay eggs that are much larger than those of *Danio* (e.g., the carp, *Cyprinus carpio*, Fig. 12.3a), and produce longer embryos with a larger number of regularly spaced neuromasts (Fig. 12.3b, c; see also Blaxter and Fuiman 1989; Pichon and Ghysen 2004). The smallest embryo that we examined, of the pygmy filefish *Rudarius ercodes*, also has the smallest number of neuromasts (Fig 12.3d, e). This variation is consistent with the idea that the embryonic pattern reflects a cyclic process of deposition that is intrinsic to the migrating primordium, and essentially conserved in all teleosts.

12.3.2 Origin of Variations in the Adult PLL Pattern

The diversity of PLL patterns observed among adult teleosts (Webb 1989c) cannot be traced back to differences in embryonic patterns, which, as far as we know, are minimal (see Sect. 12.3.1). Diversity must therefore arise during postembryonic development, suggesting that species-specific mechanisms shape the adult pattern during larval development. This aspect of PLL development has been little studied so far. Based on the understanding reached in zebrafish over the past few years, however, it has become at least feasible to propose, and in a very few number of cases, to confirm, explanatory schemes. We will consider successively variations based on each of the five mechanisms for postembryonic development outlined above.

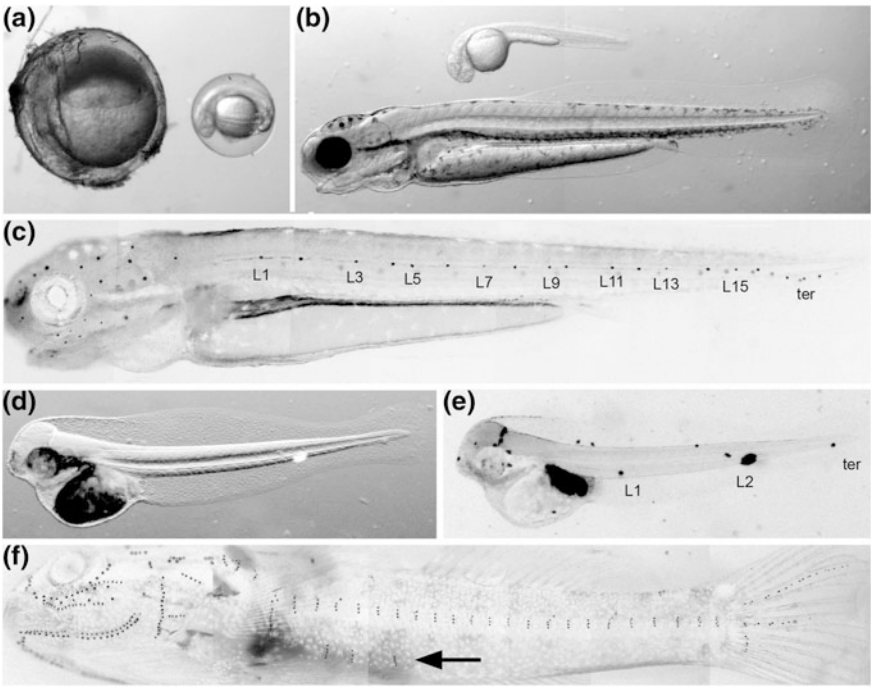


Fig. 12.3 **a**–**e** Number of embryonic neuromasts correlates with embryo size. **a** Egg of the carp *Cyprinus carpio* (Cypriniform) and egg of the zebrafish *Danio rerio* (Cypriniform), *upper right*; **b** newly hatched larvae of carp (*bottom*, 7.8 mm) and of zebrafish (*top*, 3 mm); **c** PLL of the carp embryo shown in (**b**); **d** embryo of the pygmy filefish *Rudarius ercodes* (Tetraodontiform), 2.1 mm; **e** its lateral line system, and **f** PLL in a young gobi, *Tridentiger trigonocephalus* (Gobioid, Perciform), 17 mm, with a ventral line extending to the anus (*arrow*)

12.3.2.1 PrimII and PrimD

A potential source of variation in the course of primII is the presence of a second stripe of SDF1-producing cells located at a more ventral level. This second stripe serves as a path for the migration of CXCR4-expressing germ cells toward the future gonad (Doitsidou et al. 2002), and extends caudally to the anus. In some zebrafish mutants where the lateral stripe of SDF1 is removed, primI moves ventrally, and follows this alternative pathway (David et al. 2002). We observed that a ventral line is present at the end of embryogenesis in some gobies (Fig. 12.3f). Interestingly, this ventral line stops at the level of the anus, as expected if it were driven by the ventral stripe of *sdf1* expression. We do not know, however, whether this ventral line is formed by a primordium migrating along a ventral path, or results from a ventral migration of neuromasts deposited along the myoseptum.

A second important variable is the position of the dorsal fin, as the dorsal primordium stops migrating when it reaches this structure. Thus, depending on the position of this fin, the dorsal line may be very extended, or very abridged. An extreme case is found in blue-fin tuna larvae, where the development of a dorsal fin in a very rostral position is correlated with the formation of an extremely short, almost abortive, dorsal line (Fig. 12.4c). A dorsal line of neuromasts may be well

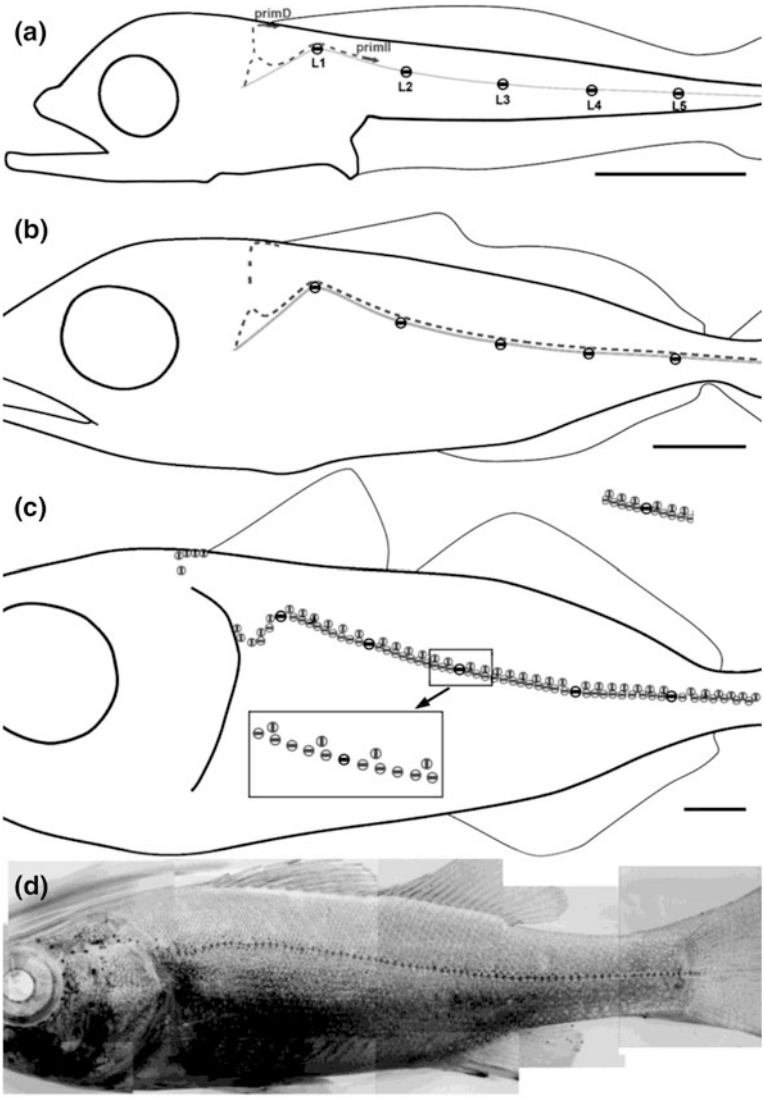


Fig. 12.4 PLL Development in perciforms. **a**–**c** Three stages of PLL development in the blue-fin tuna, *Thunnus thynnus* (Scombroid, Perciform). **d** Similar pattern in young *Lateolabrax japonicus* (Percoid, Perciform), 48 mm

tuned to respond to surface wavelets produced by fallen insects (reviewed in Bleckmann et al. 1989), and its absence would obviously be of no great concern for tuna.

12.3.2.2 Formation of Intercalary Neuromasts

The density and time of formation of intercalary neuromasts varies considerably between zebrafish and blue-fin tuna. In zebrafish, intercalary neuromasts form progressively during larval development, from anterior to posterior, at a rate of approximately one per day. They form on every intersomitic border except, in general, on those that are occupied by pre-existing neuromasts. In *Thunnus*, primI-derived intercalary neuromasts form synchronously near the end of larval development, at about three weeks of age, and their number is much larger than the number of primII-derived neuromasts. As all PLL neuromasts of *Thunnus* (except those of the diminutive dorsal line) are arranged on a single line, the relative density of AP-polarized, primI-derived and of DV-polarized, primII-derived neuromasts will affect the vectorial selectivity of the line. Very little is known about the development of intercalary neuromasts in other fish species, however, making it impossible to decide whether the proportion of the two types of neuromasts has functional relevance.

12.3.2.3 Neuromast Migration

One early difference between zebrafish and blue-fin tuna is that, in the latter species, the anterior-most embryonic neuromasts migrate dorsally, rather than ventrally as they do in zebrafish (Fig. 12.4a; Ghysen et al. 2012). In both species, primII migrates dorsal to the stripe of primI-derived cells. We do not know if this is due to an inhibitory effect that prevents primII from crossing the path of primI-derived cells, or to physical hindrance (e.g., due to attachment of primI-derived cells to the ectodermal basal lamina) preventing primII from moving across their track. Whatever the case, however, the dorsal versus ventral migration of neuromasts leads to a major difference in the final PLL pattern.

When differentiated neuromasts migrate ventrally in zebrafish, the original lateral and dorsal lines end up in more ventral positions, and the intercalary neuromasts that develop later from primII- and primD-derived interneuromast cells form two new lines, aligned along the horizontal myoseptum and the dorsal midline, respectively, (L and D lines, Fig. 12.1d). The dorsal migration of primI-derived neuromasts and the accompanying line of interneuromast cells in blue-fin tuna has the exactly opposite result: because primII cannot cross this line it migrates along it (Fig. 12.4a, b), thus resulting in a single arched line, dorsal to the horizontal myoseptum, comprising both anteroposteriorly polarized (primI-derived) and dorsoventrally polarized (primII-derived) neuromasts (Fig. 12.4c). This pattern of a single arched line is observed in many teleost species (Webb 1989c; Fig. 12.4d) and

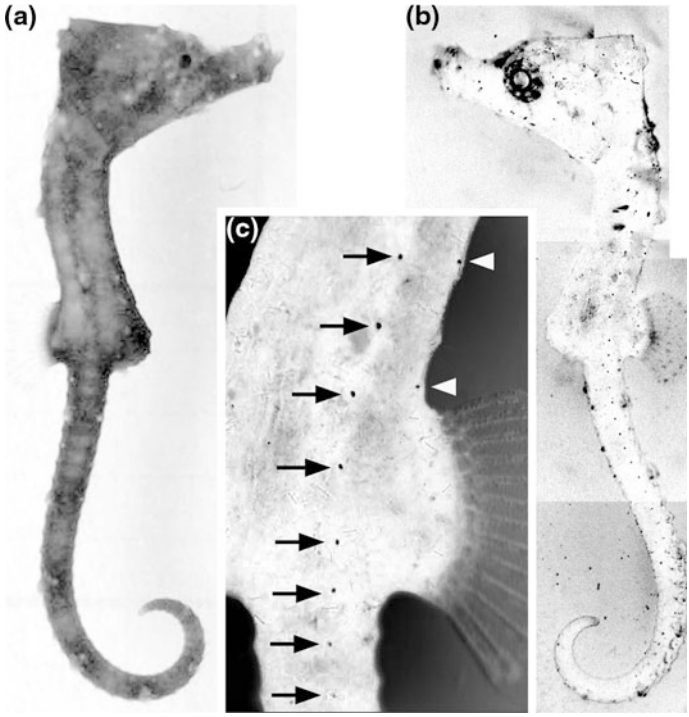


Fig. 12.5 **a** Young sea horse, *Hippocampus mohnikei* (Syngnathiform), 10 mm high, and (**b**) its PLL. **c** Higher magnification showing the neuromasts of the lateral line (*arrows*), and the neuromasts of the dorsal line stopping at the level of the dorsal fin (*arrowheads*)

illustrates how a discrete, and apparently small, change in a conserved mechanism can have drastic consequences on the outcome of later developmental processes.

A second variation arises when differentiated neuromasts do not migrate at all: such is the case of the Japanese seahorse *Hippocampus mohnikei* (locally called tatsunootoshigo, "illegitimate child of dragon"). In this case, one line remains aligned along the horizontal myoseptum, whereas a second line extends along the dorsal midline to the dorsal fin (Fig. 12.5), which is consistent with the basal pattern deduced from the work on zebrafish.

12.3.2.4 Budding and the Formation of Accessory Neuromasts

Adult patterns are derived from juvenile patterns through two processes: the formation of rows of superficial neuromasts (stitches), and the enclosure of neuromasts in canals. In zebrafish, stitches are formed by all juvenile PLL neuromasts (except for the few that become enclosed in canals, see below). Superficial neuromasts keep increasing in number through a budding process, but retain a

constant size (Münz 1985), or grow negligibly in relation to canal neuromasts (Webb and Shirey 2003; Janssen et al. 1987). More generally, superficial neuromast size is remarkably similar in teleosts and amphibians (Münz 1985), irrespective of the size of the animal, suggesting either that there is some optimal size for superficial neuromast function, or that there is a conserved mechanism for the determination of neuromast size.

The number of neuromasts within a stitch varies in the ventral-most line (V line, Fig. 12.1d), from more than 40 for the largest stitch, to less than 10 in the smallest one, in 20-month old zebrafish. Stitch size is correlated with body thickness: the largest stitches are found on the belly, and the smallest ones near the caudal peduncle (Fig. 12.2g–j). Because the number and pattern of scales remain constant throughout adult life (Levin et al. 2012), changes in fish size and shape are accommodated by changes in scale morphology, and the largest stitches are found on the largest scales. In contrast, in the pond loach *Misgurnus anguillicaudatus*, where thickness of the trunk is quite uniform along the rostrocaudal axis, stitches have essentially the same size from anterior (Fig. 12.2k) to posterior body positions (Fig 12.2l). Scale growth is not isotropic: ventral scales tend to expand ventrally, and dorsal scales dorsally. Stitch expansion seems to parallel the biased extension of the scales during adult life, as already proposed for the opercular stitch (Wada et al. 2010), where the posteriorward expansion of the stitch parallels the expansion of the opercular bone.

12.3.2.5 Morphogenetic Budding: Patterning of the Terminal System

A special case of budding is found in the terminal system, and is best illustrated by the development of the terminal neuromasts in the blue-fin tuna. At the end of embryogenesis there is only one terminal neuromast (ter1), contrary to the case of zebrafish, where there are on average three terminal neuromasts. Early during larval life, local proliferation of interneuromast cells rostral to ter1 results in the formation of a second terminal neuromast, ter2 (Fig. 12.6a). ter2 then extends a buds in a posterior direction (Fig. 12.6b). This bud becomes a third terminal neuromast, ter3 (Fig. 12.6c), which in turn buds off two additional neuromasts, first ter4 (Fig. 12.6d) and then ter5 (Fig. 12.6e). From ter1 and ter4 additional budding result in the formation of two caudal lines which, themselves, extend by budding, one neuromast at a time (Fig. 12.6f). Thus the fairly complex and highly reproducible pattern of terminal and caudal fin neuromasts in Fig. 12.6e is almost entirely generated by oriented budding events.

The development of the terminal pattern in zebrafish seems quite different, since three terminal neuromasts are already present at the end of embryogenesis (ter1–ter3 numbered from the caudalmost). Interestingly, however, it was established recently that the two species use budding as a means to establish the juvenile terminal/caudal pattern (Wada et al. unpublished). In zebrafish, the rostralmost of the three terminal neuromasts, ter3, is not involved in the formation of the juvenile pattern. The medial neuromast, ter2, undergoes budding much as

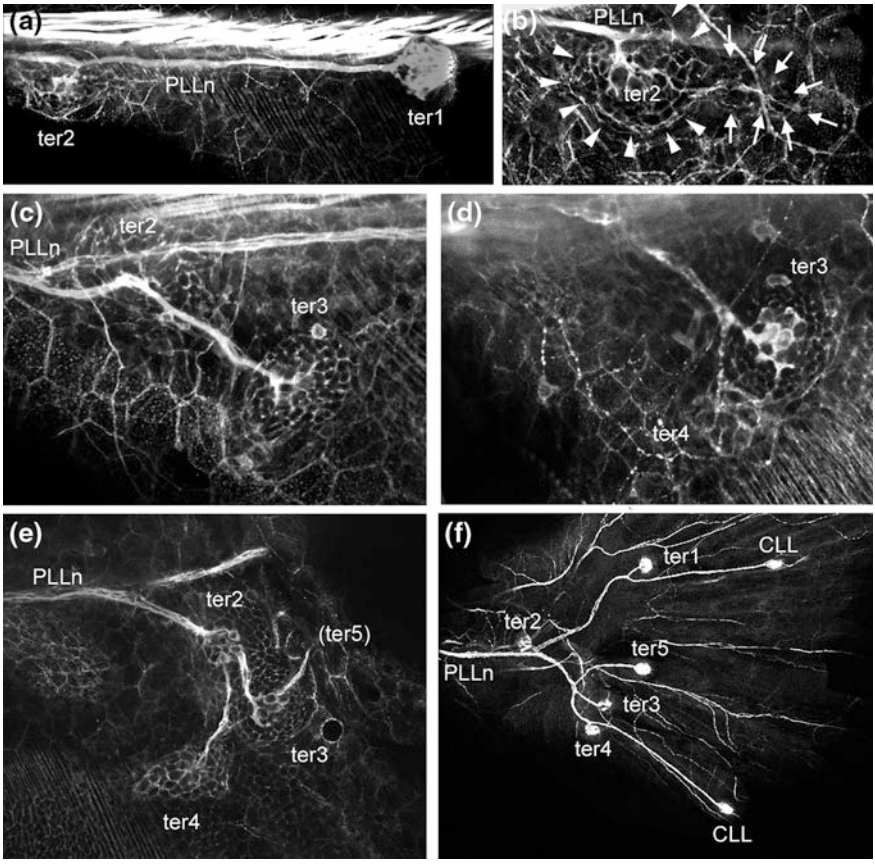


Fig. 12.6 Development of the terminal and caudal PLL in *Thunnus thynnus* (Scombroid, Perciform) as visualized in immunolabeled larvae where actin reveals cells contours, and tubulin reveals neurites and hair cells. **a** An intercalary neuromast, ter2, forms rostral to the single terminal neuromast, ter1. **b** A budding structure (*arrows*) extends from ter2 (*arrowheads*) and (**c**) forms a third neuromast, ter3. **d** ter3 in turn buds off neuromast ter4, and (**e**) ter5, out of focal plane. **f** The juvenile pattern of ter1–ter5 and the onset of the first dorsal and ventral caudal fin lines (CLL). PLLn: PLL nerve

ter2 of tuna, and generates a homolog of tuna's ter3 (called ter2′ in zebrafish). Additional lines then extend on the caudal fin, from ter1 and ter2′, through budding. Thus the principle of completing the terminal pattern and generating the caudal fin lines by budding seems conserved between the two species, even though the details of the intermediate steps vary somewhat.

An interesting variation on the zebrafish/tuna pattern is found in the medaka (*Oryzias latipes*), where a single terminal neuromast is present at the end of embryogenesis, much like in tuna, but remains single at the juvenile stage, unlike in tuna (Wada et al. 2008). Contrary to all PLL neuromasts, which never bud off

accessory neuromasts in medaka, the single terminal neuromast becomes a small stitch, but generates no caudal line. It would seem, again, that minute variations in the use of common mechanisms can generate different adult patterns starting from the same set of embryonic terminals, or similar adult patterns starting from different sets of embryonic terminals.

Unfortunately our understanding of terminal and caudal fin patterns is much too limited to draw any firm evolutionary conclusion, which is a pity because the caudal fin lines are obviously distinct from other PLL lines due to the propelling function of the caudal fin. Furthermore, based on the available evidence in zebrafish (Pujol-Marti et al. 2010; Sato et al. 2010; Olszewski et al. 2012), the neurons that innervate the terminal neuromasts play a special role in setting up neural somatotopy (Alexandre and Ghysen 1999), a major aspect of the central connectivity of most sensory systems.

12.3.2.6 Canal Formation

In many fish species, a subset of PLL neuromasts recede into the underlying scales and form a canal that extends rostrocaudally. Canal scales, also called tubular scales, often differ from other body scales in a way that is visible to the naked eye, resulting in the formation of the so-called "lateral line." Canal neuromasts are always polarized along the direction of the canal, i.e., rostrocaudally, consistent with a primI origin. In zebrafish, only the first 3–5 intercalary neuromasts of the primI-derived line become enclosed in canals. Those do not form stitches, in contrast to all other primI-derived intercalary neuromasts. This correlation suggests that the enclosure of a neuromast in a canal prevents its further budding, at the same time as it allows its further growth. On the other hand, these intercalary neuromasts form much later than the embryonic neuromasts (Nuñez et al. 2009), which remain superficial, showing that the first neuromasts to differentiate are not necessarily those that will become canal neuromasts.

Canal neuromasts are often associated with stitches of superficial neuromasts. A simple explanation for this close association could be that stitch neuromasts are bud-progeny formed by the founder neuromast before it sunk and became enclosed in a canal. If this were the case, one would expect that the same branch of the PLL nerve should innervate the canal neuromast and the surrounding superficial neuromasts, as reported in the case of *Champsodon snyderi* (Nakae et al. 2006). We observed the same result through hair cell driven, trans-synaptic labeling of afferent neurons in the sea-bass *Lateolabrax japonicus* (Fig 12.7a).

A switch between budding accessory neuromasts, and sinking into a canal, would provide for a whole range of combinations, i.e., canal neuromasts alone, canal neuromasts accompanied by superficial neuromasts, or superficial stitches not associated to canals. Support for this idea comes from a comparison of two species of the *Pseudorasbora* genus, P. *parva* and *P. pumila*. In the latter, where no canals are formed, stitches are present along the horizontal myoseptum (Fig. 12.7c). In the former, one canal neuromast is present at the center of each stitch (Fig. 12.7b).

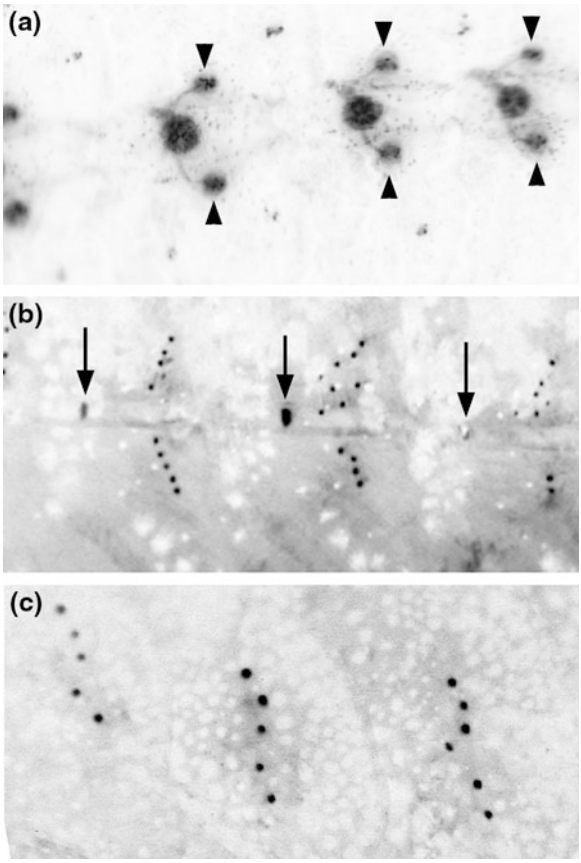


Fig. 12.7 Relation between canal and superficial neuromasts in a young adult of *Lateolabrax japonicus* (Percoid, Perciform). **a** DiAsp taken up by the hair cells has been transferred to sensory axons, revealing that the canal neuromast (*center*) and the flanking neuromasts (*arrowheads*) are innervated by branches of the same nerve, suggesting that they belong to a single stitch. **b** canal neuromasts (*arrows*) are accompanied by superficial neuromasts in *Pseudorasbora parva* (Cypriniform). **c** In the closely related species *Pseudorasbora pumila*, all neuromasts of the stitches remain superficial and no canal is formed

In other cases, a close association between canal neuromast and superficial stitches may derive from a close association of primI-derived and primII-derived neuromasts, as observed in blue-fin tuna larvae (Fig. 12.4c), where the two types of neuromasts are independently innervated (Ghysen et al. 2012 and Ghysen unpublished observations). If primI-derived neuromasts become canal neuromasts, whereas the closely apposed primII-derived neuromasts remain superficial and form stitches, this would account for the observation that in Tilapia (*Sarotherodon niloticus*, a cichlid), different fibers innervate canal and nearby surface neuromasts (Münz 1985). A close apposition of the primI- and primII-derived lines may also explain why canal and superficial neuromasts have orthogonal polarity in at least some cases (Schmitz et al. 2008).

The zebrafish PLL, where only the first 3–5 neuromasts form a short trunk canal, and the *Pseudorasbora* juveniles, where canals do or do not form in species in the same genus, suggest that canal formation is relatively easy to control independently of other PLL features. This would explain the prevalence of the

so-called "replacement neuromasts", surface neuromasts found in species that lack canals, and localized at the same positions as canal neuromasts in closely related species (Coombs et al. 1988).

12.4 Behavioral Correlates of Changes in PLL Patterns: Evolution of Development Versus Functional Adaptation

The embryonic PLL pattern is largely conserved among teleost fishes, and the system is used to trigger a fast response in both zebrafish and tuna early larvae. The response is different, however: in zebrafish the response is a C-turn followed by a forward acceleration of the body (escape reaction, Weihs 1973), whereas in tuna, it is a forward movement accompanied by jaw opening (strike reaction, unpublished observations). In yet another species, the hunting archer fish, where escape and strike reactions co-exist, the evidence suggests that the two reactions share a common network of reticulospinal neurons, or elements of it (Wöhl and Schuster 2007).

The difference between the responses of zebrafish and tuna larvae correspond well to the different conditions they encounter: the "escape" reaction of zebrafish may be very useful if lots of hiding places are at close reach, as in the shallow, slow-flowing, well-vegetated waters where zebrafish live (Engeszer et al. 2007; Spence et al. 2008). A similar response would possibly be not very meaningful in open water, because if the predator misses the first time because of an "escape reaction", it is very unlikely to miss a second time. On the other hand, the "strike" reaction of tuna may make all the difference for a larva that has to eat on its first day of larval life, because its yolk sac is exhausted on the next day, contrary to zebrafish larvae that do not need to eat before 3 or 4 days after hatching—a time when both species have developed an excellent visual system.

The behavioral difference between the escape reaction of zebrafish, and the strike reaction of blue-fin tuna, at early larval stages, suggests that the same sensory system can be used to trigger either predator avoidance or prey detection. This is reminiscent of the situation in insects: the fly larva is a worm-like maggot, whereas the grasshopper larva is a diminutive grasshopper, yet the spatial distribution of the various types of mechanosensory organs over the body surface is essentially the same in both larvae (Meier et al. 1991). Thus selection may shape neural circuitry more easily than it does sensory patterns.

The conservation of PLL pattern in early larvae of different species living in entirely different environments, suggests that the pattern of the embryonic PLL is dictated by the way it develops. Functional adaptation may be responsible for other aspects of the PLL, such as the length of the cupula. For example, the cupula is at least five times longer in tuna than in zebrafish (Kawamura et al. 2003; Ghysen et al. 2012), suggesting a very high sensitivity (Coombs and Janssen 1989;

van Netten and Kroese 1989) consistent with an early role in feeding (Mukai et al. 1994).

PLL pattern diversity appears during larval postembryonic development. Based on the scant evidence available, this diversity appears not to be the effect of diverse mechanisms, but on the diverse use of the same five mechanisms that we described in the zebrafish. Developmental mechanisms underlying postembryonic development seem conserved between zebrafish and blue-fin tuna, although they end up producing very different morphologies. Based on this example, it seems easy to imagine how the same five mechanisms could possibly generate *any* PLL pattern.

Part of the developmental variation may depend on differences in timing, as in the time-honored concept of "heterochrony" (discussed in Webb 1989b). Other elements of variation may be related to local (e.g., homeotic genes—dependent) differences in the rate of any of the postembryonic mechanisms outlined above: dorsoventral migration of neuromasts, development of intercalary neuromasts, budding, and formation of canals. Yet other causes for variation may be related to the surrounding tissues: epidermis, underlying muscles and somite boundaries, scales, etc. Clearly we have to know more about the genetic bases of these mechanisms before we can understand how they evolved, and ultimately, what is the molecular basis of pattern variation in the lateral line system.

The conservation of mechanisms governing postembryonic development raises the question of whether adult PLL patterns are adaptive, as commonly thought of, that is, are shaped as a result of a process of natural selection, or whether they are the result of developmental processes that are themselves shaped and constrained by other aspects of fish development. Although this aspect has received little experimental attention so far, partly because it is often taken for granted that all phenotypes are adaptive (i.e., the result of natural selection), at least one study on a monophyletic group of Antarctic fishes has led to the conclusion that "differences in lateral line structures, even large ones, do not necessarily have consequences for function" (Coombs and Montgomery 1994).

We cannot exclude, of course, that some changes in pattern may have adaptive value. We do not have enough comparative data on larval behavior, or on PLL development, to answer this question definitely, but we can at least make an (educated?) guess. Bearing in mind that identical PLL patterns trigger different, and appropriate, behavioral responses in early larvae of zebrafish and tuna, we propose that, in the case of the PLL, behavioral differences (motor outputs to lateral line inputs) reside mostly in neural adaptations (how brain circuits utilize lateral line sensory information) rather than in adaptations of how the sensory organs are organized peripherally. Thus adaptation would reside mostly in neural adjustment to make the best use of sensory systems that are patterned, not by functional constraints, but by developmental ones.

In a penetrating analysis of the early development of insect motor systems, Bate (1998) noted that "the evidence suggests that neurons are born and differentiate in ways that are not conditioned by their future functions as elements of neural circuits. The logic, if there is one, is a developmental one. (…) In contrast to the

apparent flexibility with which nervous systems can generate individual variations in behavior, early events such as these, that lay out the foundations of the (neural) network, appear highly stereotyped and the machinery that underlies them is increasingly well understood at a genetic as well as a cellular level." Except for the last line, one would say that the same wording exactly seems to apply to lateral line patterning. The PLL of adult fishes seems determined by "early events" that "lay out the foundations of the pattern" and thereby constrain further development. We propose that its adaptive value depends on how the nervous system makes use and sense of such patterns, and that there is possibly no direct selective pressure on their development. Further elucidation of the "machinery that underlies them" should help clarify this issue.

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