Review

Ontogenetic development of the helical heart: concepts and facts

Jörg Männer*

Department of Anatomy/Embryology, Georg-August-University of Göttingen, Kreuzbergring 36, 37075 Göttingen, Germany

Received 17 February 2006; accepted 27 February 2006

Summary

The structural and functional organization of the ventricular myocardial mass is a controversial matter that cannot be resolved by anatomical studies alone. Therefore, other approaches such as investigations of the ontogenetic development of the ventricular myocardium might help to resolve controversies about its structural and functional organization. It has recently been proposed that the spatial orientation of Torrent-Guasp’s ventricular myocardial band model (basal and apical loops) might be the mature morphological correlate of twists and torsions of the embryonic heart loop. In the present contribution, the suggestions made in this concept were analyzed in the light of currently known facts about the development of the embryonic heart. It was found that some of the suggestions made in this concept do not correspond to embryological facts, whereas other suggestions could neither be disproved nor confirmed on the basis of our current knowledge on heart development. The answer to the question as to which of the various models of myocardial fibre organization fits best with the ontogenesis of the myocardial mass awaits future studies. The myocardial units of Torrent-Guasp’s myocardial band model are said to have a functional rather than a morphological personality. Future studies on the ontogenetic development of the myocardium, therefore, should comprise not only anatomical analyses of dead specimens but should additionally comprise high resolution in vivo analyses of the development of the spatio-temporal contraction patterns of embryonic and fetal hearts.

© 2006 Elsevier B.V. All rights reserved.

Keywords: Embryology; Helical heart; Cardiac looping

1. Introduction

It is well known to anatomists that the muscle fibres of the ventricular myocardial mass are arranged in a complicated pattern of helical windings [1—4]. This pattern is so complex that up to now no generally accepted model of the myocardial fibre organization could be worked out on the basis of anatomical studies of the mature four-chambered heart [4,5]. It seems reasonable to search for other approaches that might help to gain better insight into the basic design of the anatomical and physiological organization of the ventricular myocardial mass. One of these approaches might be to clarify the ontogenetic evolution of the myocardial fibre organization. During the past decade, several studies have been conducted to clarify the ontogenetic development of the myocardial architecture [6—8]. Unfortunately, these studies primarily focus upon developmental changes in patterning of the trabecular layer of ventricular myocardium. At present, only scant information is available on the ontogenetic development of the structural and functional organization of the muscle fibres within the compact layer of ventricular myocardium.

Due to its functional and therapeutic implications, cardiovascular surgeons and cardiologists became interested in the myocardial band model of Francisco Torrent-Guasp during the past few years [9,10]. It has been proposed that the spatial orientation of Torrent-Guasp’s ventricular myocardial band (basal and apical loops) might be the mature morphological correlate of twists and torsions of the embryonic heart loop [11]. This idea might be suggested by several facts: Firstly, the anatomical dissection of the ventricular myocardial mass according to the technique of Francisco Torrent-Guasp produces a single longitudinal and stretched out myocardial band that bears some resemblance with the concept of the existence of an originally straight embryonic heart tube [11]. Secondly, in the intact four-chambered heart, the myocardial band of the Torrent-Guasp model has a helical configuration [3]. During the process of cardiac looping, the initially straight embryonic heart tube becomes transformed into a loop with a helical configuration [12—15]. Thirdly, the process of cardiac looping is generally said to bring the subdivisions of the embryonic heart tube (common atrium, atrio-ventricular region, primitive left and right ventricles, outflow tract) and the vessel primordia approximately into their definitive
topographical relationship to each other [16—22]. One might therefore speculate that — if present in the embryonic heart loop — the primordia of the myocardial units of Torrent-Guasp’s ventricular myocardial band model might also acquire the basic outline of their definitive spatial arrangement during the phase of cardiac looping.

The aims of the present contribution are, firstly, to analyze the above-mentioned embryological concept in the light of the currently known facts about the embryonic development of the heart, and, secondly, to give an outlook on future research that might facilitate the clarification of the ontogenetic development of the definitive structural and functional organization of the ventricular myocardial mass.

2. The recently introduced concept about the ontogenesis of the myocardial band model

In the recently introduced concept about the ontogenetic development of the ventricular myocardial band model, it is suggested that the following correlations might exist between the segmental organization of the embryonic heart loop and the segmental organization of Torrent-Guasp’s ventricular myocardial band [11]:

(1) The formerly called bulbus cordis segment of the embryonic heart loop, which nowadays is called the embryonic right ventricle and proximal embryonic outflow tract, is suggested to represent the future basal loop of Torrent-Guasp’s ventricular myocardial band.

(2) The formerly called ventricular segment of the embryonic heart loop, which nowadays is called the embryonic left ventricle and embryonic ventricular inflow, is suggested to represent the future apical loop of Torrent-Guasp’s ventricular myocardial band.

(3) The junction between the embryonic left and right ventricles (formerly junction between bulbus cordis and ventricle) is suggested to represent the future junction between the basal and apical loops of Torrent-Guasp’s ventricular myocardial band.

Three subsequent changes in the configuration of the embryonic heart are suspected to force the developing ventricular myocardium to acquire the structural organization of a single myocardial band with basal and apical loops:

(1) The normal positional changes of the developing ventricles with respect to the developing atria are suggested to cause 180° torsion of the heart loop at the junction between the bulbus cordis (embryonic right ventricle and outflow tract) and the ventricular segment (embryonic left ventricle) (Fig. 1). This torsion is said to generate the central fold between the basal and the apical loop of Torrent-Guasp’s myocardial band and thereby sets the stage for subsequent evolution of the helically rotated apical loop. The force leading to the 180° torsion is postulated to arise from accelerated growth of the endocardium of the ventricular segment (embryonic left ventricle) relative to the endocardium of the bulbus cordis (embryonic right ventricle and outflow tract).

(2) The evolution of the helically rotated apical loop is suspected to be the consequence of different growth rates between the internal and external layers of the left ventricular myocardial wall. A slow growing outer myocardial layer is suspected to function like a shell, which forces a fast growing internal layer to form trabeculations. The formation of trabeculations leads to establishment of a primarily spongy ventricular ‘lumen’ which, later on, becomes transformed into the definitive cavity by absorption or apoptosis of trabecular myocardium. These changes in architecture of the inner layers of embryonic myocardium are suspected to lead to formation of the descending segment of the apical loop of Torrent-Guasp’s ventricular myocardial band. There is

Fig. 1. Plasticine models of embryonic heart loops illustrating the postulated changes in configuration of the heart loop leading to the displacement of the developing ventricles from their original position (a) cranial to the atria towards their definitive position (b) caudal to the atria. The suspected changes would cause 180° torsion of the heart loop at the junction between the embryonic left and right ventricles (a). This torsion is suspected to generate the central fold between the basal and the apical loop of Torrent-Guasp’s myocardial band and thereby sets the stage for subsequent evolution of the helically rotated apical loop. The original left half of the heart tube is shown in white and the originally right half is shown in gray to stress the presence of torsions. Note that, due to such torsion, the originally right half of the embryonic heart tube is expected to form the ventral wall of the left ventricle, whereas the originally left half of the embryonic heart tube is expected to form the ventral wall of the right ventricle. Abbreviations: A: common atrium; LV: embryonic left ventricle; RV: embryonic right ventricle; OT: outflow tract.
postulation that the outer layer of embryonic myocardium forms the ascending segment of the apical loop of Torrent-Guasp’s ventricular myocardial band, and that the apex and V-shape of the mature left ventricle is caused by formation of a spiral connection between the descending and ascending segments.

3. Original facts

The formerly called bulbus cordis segment of the embryonic heart is comprised of the descending and ascending segments of the aorta, no pulmonary trunk, and no interventricular septum present in the embryonic heart. Consequently, the evolving myocardial band of embryonic hearts originally cannot run from the pulmonary trunk to the aorta as found in mature hearts. The direct physical connection between the aorta and the ascending segment of the apical loop of Torrent-Guasp’s ventricular myocardial band is suspected to be the consequence of the motion of the ascending segment along the formation of the interventricular septum that is comprised of the descending and ascending segments of the apical loop.

3. Facts

The above-mentioned suggestions sound reasonable. Up to now, however, no attempts have been made by experts in the field to test as to whether they really fit with the currently known facts about the development of the embryonic heart. Correlations between the mature heart chambers and the segments of the embryonic heart loop were traditionally made on the basis of presumed morphological and topological similarities [23]. This approach was also used to make the above-mentioned correlations between the segments of Torrent-Guasp’s ventricular myocardial band and the segments of the embryonic heart loop. Our current knowledge about the correlations between the mature heart chambers and the embryonic heart loop, however, is based on data from in vivo labelling studies made on chick embryos [21]. These data have led to a revision of the traditional textbook knowledge on heart development. In the light of these data, the validity of the above-mentioned suggestions is as follows:

1. In living chick embryos, the three-dimensional shape of the endocardial tube of the embryonic heart loop is directly visible due to transparency of the myocardium and cardiac jelly (extracellular matrix layer between embryonic myocardium and endocardium). The visibility of the endocardial tube can be improved by injection of India ink. It has been found that the transverse shape of the endocardial lumen depends on the state of myocardial contraction, being rounded during dilation and slit-like during contraction (Fig. 2) [24]. In completely contracted heart loops, the three-dimensional shape of the endocardial tube, therefore, appears as a flat band (see Fig. 3). At the end of cardiac looping, this band shows torsions at the outflow tract, which reflect the helically oriented anlagen of the outflow septa, but does not show any internal torsion between the bulbus cordis (embryonic right ventricle and outflow tract) and the ventricular segment (embryonic left ventricle) [24]. The endocardial band also does not display any regional growth differences that are suspected to provide the driving force for the caudal displacement of the developing ventricles with respect to the atria. The externally visible differences in thickness between the bulbus cordis (embryonic right ventricle and embryonic outflow tract) and the ventricular segment (embryonic left ventricle) of the heart loop correlate to regional differences in thickness of its cardiac jelly.

2. Data from studies in which the contributions of the left or right heart anlage to the formation of the embryonic heart loop were analyzed [25–27] confirm that the
positional changes of the developing ventricles with respect to the developing atria do not cause the suspected 180° torsion of the heart loop at the junction between the embryonic left and right ventricles (Fig. 1). Instead an approximately 90° torsion of the heart tube is found at the level of the common atrium (Fig. 4).

In view of these data, it seems unlikely that the segmental arrangement of Torrent-Guasp’s ventricular myocardial band into basal and apical loops can be explained on the basis of cardiac looping.

4. Outlook

Spirals and helices are universal constructive motifs in nature [10]. The vertebrate heart acquires a helical configuration already during its early embryonic development when it is a relatively simple muscular tube that propels the blood through its endocardial lumen by peristaltoid contractions of its outer myocardial wall (Fig. 5) [12–15]. The helically wound embryonic heart loop is the first morphological manifestation of visceral left–right body asymmetries [15,19,22,28]. The fact that the embryonic heart loop has a helical configuration did not receive much attention in the past [15]. We, therefore, do not know whether this fact has any functional significance for the embryonic cardiovascular system. It might be possible, however, that such an asymmetric configuration favors the directed transport of fluids through tubular structures under conditions of low Reynolds’s numbers [29]. The helical course of muscle fibres within the ventricular myocardium of the mature heart is a well-known fact. Its significance for the pumping function of the four-chambered heart has been recognized by several investigators [1,10,30]. The constructive motif of the helix, therefore, seems to be of utmost
importance for the hemodynamic function of the embryonic as well as mature heart. It is, therefore, tempting to speculate that the formation of the helical embryonic heart (cardiac looping) might lay down the blueprint of the mature helical organization of the ventricular myocardial mass.

In the present contribution, it is shown that the helical arrangement of Torrent-Guasp’s ventricular myocardial band model does not reflect the changes in configuration of the embryonic heart loop. This fact seems to be in accord with data from a recent study on situs inversus hearts suggesting that the definitive sense of twist of the helically arranged ventricular muscle fibres does not depend on the chirality (left- or right-handed) of the embryonic heart loop [31]. The ontogenetic evolution of the definitive structural and functional organization of the ventricular myocardial mass, therefore, most likely starts in the post-looping embryonic heart. This idea seems to be in accord with the fact that the myocardial wall of the looping embryonic heart tube consists only of a simple two-layered epithelium and, therefore, lacks a fibre architecture [7]. By the end of cardiac looping, epicardium-derived mesenchymal cells start to invade the embryonic myocardium and deliver the cardiac interstitium and coronary vasculature [32].

Formation of the cardiac interstitium and the initiation of myocardial nutrition via coronary vessels are the prerequisites for the transformation of the epithelial embryonic myocardium into fibrous myocardium and for the development of a thick and multi-layered compact myocardium, respectively [7,8]. I speculate that the definitive helical arrangement of the ventricular myofibres is primarily the consequence of the growth dynamics of the compact myocardium of the free ventricular wall and interventricular septum. Myocardial growth dynamics might depend on several factors such as myocardial gene activity, hemodynamics, and intramyocardial physical stress due to the contraction-dependent deformations of the ventricular myocardium. The central twist/fold between the basal and apical loops of Torrent-Guasp’s ventricular myocardial band might be formed primarily in consequence of contraction-dependent deformations (twists) of the myocardium at the junction between the two loops.

At the present time, we have excellent information about the development of the three-dimensional organization of the trabecular layer of the embryonic myocardium [6—8], but we know almost nothing about the development of the internal three-dimensional architecture of the compact layer myocardium. Due to the incompleteness of embryological data, the answer to the question as to which of the various models of myocardial fibre organization (which are recently
summarized [5]) fits best with the ontogenesis of the myocardial mass awaits future studies. The myocardial units of Torrent-Guasp’s ventricular myocardial band model are said to have a functional rather than a morphological personality [3]. This functional personality may be reflected by the sequential contraction of the myocardial units during ventricular systole [3,30]. Future studies on the ontogenetic development of the myocardium should focus not only on anatomical analyses of dead specimens, but should additionally comprise high resolution in vivo analyses of the development of the spatio-temporal contraction patterns of embryonic and fetal hearts.

Acknowledgements

The author thanks Mr Hannes Sydow for photographic assistance and Dr Wolfgang Seidl for the gift of the pictures used in Figs. 2 and 3.

References