Chapter No.: 1
Title Name: Willis

Introduction

The heart possesses a specialised conduction system that is responsible for generating and transmitting electrical stimuli to the whole heart in a specific and ordered fashion. It is composed of the sinoatrial node (SA), internodal and inter-atrial pathways, atrioventricular junction, bundle branches and Purkinje fibres (Figure 1.1). The SA contains specialised 'pacemaker' cells that have the ability to spontaneously depolarise, generating electrical impulses. The remainder of the conduction system is composed mainly of cells organised in bundles that allow conduction of the electrical stimuli. These structures are present in the walls of the heart and are interwoven with the myocardial tissue itself. It is not possible to distinguish them from the rest of the myocardium (working myocardium) with the naked eye, only with certain stains under the microscope.

The anatomy of these structures is presented in this chapter. To avoid confusion, the use of human anatomical terminology is avoided, and terminology commonly used in veterinary medicine for quadruped patients is preferred.

Given the different orientation of the heart within the chest of dogs and cats in comparison to humans, the following terms are used: cranial instead of anterior; caudal instead of posterior; dorsal instead of superior; and ventral instead of inferior. However, since some terms are so widespread in veterinary literature (e.g. left anterior or posterior fascicles), it is difficult to avoid the use of such terms even though they are not entirely appropriate.

Sinoatrial Node

Anatomy

The SA, also known as the sinus node, is found in the wall of the right atrium at its junction with the cranial vena cava in the upper portion of the terminal groove (sulcus terminalis) (Figure 1.1).

In dogs, it lies less than 1 mm beneath the epicardium and occupies almost the entire thickness of the atrial wall from epicardium to endocardium. The total size of the canine node was described as being approximately 5 mm³ with an oblong shape, although with significant variation observed amongst individuals. Other reports suggest a more extensive location of up to 3–4 cm between both venae cavae.

In cats, according to one study including five male and five female domestic shorthair cats, the SA node was located 0.06–0.11 mm beneath the epicardium with an almost triangular shape. In males the reported size was 2.78 × 2.80 × 0.54 mm, and in females it was 2.75 × 2.64 × 0.45 mm. A different study involving 12 cats produced different results. A reconstruction of the SA node based on histological and electrophysiological data was performed in five of these cats, revealing an ellipsoid shape with a total area of 10.5 ± 0.76 mm², a maximum length of 7.4 ± 0.74 mm, a maximal width of 2.2 ± 0.10 mm and a thickness of 0.41 ± 0.060 mm.

Histology

Histologically, the SA is composed of specialised muscle fibres arranged in a network. Many small bundles are present with irregular courses interspersed with connective tissue accompanied by capillary vessels and nerve cells. The surface of the SA is covered by epicardium, and the remaining areas are surrounded by atrial muscle. Each nodal fibre shows a smooth transition to ordinary atrial muscle fibres at the periphery of the SA.

Three different types of cells are present: normal working myocardial cells, transitional cells and P (pacemaker) cells.

The P cells are responsible for the ability of the SA to spontaneously generate electrical stimuli. They represent approximately 50% of the cells in the SA and are also present in other areas of the conduction system.
(e.g. atrioventricular node [AVN]) in fewer numbers. They are organised in small groups of approximately five cells surrounded by connective tissue that function as a unit.

The transitional cells are also present in other parts of the conduction system (e.g. internodal tracts and the atrioventricular junction) and seem to provide a link between the specialised cells and the normal working myocardium.

**Sinoatrial Exit Pathways**

The existence of discrete exit sites has been described at the cranial and caudal ends of the canine sinus node. Ablation of these sites resulted in sinoatrial block, suggesting that the SA was not anatomically continuous with the atrial myocardium. It was suggested that vessels and connective tissue around the SA tissue were responsible for anatomical and physiological blocks on both sides of the node with the exception of the exit sites. These findings, together with the reports of a length of up to 3–4 cm, provide a plausible explanation for the occurrence of ‘wandering pacemaker’ in this species (see chapter 5).

**Internodal Pathways**

The presence of preferential pathways that connect the SA and AVN has been the subject of debate for the past century, and there is still disagreement about their existence and significance. In the dog, there is anatomical and electrophysiological evidence to support the presence of three distinct pathways in the right atrium, with cells that possess characteristics similar to those of Purkinje cells. However, these pathways are not insulated from neighbouring atrial muscle and are not composed of specialised conduction cells only. This raises questions about their role, and some argue that they should not be termed bundles for this reason. Nonetheless, surgical resection of these pathways was shown to result in a junctional rhythm in dogs, supporting their role as internodal pathways.

The anterior internodal pathway originates in the sinus node and courses through the cranial aspect of the cranial vena cava, at which point it bifurcates into Bachmann’s bundle (see the ‘Inter-atrial pathways’ section) and a branch that courses ventrally through the cranial inter-atrial septum to join the cranial aspect of the AVN (Figure 1.1).

The middle internodal pathway originates in the sinus node and travels downwards cranially to the fossa ovalis towards the AVN (Figure 1.1).

The posterior internodal pathway originates in the sinus node, then it courses along the crista terminalis and downwards through the caudal aspect of the inter-atrial septum, past the coronary sinus (CS) ostium and joining the caudal aspect of the AVN (Figure 1.1).

**Inter-atrial Pathways**

At least four distinct inter-atrial electrical connections have been identified in dogs. Bachman’s bundle, or the inter-atrial band, originates close to the SA and traverses the upper portion of the inter-atrial septum towards the left auricle (Figure 1.1).
It is composed of normal atrial muscle and of specialised conducting fibres capable of rapid conduction, similar to the Purkinje fibres in the ventricles. Another connection is present ventrally via striated muscle fibres identical to atrial myocardium that surround the CS. These fibres are continuous with the right atrial myocardium at the level of the CS ostium and with the left atrial myocardium from which they separate approximately 20–30 mm from the CS ostium. A tract of atrial muscle that terminates blindly within the ligament or vein of Marshall (a remnant of the left cranial vena cava) has been proposed as the terminal end of this pathway in the left atrium, and the term inferior interatrial pathway was used to describe it. Additional connections exist at the level of the atrial septum craniodorsally, in the proximity of the fossa ovalis, and caudoventrally, possibly via the subepicardial band that connects the left atrium and cavoatrial junction ventrally. Bachman’s bundle and the CS musculature are believed to be the major connections and the preferred pathways for conduction of electrical stimuli between the atria.

**The Atrioventricular Junction**

The atrial and ventricular myocardium are separated by a fibrous skeleton that consists of the distinct valve annuli and intervening fibrous trigones. This structure provides attachment for the valve leaflets and the myocardium itself. As a consequence, the atrial and ventricular myocardium are electrically isolated, which is important to ensure that atrial and ventricular contractions occur in a coordinated fashion. The only point of electrical connection is provided by a specialised conduction structure that traverses the central portion of the fibrous skeleton (the central fibrous body), commonly described as the atrioventricular node or junction (Figures 1.1 and 1.2). It is located approximately 1 mm beneath the epicardium on the floor of the right atrium in an area known as the triangle of Koch (Figure 1.2). The CS ostium limits the base of this triangle, and the apex is formed by the junction between the fibrous tendon (tendon of Todaro) and the septal leaflet of the tricuspid valve (Figure 1.2). In the dog, the AVN has an elongated shape with a concave surface facing the central fibrous body. It averages approximately 2–4 mm in length, 2 mm in width and 0.5–1 mm in thickness. In the cat, an elongated oval shape has also been reported that is approximately 1.2–1.8 mm in length, 0.2–0.5 mm in width and 0.4–0.6 mm in thickness. Male cats appear to have a larger AVN than females.

The AVN can be divided into an atrionodal region formed by atrionodal bundles that converge into a proximal atrioventricular bundle, the compact node and the distal atrioventricular bundle (DAVB; Figure 1.2). This division is based on histological differences between each area. The remainder of this section focuses on canine anatomy.

**Atrionodal Bundles and the Proximal Atrioventricular Bundle**

Three distinct atrionodal bundles have been described in the dog and are thought to be the continuation of the internodal pathways (Figure 1.2). They are associated
with epicardium of the medial right atrial wall and the crest of the ventricular septum, approximately 1 cm away from the annulus fibrosus. The cells are organised into small fascicles of myofibres surrounded by collagen without connection to ordinary atrial myocardium. The myofibres run in a parallel fashion.

The superior (dorsal) atrionodal bundle is located beneath the epicardium of the dorsal-cranial aspect of the medial right atrial wall, closely apposed to the crest of the interventricular septum.

The middle atrionodal bundle is located beneath the epicardium on the dorsal-caudal aspect of the medial right atrial wall, opposed to the medial aspect of the tendon of Todaro, associated with the dorsal-medial aspect of the CS ostium.

The lateral atrionodal bundle input is located beneath the epicardium on the caudal-ventral aspect of the medial right atrial wall, subjacent to the lateral aspect of the CS ostium.

The presence of additional atrionodal bundles has not been proved but was suggested. Remnants of bundles extending into the left atrium have been described, but further studies are necessary to determine their significance.

The atrionodal bundles converge into the proximal atrioventricular bundle (PAVB) that is continuous with the compact node (Figure 1.2). It is located beneath the epicardium of the right atrial medial wall, cranially to the floor of the CS ostium, medially to the tendon of Todaro and approximately 1 cm away from the hinge point of the tricuspid leaflet at the annulus fibrosus. At this level, the myofibres are tightly coiled in single strands that form fascicles running in parallel. A small number of intercalated discs are present in comparison to the atrionodal bundles. The PAVB is also characterised by numerous ganglia nestled amongst its fascicles, blood vessels and fat vacuoles and particularly prominent at the ventricular septal apposition.

Compact Node

The compact node rests on the atrial aspect of the central fibrous body (Figure 1.2). In the dog, it is approximately 1–1.5 mm in length. From caudal to cranial, it appears initially as two half-ovals separated by the nodal artery that become fused cranially. It is composed of closely interwoven fibres which frequently connect with each other within a sparse collagen framework. The nodal cells are small and are arranged in a parallel fashion on the caudal aspects of the node. Cranially, they are arranged in interweaving fascicles on the left margin, and on the right the cells become larger and are arranged in a more parallel fashion. This arrangement is also seen in the proximal part of the DAVB.

Distal Atrioventricular Bundle

The DAVB extends cranially from the compact node approximately 3 mm to a branching point at the cranial edge of the tricuspid septal leaflet (Figure 1.2). It resides in the cranial part of the central fibrous body, where it penetrates the septum fibrosum bridging the atria and ventricles. The myocytes are larger in the DAVB, and the myofibres and fascicles run in a parallel fashion as in the atrionodal bundles. Given that the initial part of the DAVB is often histologically similar to the compact node, some authors only consider the bundle where it becomes surrounded by the tissues of the fibrous body. The term bundle of His is commonly used for this structure, named after Wilhelm His Jr., who described it for the first time. In dogs, it is approximately 8–10 mm long and has a width of 1.5–2.0 mm. The presence of two distinct functional strands within the common trunk of the canine His bundle has been described. According to this report, a dorsal strand extends from the dorsal part of the compact node and continues ventrally with the right bundle branch, and a ventral strand extends from the ventral part of the compact node to continue with the left bundle branch. The electrophysiological properties of both strands are similar, with the exception of the conduction velocity which seems to be faster in the ventral strand. Traversing bridges are present between the strands and ensure their activation as a single conducting structure.

The Bundle Branches

The DAVB divides into several branches that supply the Purkinje network of the right and left ventricles (Figures 1.1 and 1.3). A division into right and left bundle branches is common, although variations exist amongst individuals. This division occurs at the level of the upper portion of the interventricular septum beneath the non-coronary and the right aortic leaflets.

The right bundle branch courses in the subendocardial of the right side of the interventricular septum. Proximally, it branches from the DAVB approximately 2–3 mm away from the insertion of the septal leaflet of the tricuspid valve and runs as a single chord until it reaches the cranial (anterior) papillary muscle. At this level, it divides into three branches:

1) Ramification for the conus pulmonalis: These branches separate from the right bundle at the level of the base of the papillary muscle and spread over the cranial part of the interventricular septum with an irregular pattern to supply the Purkinje fibres in the area of the conus pulmonalis.

2) Ramification for the free wall: After the branching for the conus, the right bundle courses around the base of the papillary muscle and proceeds downward, giving
1) Cranial (anterior) group: The first branch to divide from the trunk splits into a few small branches that run cranially beneath the endocardium for approximately 10–15 mm until they change into bands that project into the ventricular cavity – ‘pseudotendons’. Once they reach the base of the cranial (anterior) papillary muscle, they spread to the cranial area of the left ventricle in a mesh pattern.

2) Caudal (posterior) group: Another few small branches run approximately 10–15 mm beneath the endocardium in parallel with each other like a chord until they change into pseudotendons, projecting into the ventricular cavity towards the caudal (posterior) papillary muscle. From this point, the Purkinje fibres from the pseudotendons spread over the caudal area of the left ventricle.

Another small subendocardial network of branches from the left bundle has been described between the cranial and caudal groups spreading directly over the septum without giving off pseudotendons – the intermediate group.7 The terms anterior and posterior fascicles are often used to describe the cranial and caudal divisions of the left bundle, respectively.

The Purkinje Fibres

The bundle branch subdivisions give rise to numerous small branches that spread all over the subendocardium of both ventricles.7 These branches are composed of Purkinje cells and form a network connecting the conduction system to the ventricular myocardium. They are more abundant over the base of the papillary muscles and apical regions of the heart. A similar density of Purkinje fibres has been reported in the free wall of both ventricles, but it is higher in the left side of the interventricular septum due to the existence of the intermediate group. As a consequence, the peripheral ramifications are denser in the left ventricle, which makes sense due to its larger dimensions and higher contractile force.

Blood Supply

Sinus Node

The canine SA artery has been reported to derive in most instances (90%) from the distal right atrial branch, a terminal branch of the right coronary artery, and less commonly from a branch of the left coronary artery.1,28–30 However, other reports showed that the blood supply to the sinus node was instead derived from branches of the left circumflex coronary artery either alone or in combination with distal branches of the right coronary artery.31,32 This highlights the high
degree of variation possible in this species. The venous return occurs via tiny valveless veins – *Thebesian veins* – that are present in the endocardium and empty directly into the right atrium.

The blood supply of the feline SA also shows a high degree of variation. In most instances, the supply was seen to originate from collaterals of the right circumflex or right coronary arteries, and less frequently from the proximal left atrial branch originating from the left coronary artery.33

**Atioventricular Junction**

The blood supply to the atioventricular junction in the dog has been described as originating from two branches from the right coronary artery and one from the left, as well as anastomoses of these vessels in the septum.34 The DAVB is supplied by the septal artery and the dorsal left artery which are both branches from the left coronary artery. Additionally, perfusion is provided in part by the accessory ventral right atrial branch of the right coronary artery. The venous return occurs via Thebesian veins.

**Innervation**

The SA and AVN regions of the canine heart are richly innervated by the autonomic nervous system.35 The SA is especially responsive to parasympathetic stimulation, whereas the AVN is preferentially sensitive to sympathetic tone. The effects of both are discussed in chapter 2.

Sympathetic innervation of both the SA and AVN is provided by sympathetic efferents from the ansae subclaviae via branches of the cervicothoracic ganglia and the middle cervical ganglia.36 Parasympathetic innervation of the SA is provided by the right vagus, whilst the AVN is innervated by both the right and left vagus nerves. The parasympathetic fibres synapse in ganglia located in the heart and short postsynaptic fibres, then supply the relevant cardiac structures (e.g. the SA and AVN). These ganglia are located in fat pads at the level of the junction between the cranial vena cava and aorta, the caudal vena cava and left atrium and the junction of the right pulmonary vein with the atrium.37,38 The bundle branches and its ramifications do not seem to be innervated, although autonomic fibres have been identified in close proximity to the subendocardial Purkinje fibres.39

**References**


39 Tcheng KT. Innervation of the dog’s heart. Am. Heart J. 1951;41:512–524.