Supernormal conduction, that is, conduction which is better than anticipated or conduction that occurs when block is expected, can theoretically be caused by a variety of mechanisms including the presence of a period of supernormal excitability (127, 561). The term supernormal excitability refers to a reduced current requirement to excite a tissue at a specific period of its activity cycle. Periods of supernormal excitability were first described for nerve in 1912 by Adrian and Lucas (4) and for heart muscle in 1938 by Hoff and Nahum (158). In these early experiments the tissues were excited by electrodes placed on the surface. Recent studies have emphasized the complexity of surface stimulation in testing myocardial excitability (158, 170, 380). Because a conducted beat relies on depolarizing currents for its propagation, in situations where one is interested in correlating changes in membrane excitability with characteristics of conduction, a pure depolarizing current is more appropriate for evaluating excitability. A pure depolarizing current can be delivered to a cell through an intracellular microelectrode. Using this technique Weidmann (898) first demonstrated a period of supernormal excitability in sheep Purkinje fibers and Childers et al. (125) showed that specialized atrial fibers within Bachmann's bundle in dogs possessed a period of supernormal excitability. The present studies will describe attempts to correlate supernormal excitability in the Purkinje system of the dog with associated conduction phenomena in this tissue.

THE TECHNIQUE OF INTRACELLULAR STIMULATION

Figure 1 demonstrates the technique for measuring excitability utilizing depolarizing current passed to the cell by way of an intracellular microelectrode. False tendons were removed from right and left ventricles of anesthetized dogs and equilibrated in Tyrode's solution with 95% oxygen and 5% carbon dioxide. The tissues were maintained at 37°C. In figure 1, PF₁ is a recording from a Purkinje fiber with a microelectrode capable of both stimulation and recording. PF₂ is a differential recording from an impalement within a space constant of the PF₁ fiber. The second pair of action potentials in the PF₁ and PF₂ records were evoked by applying a depolarizing current through the PF₁ electrode at just threshold intensity. The record labelled (PF₂) is the PF₂ action potential evoked by intracellular stimulation displayed on an expanded time scale. The intensity of the current utilized to evoke the response is shown on the same expanded time scale below the

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Fig. 1. Analog data demonstrating the technique used to measure excitability and threshold potential. All traces were recorded simultaneously. The 100 msec time pulses apply to traces PF1, PF2. The 1 msec time pulses apply to traces (PF2) and the current record. PF1 indicates transmembrane action potentials recorded with a microelectrode capable of both passing current and recording potentials. The PF2 transmembrane action potential were recorded within a space constant of the PF1 recording site using a difference amplifier. The second action potentials in the PF1 and PF2 records were evoked by a threshold depolarizing current delivered through the PF1 electrode. The PF2 action potential evoked as a result of this current is shown on the expanded time scale below as (PF2).

(PF2) record. By scanning the conducted beat with threshold depolarizing pulses, the excitability of the tissue could be obtained throughout the time course of an action potential. In the (PF2) record the threshold potential was determined as the potential at which the rapid upstroke of the action potential was initiated. Because of the complications of cable properties that play a role in cardiac excitation when current is injected at a single point in the tissue, the threshold potential indicated in (PF2) of figure 1 is not the true membrane threshold potential. During intracellular injection of a depolarizing current a certain minimum amount of surrounding membrane (liminal length of membrane) must be raised above the membrane threshold potential to counter the repolarizing effect of local currents from adjacent inactive membrane (709). Changes in excitability as measured by intracellular stimulation can be due at least in part to changes in cable properties of the membrane. However, since a conducted wave of activity relies on local depolarizing current to excite fibers downstream, the factors that modify excitability as measured by intracellular stimulation in these experiments would be expected to similarly modify excitability in the case of a conducted beat.