In the General Introduction (chapter 1) several questions were posed to which we can now give at least partial answers.

The gills of the carp are innervated by branchial branches of the IXth and Xth cranial nerves (chapter 2). Each branchial nerve comprises an epibranchial ganglion, formed by cell bodies of sensory neurons, from which three nerve branches emerge: (i) a dorsal pharyngeal branch; (ii) a pretrematic branch and (iii) a posttrematic branch. A small bundle of motor fibres bypasses the ganglion and anastomoses distally with the posttrematic branch. The hemibranchs and gill rakers of neighbouring gills bordering a gill slit are innervated by the same branchial nerve. The first gill arch receives a posttrematic branch of the glossopharyngeal (IX) and a pretrematic branch of the vagal (X) nerves. The other, more caudally located gill arches are innervated solely by posttrematic and pretrematic branches of the vagus nerve. Each branch splits into an external bundle that terminates in the gill filaments, and an internal bundle that innervates the buccal side of the gill, including the gill rakers. The dorsal pharyngeal branch terminates in the palatal organ in the roof of the buccal cavity.

Electrophysiological recording from epibranchial vagal ganglia revealed the sensory input from gill mechanoreceptors that is transmitted to the central nervous system of the carp. Mechanoreceptors are present in the gill filaments and gill rakers (chapter 3), and gill arch proprioceptors appear to be located in or around the cartilaginous band between the main bony elements of each gill (chapter 4). The gill filament and gill raker mechanoreceptors are not active during normal respiration. In contrast, the gill arch proprioceptors provide the central nervous system with rhythmic sensory input. The discharge of these proprioceptors is linearly related to gill arch position and, hence, they monitor the degree of expansion of the branchial basket. Since the gills move rhythmically during respiration the firing pattern of these proprioceptors is respiration-modulated.

Two sets of experiments were performed to elucidate the effect of this pattern of sensory input on the respiratory rhythm. First, epibranchial vagal ganglia were stimulated electrically, and second, the gill arches were moved artificially. Electrical stimulation, used to mimic afferent input, showed that sensory signals from the gills have a significant influence on respiration.
A single pulse or pulse train could shorten or (to a lesser degree) lengthen breathing cycle duration, depending on the moment of application of the stimulus in the breathing cycle, and as a consequence, could reset the respiratory rhythm. Increase of stimulus intensity evoked coughing, thus delaying the onset of following breathing cycles. Rhythmical stimulation, mimicking rhythmical sensory input, could entrain the breathing rhythm in a one-to-one ratio within certain limits. It was easier to increase than to decrease the respiratory rhythm. Stimulation at intervals which were at least 10 to 15% longer or shorter than the spontaneous respiratory cycle period could result either in a cyclic pattern of cycle modification ('relative coordination') or in entrainment patterns with coupling ratios of e.g. 2:1 or 2:3. During entrainment the frequency of spontaneous coughing decreased or even stopped. Normal respiratory movements and coughs both result from contraction of the same set of muscles, and thus result from the same set of motoneurons, although they are active in a slightly different pattern. The experiments presented in chapter 5 indicate that different central mechanisms are involved in the generation of both types of movements. Electrical stimulation not only influenced the respiratory rhythm during the stimulation period, but also had an after-effect.

In chapter 5 it was postulated that input from gill arch proprioceptors plays a role in resetting and entrainment of the respiratory rhythm. Therefore, oscillatory movements were imposed onto the gill arches in order to provide a more natural and more selective stimulus than electrical stimulation (chapter 6). The applied movements elicited similar responses of the respiratory rhythm. This finding confirms the hypothesis that gill arch proprioceptors contribute to these respiratory responses.

Vagal sensory signals from these proprioceptors might play a role in adjustment of gill arch positioning during respiration to ensure the continuity of the 'gill curtain', and to control the mesh width of the gill sieve during feeding. The long-lasting influence of rhythmic vagal sensory input on the respiratory rhythm may serve to stabilize the pattern generator for respiration, thus making it less susceptible to perturbations. The gill filament and gill raker mechanoreceptors do not seem to play a role in normal respiratory control. They might, however, serve a protective function. Mechanical stimulation of filaments and rakers evoked a phasic response in these receptors (chapter 3). The location of their receptive fields coincides with the innervation pattern described in chapter 2. The local adduction of filaments, observed when the gills were stimulated mechanically, is an example of such a protective response.

The observation that vagal sensory input can reset and entrain the respiratory rhythm indicates that vagal afferent fibres must have direct or indirect inputs to, and interact with, the central mechanisms that generate the normal respiratory movements and coughs. This interaction results in modula-
tion of the respiratory rhythm and determines the final motor program. The impact of sensory input is, however, limited. This is illustrated by the observation that entrainment only occurs after several 'transient' breathing cycles and can be established only over a limited range of stimulation frequencies.

Sensory fibres from the branchial nerves terminate in different locations within the central nervous system. Possible pathways which may be involved in respiratory control were evaluated on the basis of the neuroanatomical literature (chapter 7). Mechanoreceptive input from the gills can reach the motor nuclei that provide the efferent innervation of the respiratory pump muscles and the branchial muscles, via several integrating nuclei in the medulla oblongata.

First, vagal connections with the descending trigeminal nucleus and the medial funicular nucleus are potential pathways for sensory input from gill arch proprioceptors. Convergence of proprioceptive input from respiratory pump muscles and gill arches in these nuclei may be important in relating the contraction of respiratory pump muscles, which results in expansion or contraction of the entire respiratory system, to the degree of expansion of the branchial basket.

Second, there are branchial connections via the reticular formation to the trigeminal and facial motor nuclei that innervate the respiratory pump muscles, and to those vagal motoneurons that innervate the branchial muscles. These pathways may play a role in peripheral responses to mechanical stimulation of the gills, such as adduction of gill filaments and coughing. In addition, input from gill arch proprioceptors to the vagal motor nucleus may serve to control the contraction intensity of gill arch levator muscles, which are known to adjust gill arch position. From the innervation pattern of the gills (chapter 2) it was concluded that these small muscles are devoid of sensory innervation, and thus probably lack receptors. Gill arch proprioceptor information might be an alternative for regulation of the activity of these muscles.