Sensory functions of the chorda tympani nerve in the chicken

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Summary. The peripheral course of the chorda tympani nerve in the chicken was described and the area of the mouth it innervates was investigated by mechanical stimulation of the oral epithelium. Afferent neural activity recorded from the chorda tympani nerve showed that it relays information from oral chemoreceptors, mechanoreceptors, thermoreceptors and possibly nociceptors. The results indicate that the previously held ideas on the function of the chorda tympani nerve in the chicken are incorrect.

Key words. Chicken; chorda tympani nerve; neural activity, afferent; sensory function.

The avian chorda tympani nerve (CT) is generally considered to contain mainly preganglionic parasympathetic fibers. These synapse with cells in the mandibular ganglion from which postganglionic fibers run to the floor of the oral cavity and innervate the mandibular salivary glands[1-3]. It may also contain general visceral afferent fibers[2]. The presence of special visceral afferent fibers associated with the sense of taste are denied by most authors[3-6]. No mention is made however, of the results of Saito[7] who described taste buds associated with the anterior mandibular salivary glands. This work has been confirmed recently (Gentle & Hunter, unpublished observations) and a preliminary note has been published to show that the CT does conduct gustatory information from within anterior mandibular area[8].

A description of the peripheral course of the CT by Baumel[4] is based on the account by Cords[9] and describes the CT leaving the genu of the VIIth nerve where it turns rostrally and runs in the canal medial to the external ophthalmic blood vessels. Leaving the rostral end of the canal it turns ventrally and rostrally along the medialdorsal side of the quadrate bone. It runs rostroventral to the quadrato-mandibular articulation where it enters the articular bone and travels diagonally inside the mandible. Near the ventral edge of the mandible the CT leaves its canal, runs under the periosteum, and enters another canal ventral to the mandibular foramen. This canal lies medially to the intermandibular ramus of the mandibular nerve within the bone, travels past the intermandibular ramus and joins the sublingual ramus of the mandibular nerve with which it becomes incorporated.

Apart from a short note[8] the CT nerve of the chicken has not been investigated experimentally and the present work was planned to identify qualitatively the afferent sensory information relayed in the CT nerve originating in the area of the mouth it innervates. Also a number of dissections of the nerve were performed to establish the best surgical approach. These findings are presented because the peripheral course of nerve in the birds used in this study has been found to differ markedly from the account given by Cords[9].

Materials and methods. Ten 15-week-old Brown Leghorn hens were used. The general surgical procedures and electrical recording techniques were the same as those used previously[8]. The anterior buccal epithelium was stimulated for approximately 10 sec with 10 ml of the required solution maintained at body temperature delivered by a syringe placed close to the epithelium. The solutions used were 1 M potassium, calcium, sodium and ammonium chlorides, 1 M fructose and sucrose, 0.1 M quinine hydrochloride, 0.05 M acetic, citric and hydrochloric acids, distilled water and Tyrode ringer (without glucose). Glass distilled water (pH 4.5) was used to make up the salts and acids and Tyrode ringer was used for the other solutions.

Neural activity was recorded for 2 min after the test solution was placed on the preparation. After this, the buccal epithelium was washed with 30 ml of distilled water followed by 20 ml of ringer. The preparation was allowed a 3-min period of rest before another thest solution was applied.

In addition to chemical stimulation the buccal epithelium was explored with a hand-held blunt glass probe (tip diameter 1 mm). The probe was initially gently stroked over the epithelium and then applied with a greater pressure to produce a slight indentation. When a response was obtained the probe was held there for periods varying from 1 to 35 sec before being removed.

Temperature sensitivity was investigated by passing ice water over the buccal epithelium using otherwise the same method as that used with the chemical stimulation.

Finally the effects of drying the mouth were investigated by placing a swab of dry cotton wool on the epithelium, leaving it there for approximately 8 sec and then removing it.

Results. Peripheral course of the CT. It was found that up to the point where the nerve approaches the quadrate-mandibular articulation the course of the CT follows that described by Cords[9]. In the birds used in the present study the nerve did not enter the articular bone or the mandible at this point. The nerve ran between the muscle layers on the medial inner face of the mandible up to the level of the mandibular foramen where, it entered the mandibular canal and fused with the sublingual ramus of the mandibular nerve.

Area innervated by the CT. The area over which responses were obtained following mechanical stimulation of the oral epithelium is shown in figure 1. It consisted of the ventral buccal epithelium beneath the tongue extending caudally to part of the epithelium on the underside of the posterior area of the tongue and laterally up to a line level with the edge of the mandible. No responses were obtained from the inner keratinized beak surface, the outside of the beak or skin, the laryngeal area, the anterior part of the tongue or from the dorsal or dorso-lateral parts of the posterior tongue.

Afferent activity. In the majority of preparations there was a pronounced increase in neural activity which lasted for long periods following stimulation with all of the chemical solution tested except sucrose (fig. 2). Sucrose (not shown in fig. 2) did not produce a clear response in most of the preparations but in

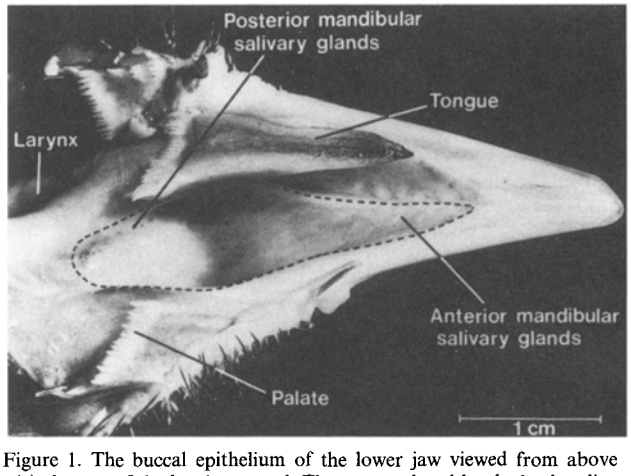

Figure 1. The buccal epithelium of the lower jaw viewed from above with the rest of the head removed. The area enclosed by the broken line gave responses following mechanical stimulation of the epithelium.

2 instances small questionable responses were obtained. The overall level of activity varied between preparations. The effect of the acids persisted even after repeated washings with ringer and distilled water. Distilled water gave a marked response in most but not all of the preparations, whereas Tyrode ringer only produced a short burst of activity during part of the stimulus period.

The mechanical responses to the glass probe consisted of 2 types, a rapidly adapting and a more slowly adapting response.

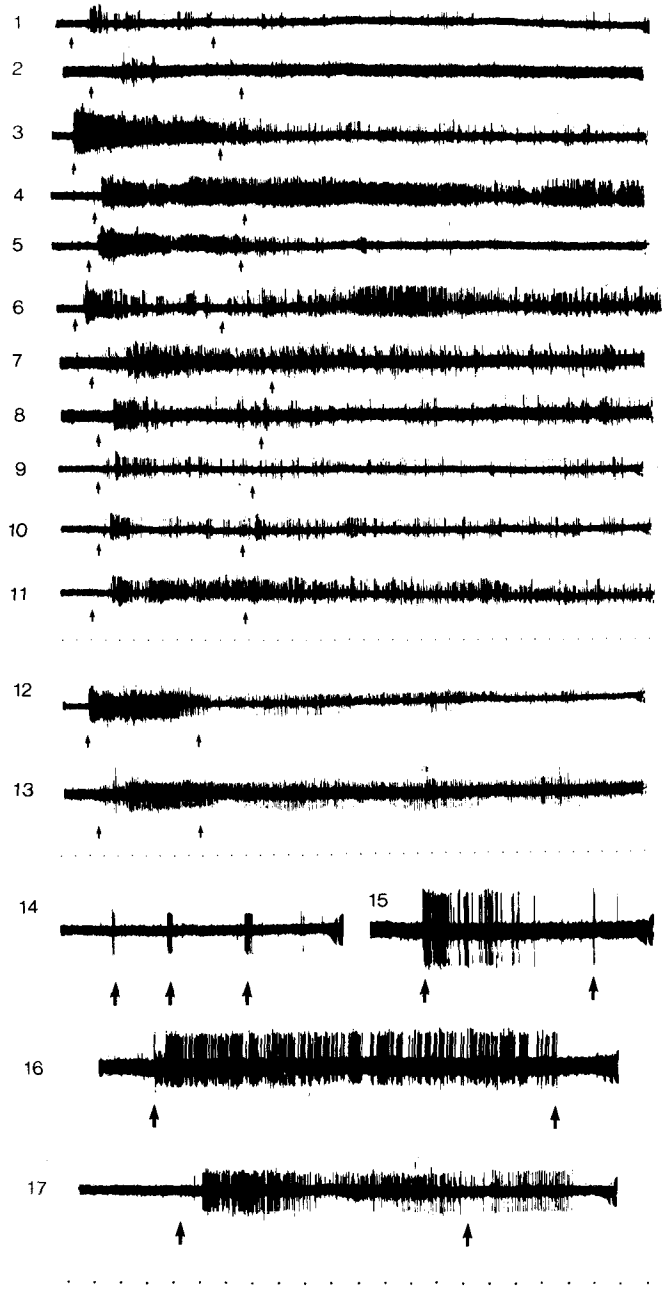

Figure 2. Recordings from the chorda tympani nerve following. *1* Distilled water; *2* Tyrode ringer; *3* 1 M potassium chloride; *4* 1 M sodium chloride; *5* 1 M calcium chloride; *6* 1 M ammonium chloride; *7* 1 M fructose; *8* 0.1 M quinine hydrochloride; *9* 0.05 M acetic acid; *10* 0.05 M citric acid; *11* 0.05 M hydrochloric acid; *12* drying the mouth; *13* high intensity mechanical stimulation; *14* rapidly adapting response to mechanical stimulation; *15* and *16* slowly adapting response to mechanical stimulation; *17* ice water. The arrows mark the beginning and end of the stimulus and the time works for all except 16 are 1-sec intervals. The time marks in 16 are 2-sec intervals.

The rapidly adapting response usually consisted of a short burst of activity when the stimulus was applied but showed no further activity under static displacement (fig. 2).

Very rapidly adapting responses, i.e., 1 response per stimulus, were not observed but they would be difficult to identify in multiunit preparations. The more slowly adapting response showed a more prolonged increase in activity which in some cases declined before the end of the stimulus period (fig. 2). In other cases the activity persisted for the duration of the stimulus (fig. 2). Several units were identified which only responded to high threshold mechanical stimulation (stimulus sufficient to produce a dent in the epithelial surface) and they often showed persistent activity after the stimulus was removed (fig. 2). In all of the mechanoreceptor units identified the responses were repeatable.

Stimulation with ice water produced a marked response (fig. 2) which persisted after the stimulus was removed.

Drying the epithelium produced a pronounced response while the cotton wool was in contact with the epithelium and this persisted for a period of 30 sec or longer after the cotton wool was removed (fig. 2).

Discussion. The peripheral course of the CT found in the birds used in the present experiment agrees with that shown by Hsieh[20] but not to the course described by Cords[9].

Bubién-Waluszewska[2] reported that in some birds the CT lies on the medial face of the ramus of the mandible but makes no mention of the species involved. From the illustration presented by Zweers[10] one can infer that in the pigeon the CT runs between the buccal epithelium and muscle layers attached to the mandible. In the chicken the CT lies much closer to the mandible than in the pigeon and runs between the muscle layers. It does not enter the mandible until it fuses with the sublingual ramus of the trigeminal nerve within the mandibular canal.

The CT innervates the mucous membrane of the floor of the mouth rostral and lateral to the tongue and unlike mammals does not innervate the tongue.

The pronounced activity in the CT nerve in response to stimulation with a variety of chemical solutions demonstrates conclusively that contrary to previous reports[3-6] this nerve relays gustatory information from the anterior mandibular taste buds to the central nervous system. The average number of taste buds in this region is 84.4[7] compared to 12 in the tongue, 196 in the palate and 67.8 in the rest of the floor of the oral cavity. The anterior mandibular taste buds therefore represent a significant proportion of the total receptor population. Hence the CT plays an important role in gustatory perception and has a comparable function to the mammalian CT nerve. While in general the results from the CT nerve agree with previous reports of taste responses from the lingual nerve[11-13] detailed comparisons are difficult since not only were different concentrations of test substances used but 2 of the studies[11,12] used integrator records. The response to distilled water in the present experiment is of interest because Kitchell et al.[11] also reported a clear response in the lingual nerve whereas Kadono et al.[13] did not. There are also other discrepancies; for example the response to 15% sucrose in ringer was doubtful in the experiments of Kitchell et al.[11] and this was also the case in the present experiment but 1 M sucrose made up in distilled water gave a clear response in the preparations used by Halpern[12] and Kadono et al.[13]. Ringer did not produce a marked effect in the present experiment or in previous experiments using the lingual nerve.

The rapidly and slowly adapting responses to mechanical stimulation are similar to those seen in recordings from the trigeminal nerve in other avian species[14-18]. The persistent responses after high threshold mechanical stimulation are of interest. The high threshold stimulus would activate nociceptors but in general unless they are damaged they do not show persistant responses after stimulation (Breward and Gentle, unpublished

observation). The fact that those results were repeatable would suggest the receptors were not extensively damaged. One possible explanation is that the responses were originating from nociceptors in an area of the mouth where there had been some pathological change (e.g., buccal erosion) which was not clearly visible.

It is not surprising that the CT showed a clear response to cooling of the mouth as cold receptors have been identified in both the lingual[11] and trigeminal nerves[18,19].

The persistent responses to drying of the buccal epithelium is of considerable interest. It is too early to speculate as to the nature of the receptors involved but it does suggest that it may be the physiological basis of the dry mouth sensation which is often used to explain prandial drinking in animals fed a dry diet.

In conclusion the CT, in addition to the preganglionic parasympathetic fibers which it was generally considered to contain, contains a wide variety of afferent sensory fibers giving information to the bird about taste, touch, temperature and pain.

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Liver function during chronic renal failure in rabbits

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Summary. In rabbits with chronic renal insufficiency the prothrombin index was increased by 25% and the alanine aminotransferase activity decreased by 20%; the results of other routine tests of hepatic function were not affected. The galactose elimination capacity was decreased by 12%, whereas the body clearance of antipyrine was unchanged. No change in hepatocytic structure was found.

Key words. Rabbits; renal failure, chronic; liver function; prothrombin index.

Evidence of altered liver function in patients with chronic renal failure (CRF) consists of increased serum levels of various coagulation factors[2,3], decreased activity of serum transaminases[4] and altered hepatic drug metabolism[5]. The present study concerns quantitative and qualitative measures of hepatic function and liver morphology in rabbits with CRF.

Material and methods. Chronic renal failure (CRF) was induced in young adult male rabbits of the White Danish Country strain by a 2 step procedure. During general anesthesia two-thirds of the surface of the left kidney was cauterized through an abdominal incision and 3 weeks later the right kidney was removed[6]. Control rabbits were sham-operated twice. Three months after surgery the glomerular filtration rate was measured as the total plasma clearance rate of ^{51}Cr-EDTA[6]. The galactose elimination capacity (GEC) was measured by injecting a weighed amount of galactose (4 mmol/kg b.wt) i.v. and during the next 3 h 15–19 arterial blood samples were obtained. The urinary bladder was emptied and irrigated with 2 × 10 ml of isotonic saline. The galactose concentrations in blood and urine samples were determined enzymatically[7]. The GEC was calculated as $\frac{A-U}{t_{c=o}+7}$, where A is the amount of galactose injected, U the amount excreted in the urine, $t_{c=o}$ the intercept on the time axis of the linear regression of arterial galactose concentration with time, and 7 is a correction for the equilibration of galactose during the elimination[8]. The regression analysis included samples obtained from 25 min after the injection until the concentration was below 2 mmol/l.

The clearance of antipyrine was determined by injecting a weighed amount of antipyrine (60 mg/kg b.wt) into an ear vein. Four venous blood samples were drawn from the other ear 3–7 h after the injection and analyzed for antipyrine[9]. The clearance was calculated from the linear regression of log concentration over time as clearance = $k \cdot \text{dose}/C_0$, where k is the elimination konstant and C_0 is the extrapolated concentration at time zero.

The serum concentrations of creatinine, urea, protein and bilirubin and the activities of alkaline phosphatase and alanine aminotransferase were measured by an autoanalyzer (ACA, Dupont Instruments). Albumin was determined by the succinic acid buffer method and the prothrombin index by the Owrens