

Sensory involvement in the control of food intake in poultry

By MICHAEL J. GENTLE, *Agricultural and Food Research Council's Poultry Research Centre, Roslin, Midlothian EH25 9PS*

To be able to satisfy the varying nutritional needs of the animal, the selection and ingestion of food items from the environment must be closely monitored both qualitatively and quantitatively. This monitoring is accomplished by a variety of sensory systems of which a simplified outline is presented in Fig 1.

While it is simpler to consider the stages of food ingestion separately, it must always be stressed that they do not occur in isolation but form a continuum with each phase being closely integrated with the preceding and succeeding ones.

Food recognition

Birds appear to rely almost exclusively on vision to select food items from the environment but they do have a functional olfactory system so that olfaction cannot be completely excluded. The domestic hen is a nidifugous bird and because the chicks are not fed directly by the parents there is an elaborate system of innate behavioural patterns which protect the animal from ingesting noxious diets. These innate reflexes are subsequently modified by new experiences allowing the birds to

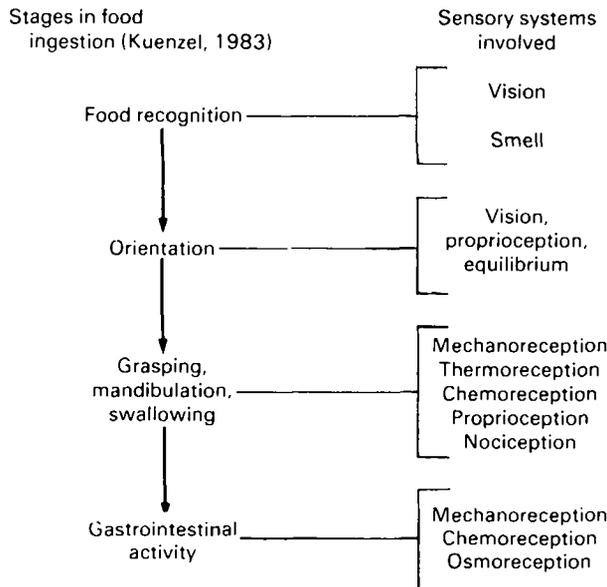


Fig. 1. Stages in food ingestion and sensory systems involved.

exploit a variety of available food sources. The visual factors can be separated into those which relate directly to the food and those which do not.

Food-related factors

Newly-hatched chicks appear to have innate preferences for food of certain colours. Hess (1956) reported a bimodal colour preference with peaks in the orange and blue region of the spectrum. A preference for green over red was found in domestic-fowl chicks (Capretta, 1969) and in 1-d-old turkeys (Cooper, 1971). In contrast, 1-d-old chicks reared in the dark have been reported to have an initial preference for red and blue (Salzen *et al.* 1971) but work by Kovach (1971) suggests that these preferences result from the birds being reared in the dark; they can be eradicated by giving chicks previous experience with achromatic light. Colour preference has also been reported in adult birds (Hurnik *et al.* 1971).

Innate food preferences are not restricted to colour but also extend to shape (Fantz, 1957; Dawkins, 1968) and size (Schrenk *et al.* 1963) of the food particles. These innate preferences are easily modified by experience. Taylor *et al.* (1969) and Capretta (1969) have both shown that the attractiveness of an innately non-preferred colour can be increased by simple exposure to it. The chicken also has a strong bias to use colour in learning situations and on the basis of colour will learn to avoid substances which after ingestion produce illness (Martin *et al.* 1977; Gillette *et al.* 1980). Novelty seems to be an important component in these learned illness-induced aversions (Ionescu & Bures, 1976; Gaston, 1977) and in the discernment of unpalatable substances (Shettleworth, 1972*a,b*).

The development of food recognition by young, newly-hatched chicks has been extensively studied by Hogan (1971, 1973*a,b*, 1975, 1977) and by Hogan-Warburg & Hogan (1981). Young chicks given food and sand learn to ingest primarily food but will still ingest some sand. The increase in food ingestion was probably the result of an association between the visual-tactile-gustatory stimuli from the food and the positive long-term effects of the food ingestion.

Non-food-related factors

A number of non-food related visual factors are involved in controlling food intake. In the natural environment the mother hen is important in directing attention to food sources (Turner, 1964; Hogan, 1973*a*; Savory *et al.* 1978). Young chicks eat more food in the presence of an active companion than in isolation and this has been called social facilitation (Tolman, 1964, 1965, 1968; Tolman & Wilson, 1965). It has been argued that social facilitation is responsible for the increase in growth rate of group-reared chicks (Schrenck *et al.* 1963) but Savory (1975) showed that these differences in growth rate were due to food conversion efficiency. Social facilitation seems to play an important role in the initiation of pecking (Strobel & Macdonald, 1974). These social factors in chicks have the effect of synchronizing the feeding of whole groups and a similar tendency is seen in adult birds (Hughes, 1971).

Olfaction

The sense of smell in birds has received very little attention but there is experimental evidence to show that kiwis, petrels and shearwaters can locate their food by smell (Wenzel, 1968; Grubb, 1972). The chicken has a functional olfactory system (Tucker, 1965; Tolhurst & Vince, 1976) and by using operant-conditioning techniques, olfactory thresholds to various hydrocarbons have been determined (Stattelman *et al.* 1975). Some recent work (Jones & Gentle, 1985) suggests that domestic chicks can regulate their behaviour in response to olfactory factors. While there is no direct evidence for the chicken using olfaction in feeding, studies involving olfactory-bulb ablation in relation to food intake and obesity (Robinson *et al.* 1977) suggest that it cannot be excluded.

Orientation

It is self-evident that the sensory systems responsible for maintaining the position of the head relative to the body are vital for feeding. A number of studies have shown that certain brain lesions in areas not directly involved in primary sensation will greatly interfere with the animals' ability to orientate correctly to food. Salzen & Parker (1975) proposed that the hyperstriatum provides a fine degree of orientation and produces arousal to fine stimulus differences: because it receives a wide variety of sensory inputs it can distinguish the detailed features of the stimulus object or situation. Following hyperstriated ablation, several birds were observed to show long periods of aphagia (Gentle *et al.* 1978). Deficits in the orientation phase of feeding behaviour resulted from bilateral lesions in the ansa lenticularis (Kuenzel, 1982). After bilateral lesion the birds approached grains of food but when they attempted to consume them they either pecked the air or struck a matted surface to the left or right of the food particles.

Grasping, mandibulation, swallowing

The amount and type of food eaten during a meal results from a combination of various internal and external signals, particularly oropharyngeal stimulation by the sensory characteristics of the food. To be able to grasp, mandibulate and swallow food, feedback from receptors in the oral cavity, pharynx and upper oesophagus is required. The cranial nerves which relay this sensory information to the brain are the trigeminal, facial, glossopharyngeal, vagus and hypoglossal nerves. The alteration of sensory feedback from the mouth results in a marked reduction in food intake. Section of the trigeminal nerves in the pigeon (Zeigler, 1973, 1975) or lesions in the trigeminal system in the brain (Zeigler & Karten, 1973*a,b*) resulted in aphagia, which may last for several days or months, followed by a period of anorexia during which body-weight is regulated at less than that of free feeding control animals. Since neither drinking nor preening behaviour was disrupted, it was postulated that deafferentation affects neural processes specific to the control of responsiveness to food (i.e. hunger) rather than reflecting a more generalized disruption of the sensorimotor mechanisms involved in pecking behaviour. A

detailed account of trigeminal sensorimotor circuit for pecking, grasping and feeding in the pigeon has been recently presented by Wild *et al.* (1984). Macleod (1978) has, however, proposed that trigeminal nerve section alters the bird's perception of food to such an extent that it was no longer regarded as food. Aphagia as a result of sensory deafferentation is thus analogous to food neophobia and, in a series of experiments giving birds novel diets, he was able to show that they exhibited a marked aphagia and one animal would not accept the novel diet at all.

Aphagia followed by a period of anorexia is also seen following section of the lingual and laryngo-lingual branches of the glossopharyngeal nerves (Gentle, 1971, 1978). It is interesting to note that following lingual nerve section the birds also showed a pronounced neophobia.

The receptors present in the mouth consist of mechanoreceptors, thermoreceptors, chemoreceptors and nociceptors. In considering oral receptors it must be stressed that they are not acting in isolation; for example, gustatory stimuli normally have concomitant tactile and thermal components.

Mechanoreceptors

Physiologically there are two types of mechanoreceptors present in the oral cavity: those which adapt rapidly, and those which adapt slowly to a mechanical stimulus.

The rapidly-adapting mechanoreceptors are of two types: those which give a single response to a mechanical displacement and those which give a short group or burst of responses to the same displacement. Herbst's corpuscles are thought to be responsible for the single-response type and Grandry corpuscles for the short-burst type (Malinovsky, 1967; Dorward, 1970; Gregory, 1973; Gottschaldt, 1974; Leitner & Roumy, 1974a; Saxod, 1978; Berkhoudt, 1980). Both of these rapidly adapting mechanoreceptors respond only to the onset of the stimulus and do not respond to a static displacement. The Herbst corpuscles, unlike the Grandry corpuscles, respond to a vibrating mechanical stimulus in the response range of 40–1500 Hz.

The slowly-adapting mechanoreceptors give a prolonged response to mechanical displacement and are common in the trigeminal system of geese (Gottschaldt, 1974) and pigeons (Necker, 1973). Slowly-adapting mechanoreceptors have been identified in the oral cavity of the chicken. We have recently recorded the electrical activity from single cells in the geniculate ganglion and have identified slowly-adapting mechanoreceptors from various branches of the facial nerve. It is thought that these slowly-adapting mechanoreceptors may be responses from free nerve endings.

Thermoreceptors

Cold receptors have been identified in the mouth and they respond to cooling of the surface of the beak and oral epithelium (Kitchell *et al.* 1959; Gregory, 1973; Necker, 1973; Leitner & Roumy, 1974b). Warm receptors responding to an

increase in temperature, have been found in the pigeon (Necker, 1972, 1973; Necker & Reiner, 1980) but not in the chicken (Kitchell *et al.* 1959).

Chemoreceptors

As in mammals, the chemoreceptor cells of avian species are clustered into taste buds, there being an average 360 taste buds in the oral cavity of the chicken (Saito, 1966); this is about half the number found in the hamster (Miller & Smith, 1984) and 29% of those found in the rat (Miller & Spangler, 1982). The distribution of the taste buds in the chicken is of interest as 54% are in the palate, 42% in the floor of the oral cavity and only 4% in the tongue. In the hamster (Miller & Smith, 1984) 73% are in the tongue and only 13.8% in the palate. In the Mallard the taste buds are situated in the areas of the mouth where there is prolonged contact with food and would thus enable better gustatory discrimination (Berkhoudt, 1977); a similar argument may hold for the chicken.

It was originally thought that taste information was relayed to the brain entirely along branches of the glossopharyngeal nerve (Kitchell *et al.* 1959) but recent work has shown that the chorda tympani branch of the facial nerve has an important role in taste perception (Gentle, 1983). The chorda tympani relays taste information from those taste buds in the anterior mandibular area. Some recent recordings we have taken from the geniculate ganglion show that many of the taste buds in the palate also send information to the brain along other branches of the facial nerve.

Chickens have an acute sense of taste (Gentle, 1975) and changes in taste preferences occur readily following experimental manipulation. When fed on a diet adequate in energy, the chicken did not exhibit any marked preference for a sucrose solution (100 g/l) but when fed on a diet low in energy they showed a marked preference for the sucrose (Kare & Maller, 1967). Gustatory cues are also used to select calcium carbonate-supplemented diets when Ca is lacking (Hughes & Wood-Gush, 1971). In these experiments the birds' gustatory behaviour is altered as a result of the consequences of ingesting the food and this is very clearly demonstrated in condition-aversion studies. Birds rapidly form conditioned aversion to weakly-flavoured solutions (Lett, 1980; Westbrook *et al.* 1980; Gillette *et al.* 1983) but not to strongly-flavoured foods (Gillette *et al.* 1980; Gillette *et al.* 1983). Even after short periods of water deprivation, the chicken will accept solutions which would have been unacceptable previously (Gentle, 1976) and it was suggested that this increase in acceptability may be due to changes in taste sensitivity. Changes in hydration will also affect the birds' response to water: after deprivation, water is positively rewarding but after loading the crop with water further water in the mouth is stressful (Gentle, 1974). Many of the conditions which alter the animals' behavioural responses to gustatory stimuli also evoke visceral afferent activity. Both gustatory (Dubbeldam *et al.* 1976, 1979; Dubbeldam, 1984; Gentle 1979a) and visceral afferents (Katz & Karten, 1983) project on to the nucleus of the solitary tract within the medulla. How visceral afferent information affects behaviour is not known but one possibility is that it interacts with oral or gustatory activity (Norgren, 1983). This interaction might

take place in the nucleus of the solitary tract or caudal brain stem and in the rat, neurons responsive to chorda tympani as well as cervical vagus nerve stimulation were identified electrophysiologically in the caudal brain stem (Bereiter *et al.* 1981).

Oral behaviour in response to gustatory stimulation usually consists of mandibulatory movements of the beak coupled with movements of the tongue and swallowing. Head-shaking and beak-wiping where the birds rapidly stroke alternate sides of the beak on the sides or floor of the cage are also seen. The behavioural sequence is not rigid. Although beak and tongue movements occur over several minutes, beak-wiping does not necessarily follow a period of head-shaking and the ratio of the different behaviour components to each other does not remain the same (Gentle & Harkin, 1979). Changes in oral behaviour can occur following both vitamin A (Gentle & Dewar, 1981) and zinc deficiencies (Gentle *et al.* 1981). Of these behaviour patterns, beak-wiping was abolished by removal of the anterior telencephalon and head-shaking by the removal of both the telencephalon and diencephalon. Beak and tongue movements are still present after this surgery and are therefore organized in, or caudal to, the midbrain (Gentle, 1981).

Nociceptors

The presence of specific nociceptors which respond to various thermal or mechanical stimulation, or both, have been identified in the chicken beak (Breward, 1984). The thermal response threshold was found to be in the range 41–56°. These results explain the observations that chickens drink very little, if any, water if it is at 45° (Gates & Kare, 1961; Gentle, 1979*b*). While it is unlikely that birds would normally encounter water at 45° they are likely to peck at solid items at that temperature and damage the oral epithelium and stimulate nociceptors.

Gastrointestinal activity

We know least of all about the receptors in the gastrointestinal tract. Work by Richardson (1970) showed that the artificial inflation of the crop by a permanently-implanted balloon reduced the amount of food a bird ate. Subsequently, Hodgkiss (1981) has demonstrated the presence of two types of distension-sensitive receptors in the crop of the chicken, slowly-adapting receptors and rapidly-adapting receptors, the former being encountered about four times more frequently than the latter. The slowly-adapting receptors are capable of signalling distension of the crop for prolonged periods of time although small local changes in tension may modulate the firing rate. The only other piece of direct evidence for gastrointestinal receptors comes from the work of Duke *et al.* (1977) who reported mechanoreceptors present in the gizzard. A number of studies (Gentle & Richardson, 1972; Richardson & Gentle, 1972; Shurlock & Forbes, 1981*a*; Gentle *et al.* 1982) have suggested the presence of thermoreceptors, chemoreceptors or osmoreceptors in the crop and duodenum. The work of Shurlock & Forbes (1981*a*) is of interest as it suggests that in relation to food

intake there is a major osmotic control in the duodenum which may affect a secondary control system in the upper gastrointestinal tract. Further work by the same authors (Shurlock & Forbes, 1981*b*) has demonstrated a glucose-dependent mechanism for the control of food intake which exists in the hepatic area of the chicken.

Conclusions

In the present paper I have examined the role of some of the sensory systems involved in controlling food intake by considering their role in monitoring food items qualitatively and quantitatively. Our knowledge is, however, only fragmentary and we have little information on the receptors present in the alimentary canal or those receptors which measure circulating nutrients. For food intake to be controlled effectively the activity of this vast array of receptors, both internal and external, are integrated within the central nervous system where the fine adjustments can be made.

REFERENCES

- Bereiter, D. A., Berthoud, H. R. & Jeanrenaud, B. (1981). *Brain Research Bulletin* **7**, 261–266.
- Berkhoudt, H. (1977). *Netherlands Journal of Zoology* **27**, 310–331.
- Berkhoudt, H. (1980). *Netherlands Journal of Zoology* **30**, 1–34.
- Breward, J. (1984). *Journal of Physiology* **346**, 56P.
- Capretta, P. J. (1969). *Animal Behaviour* **17**, 229–231.
- Cooper, J. B. (1971). *Poultry Science* **50**, 1892–1893.
- Dawkins, R. (1968). *Zeitschrift für Tierpsychologie* **25**, 170–186.
- Dorward, P. K. (1970). *Comparative Biochemistry and Physiology* **35**, 729–735.
- Dubbeldam, J. L. (1984). *Brain Behaviour and Evolution* **24**, 47–57.
- Dubbeldam, J. L., Brus, E. R., Menken, S. B. J. & Zeilstra, S. (1979). *Journal of Comparative Neurology* **183**, 149–168.
- Dubbeldam J. L., Karten, H. J. & Menken, S. B. J. (1976). *Journal of Comparative Neurology* **170**, 415–420.
- Duke, G. E., Kuhlman, W. D. & Fedde, M. R. (1977). *Poultry Science* **56**, 297–299.
- Fantz, R. L. (1957). *Journal of Comparative and Physiological Psychology* **50**, 422–430.
- Gaston, K. E. (1977). *Behavioural Biology* **20**, 441–453.
- Gates, J. D. & Kare, M. R. (1961). *Poultry Science* **40**, 1407.
- Gentle, M. J. (1971). *British Poultry Science* **12**, 77–86.
- Gentle, M. J. (1974). *Physiology and Behaviour* **13**, 15–19.
- Gentle, M. J. (1975). In *Neural and Endocrine Aspects of Behaviour in Birds*, pp. 305–318 [P. Wright, P. G. Caryl and D. M. Vowles, editors]. Amsterdam: Elsevier.
- Gentle, M. J. (1976). *Chemical Senses and Flavour* **2**, 121–128.
- Gentle, M. J. (1978). *Chemical Senses and Flavour* **3**, 325–329.
- Gentle, M. J. (1979*a*). *Journal of Comparative Physiology* **130**, 259–264.
- Gentle, M. J. (1979*b*). *British Poultry Science* **20**, 533–539.
- Gentle, M. J. (1981). *Behaviour Processes* **6**, 109–120.
- Gentle, M. J. (1983). *Experientia* **39**, 1002–1003.
- Gentle, M. J. & Dewar, W. A. (1981). *British Poultry Science* **22**, 275–279.
- Gentle, M. J., Dewar, W. A. & Wright, P. A. L. (1981). *British Poultry Science* **22**, 265–273.
- Gentle, M. J., Dewar, W. A., Wright, P. A. L. & Dick, K. M. (1982). *Appetite* **3**, 53–60.
- Gentle, M. J. & Harkin, C. (1979). *Chemical Senses and Flavour* **4**, 183–190.
- Gentle, M. J. & Richardson, A. (1972). *British Poultry Science* **13**, 163–170.
- Gentle, M. J., Wood-Gush, D. G. M. & Gordon, J. (1978). *Behavioural Processes* **3**, 137–148.
- Gillette, K., Martin, G. M. & Bellingham, W. P. (1980). *Journal of Experimental Psychology: Animal Behaviour Processes* **6**, 99–111.

- Gillette, K., Thomas, D. K. & Bellingham, W. P. (1983). *Chemical Senses* **8**, 41–57.
- Gottschaldt, K. M. (1974). *Journal of Comparative Physiology* **95**, 29–47.
- Gregory, J. E. (1973). *Journal of Physiology* **229**, 151–164.
- Grubb, T. C. (1972). *Nature* **237**, 404–405.
- Hess, E. H. (1956). *Psychological Reports* **2**, 477–483.
- Hodgkiss, J. P. (1981). *Comparative Biochemistry and Physiology* **70A**, 73–78.
- Hogan, J. A. (1971). *Behaviour* **39**, 128–201.
- Hogan, J. A. (1973a). *Journal of Comparative and Physiological Psychology* **83**, 355–366.
- Hogan, J. A. (1973b). *Journal of Comparative and Physiological Psychology* **83**, 367–373.
- Hogan, J. A. (1975). *Journal of Comparative and Physiological Psychology* **89**, 95–104.
- Hogan, J. A. (1977). *Journal of Comparative and Physiological Psychology* **91**, 839–850.
- Hogan-Warburg, A. J. & Hogan, J. A. (1981). *Animal Behaviour* **29**, 143–154.
- Hughes, B. O. (1971). *British Poultry Science* **12**, 359–366.
- Hughes, B. O. & Wood-Gush, D. G. M. (1971). *Animal Behaviour* **19**, 490–499.
- Hurnik, J. F., Jerome, F. M., Reinhart, B. S. & Summers, J. D. (1971). *Poultry Science* **50**, 944–949.
- Ionescu, E. & Bures, J. (1976). *Behavioural Processes* **1**, 233–241.
- Jones, R. B. & Gentle, M. J. (1985). *Physiology and Behaviour* **34** (In the Press).
- Kare, M. R. & Maller, O. (1967). *Journal of Nutrition* **92**, 191–196.
- Katz, D. M. & Karten, H. J. (1983). *Journal of Comparative Neurology* **218**, 42–73.
- Kitchell, R. L., Strom, L. & Zotterman, Y. (1959). *Acta Physiologica Scandinavica* **46**, 133–151.
- Kovach, J. K. (1971). *Journal of Comparative and Physiological Psychology* **75**, 386–398.
- Kuenzel, W. J. (1982). *Society for Neuroscience* **8**, 599.
- Kuenzel, W. J. (1983). *Bird Behaviour* **5**, 2–15.
- Leitner, L. M. & Roumy, M. (1974a). *Pflugers Archiv für die gesamte Physiologie des Menschen und der Tiere* **346**, 141–150.
- Leitner, L. M. & Roumy, M. (1974b). *Pflugers Archiv für die gesamte Physiologie des Menschen und der Tiere* **346**, 151–155.
- Lett, B. T. (1980). *Animal Learning and Behaviour* **8**, 193–198.
- Macleod, H. A. (1978). Control of feeding patterns in the Banbury dove (*Streptopelia risoria*). PhD Thesis, University of Edinburgh.
- Malinovsky, L. (1967). *Zeitschrift für mikroskopisch – anatomische Forschung* **77**, 279–303.
- Martin, G. M., Bellingham, W. P. & Storlien, L. H. (1977). *Physiology and Behaviour* **18**, 415–420.
- Miller, I. J. Jr & Smith, D. V. (1984). *Physiology and Behaviour* **32**, 275–285.
- Miller, I. J. Jr & Spangler, K. M. (1982). *Chemical Senses* **7**, 99–108.
- Necker, R. (1972). *Journal of Comparative Physiology* **78**, 307–314.
- Necker, R. (1973). *Journal of Comparative Physiology* **87**, 379–391.
- Necker, R. & Reiner, B. (1980). *Journal of Comparative Physiology* **135**, 201–208.
- Norgren, R. (1983). *Journal of the Autonomic Nervous System* **9**, 67–77.
- Richardson, A. J. (1970). *Animal Behaviour* **18**, 633–639.
- Richardson, A. J. & Gentle, M. J. (1972). *British Poultry Science* **13**, 171–173.
- Robinson, B., Snapir, N. & Perek, M. (1977). *Brain Research Bulletin* **2**, 465–474.
- Saito, I. (1966). *Bulletin of the Faculty of Agriculture, Miyazaki University* **13**, 95–102.
- Salzen, E. A., Lily, R. E. & McKeown, J. R. (1971). *Animal Behaviour* **19**, 542–547.
- Salzen, E. A. & Parker, D. M. (1975). In *Neural and Endocrine Aspects of Behaviour in Birds*, pp. 205–242 [P. Wright, P. G. Caryl and D. M. Vowles, editors]. Amsterdam: Elsevier.
- Savory, C. J. (1975). *British Poultry Science* **16**, 343–350.
- Savory, C. J., Wood-Gush, D. G. M. & Duncan, I. J. H. (1978). *Applied Animal Ethology* **4**, 13–27.
- Saxod, R. (1978). In *Handbook of Sensory Physiology*, vol. 9, pp. 338–417 [M. Jacobson, editor]. Berlin: Springer Verlag.
- Schrenk, P. K., Sterritt, G. M., Smith, M. P. & Stilson, D. W. (1963). *Animal Behaviour* **11**, 306–309.
- Shettleworth, S. J. (1972a). *Animal Behaviour* **20**, 29–35.
- Shettleworth, S. J. (1972b). *Journal of Comparative and Physiological Psychology* **80**, 175–198.
- Shurlock, T. G. H. & Forbes, J. M. (1981a). *British Poultry Science* **22**, 323–331.
- Shurlock, T. G. H. & Forbes, J. M. (1981b). *British Poultry Science* **22**, 333–346.

- Stattelman, A. J., Talbot, R. B. & Coulter, D. B. (1975). *Comparative Biochemistry and Physiology* **50A**, 807-809.
- Strobel, M. G. & Macdonald, G. E. (1974). *Journal of Comparative and Physiological Psychology* **86**, 493-502.
- Taylor, A., Sluckin, W. & Hewitt, R. (1969). *Animal Behaviour* **17**, 3-8.
- Tolhurst, B. E. & Vince, M. (1976). *Animal Behaviour* **24**, 772-779.
- Tolman, C. W. (1964). *Animal Behaviour* **12**, 245-251.
- Tolman, C. W. (1965). *Animal Behaviour* **13**, 493-496.
- Tolman, C. W. (1968). *Behaviour* **30**, 275-286.
- Tolman, C. W. & Wilson, G. F. (1965). *Animal Behaviour* **13**, 134-142.
- Tucker, D. (1965). *Nature* **207**, 34-36.
- Turner, E. R. A. (1964). *Behaviour* **24**, 1-46.
- Wenzel, B. M. (1968). *Nature* **220**, 1133-1134.
- Westbrook, R. F., Clarke, J. C. & Provost, S. (1980). *Behavioural and Neural Biology* **28**, 398-407.
- Wild, J. M., Arends, J. J. A. & Zeigler, H. P. (1984). *Brain Research* **300**, 146-151.
- Zeigler, H. P. (1973). *Science* **182**, 1155-1157.
- Zeigler, H. P. (1975). *Journal of Comparative and Physiological Psychology* **89**, 827-844.
- Zeigler, H. P. & Karten, H. J. (1973a). *Journal of Comparative Neurology* **152**, 59-82.
- Zeigler, H. P. & Karten, H. J. (1973b). *Journal of Comparative Neurology* **152**, 83-102.