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STUDIED BY THE METHOD
OF CONDITIONED REFLEXES

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FROM THE PHYSIOLOGICAL
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DOOR

WILLEM GEORGE WALTER

GEBOREN TE AMSTERDAM

Promotor: Prof. Dr. J. ten Cate.

T.P.

Point n'est besoin d'espérer pour entreprendre,
ni de réussir pour persévérer.

SAMENVATTING.

Inleiding en Hoofdstuk 1. Hoewel de anatomische gegevens over het reukorgaan van vogels de verwachting wekken dat deze dieren een vrij goed reukvermogen hebben, vermeldt de physiologische literatuur zulke tegenstrijdigheden, dat hierover geenszins zekerheid bestaat. Inzonderheid aan roofvogels werd een zeer goed reukvermogen toegekend. Het is evenwel waarschijnlijk dat hierbij niet voldoende werd rekening gehouden met het buitengewoon scherpe gezichtsvermogen van deze vogels, waaraan ongetwijfeld geheel het bijzondere gedrag van roofvogels bij het zoeken en vinden van de prooi is toe te schrijven. De proeven met roofvogels, waarvan de resultaten den auteurs aanleiding gaven het aanwezig zijn van een reukvermogen aan te nemen, kunnen de critiek niet doorstaan. Daartegenover staan de resultaten van een aantal experimenten, waaruit men de overtuiging krijgt dat roofvogels bij het zoeken naar voedsel in het geheel niet door den reuk worden geleid. Vele proeven met andere vogels voldoen evenmin aan de eischen die men aan bewijzende experimenten kan stellen. Bovendien heeft geen van de auteurs die tot het aanwezig zijn van een reukvermogen hebben geconcludeerd, de beslissende proef genomen de reukzenuwen door te snijden. Alle reacties zouden dan onmiddellijk moeten verdwijnen. In de artikelen waarin dressuurproeven en observaties, gedaan aan vogels bij het eten van ruikend voedsel, zijn beschreven, zijn ongeveer evenveel pleidooien voor, als tegen het aanwezig zijn van een reukvermogen te vinden. Slechts eenmaal werd het probleem bestudeerd met de methode van de voorwaardelijke reflexvorming. Dit is te betreuren, aangezien deze onderzoekingswijze den proefnemer het best in staat stelt de factoren in het experiment te beheerschen en, mits toegepast met de noodzakelijke contrôleproeven, waarschijnlijk de beste inlichtingen geeft omtrent de zintuiglijke waarnemingsmogelijkheden van dieren.

Het leek mij noodzakelijk deze proeven uit te breiden, waarbij is nagegaan in hoeverre ik de resultaten van de vroegere auteurs kon bevestigen. Bovendien heb ik dressuurproeven verricht en, wat daarmede in nauw verband staat, vrije voedingsproeven. Tenslotte heb ik getracht iets te onthullen van de processen die in de hersenen plaats hebben, wanneer het neusslijmvlies met reukstoffen wordt geprikkeld. Hiertoe heb ik de electrische verschijnselen van de hersenen afgeleid en den invloed nagegaan die verschillende stoffen, aan de ademhalingslucht toegevoegd, op het electro-encephalogram hebben. Hierbij is een aanwijzing verkregen dat stoffen die bij den mensch uitsluitend den n. olfactorius prikkelen, geen veranderingen in het electro-encephalogram ten gevolge hebben, dat dit daarentegen wel wordt beïnvloed door stoffen die voor den mensch (tevens) prikkelend werken op den n. trigeminus. Deze proeven zijn evenwel nog niet in een zoo ver gevorderd stadium dat de resultaten ervan uitvoerig kunnen worden medegedeeld.

Hoofdstuk 2. Hoewel in het algemeen zeer geringe prikkels reeds voldoende zijn om de ademhaling van een duif te veranderen, bleek het dat met reukstoffen de ademhaling in het geheel niet was te beïnvloeden, mits het was uitgesloten dat hierbij andere prikkels werden gegeven. Ook is het niet gelukt een voorwaardelijke reflex te vormen waarbij een reukprikkel als voorwaardelijke prikkel werd gecombineerd met een pijnprikkel die langs onvoorwaardelijken weg een ademversnelling gaf. Een duif werd gedurende 240 combinaties geconditioneerd op pyridine en een andere gedurende 250 op amylacetaat. Zelfs na dit groote aantal combinaties kon er niet de minste verandering in de ademhaling worden bespeurd wanneer de reukprikkel alleen werd gegeven. Op een zwakken acoustischen prikkel kon evenwel reeds na korten tijd een voorwaardelijke ademversnelling worden geconstateerd.

Hoofdstuk 3. Ook bij gebruikmaking van een methode geheel gelijk aan die der vroegere auteurs is het me niet gelukt hun resultaten te bevestigen. De onvoorwaardelijke pootbeweging door inductieslagen aan den poot kon niet als voorwaardelijke reactie worden teweeggebracht door den reukprikkel, hoewel deze gedurende geruimen tijd met den onvoorwaardelijken prikkel was gecombineerd. De toegediende reukstoffen waren bij een duif eau de Cologne, bij een andere duif en bij een eend methylsalicylaat. Het aantal malen dat de combinatie werd gegeven was respectievelijk 88, 92 en 102. Om na te gaan of voor de vogels de mogelijkheid bestaat de reukstoffen te percipieeren in vochtige lucht, werden overeenkomstige proeven verricht met een tweetal duiven, waarbij de reukstoffen werden toegevoegd aan met waterdamp verzadigde lucht. Deze duiven kregen respectievelijk pyridine in 128, en methylsalicylaat in 129 combinaties. Ook aan het eind van deze proefreeksen was het niet mogelijk door het geven van de reukstof zonder onvoorwaardelijken prikkel, eenig effect te verkrijgen.

Hoofdstuk 4. Dressuurproeven met drie sijsjes en twee parkieten hebben slechts het negatieve resultaat opgeleverd, dat dressuur op lavendelolie, anijsolie, jasmijn-essence, kruidnagelolie, pyridine en scatol niet mogelijk was. Bij de dressuurproeven met de vrouwelijke parkiet werden oogenschijnlijk goede resultaten verkregen op kruidnagelolie. Het aantal goede keuzen verminderde evenwel niet nadat de reukzenuwen waren doorgesneden. Bij de dressuur zijn er dus prikkels geweest die onafhankelijk van, maar gelijktijdig met, de olfactorische prikkels zijn gegeven en die voor het resultaat verantwoordelijk waren.

Voor en gedurende den tijd dat deze dressuur werd verricht, is nu en dan het gedrag van de vogeltjes geobserveerd wanneer vreemde stoffen aan het voedsel waren toegevoegd. Men zou verwachten dat wanneer deze stoffen een olfactorische gewaarwording zouden kunnen geven dit aan de reacties van de proefdieren zou zijn te zien. Een reactie werd evenwel uitsluitend waargenomen wanneer de gegeven stoffen tot de groep van reukstoffen behoorden die bij den mensch (naast een reukgewaarwording) gewaarwordingen geven tengevolge van prikkeling van de trigeminus uiteinden. De stoffen die voor menschen zuivere reukstoffen zijn, gaven evenwel nooit aanleiding tot eenig van het normale afwijkend gedrag.

Hoofdstuk 5. Met twee eenden zijn vrije voerproeven verricht. Nadat gedurende langen tijd een sterk ruikend vischmeel het eenige voedsel was geweest, werden de oogen dichtgeplakt. De eenden waren niet in staat het voedsel te vinden. Hierna werd enucleatio bulbi verricht, maar na twee maanden met het vischmeel te zijn gevoerd, waaraan bovendien als reukstof pyridine resp. amylacetaat was toegevoegd, konden de blinde eenden het voedsel niet vinden. Blijkbaar was er geen reukvermogen aanwezig om hen te leiden bij het zoeken naar voedsel.

Hoofdstuk 6. Bij vijf eenden met canules in de kliermaag werd getracht de maagsapsecretie op reukprikkels te conditioneeren, om zoo te pogen een vegetatieve voorwaardelijke reflex te vormen. Respectievelijk werden de proeven verricht met scatol in 181 combinaties, pyridine in 244, toluol in 202, anijsolie in 331 en toluol in 331 combinaties. In geen van de gevallen werd een voorwaardelijke maagsapsecretie verkregen als de reukprikkel zonder de (onvoorwaardelijke) voedseltoediening werd gegeven.

Op acoustische en optische prikkels kon evenwel zeer gemakkelijk een voorwaardelijke secretie worden verkregen.

Alle proeven leiden tot de conclusie dat bij de vogels waarmede hier is gewerkt noch een voorwaardelijke reflex kan worden gevormd op reukstoffen, noch een dressuur daarop mogelijk is. Bij het zoeken naar voedsel blijkt de reuk ervan de vogels niet te leiden. Dit alles wijst erop dat de onderzochte vogels geen reukvermogen bezitten.

CONTENTS

INTRODUCTORY.

The controversy around the problem of the sense of smell in birds became only accentuated as the number of publications on the subject increased. Whereas some authors consider birds to be microsmatics, there are investigators who attribute to birds a sense of smell equalling the dog's olfactory sense. But on the other hand many scientists are of the opinion that birds are absolutely anosmatic. The problem has a larger bearing than might be apparent at first sight. If birds are absolutely anosmatic, then we are faced with the remarkable fact that in this group the olfactory organ is still developed to some extent, but that these animals are not able to use it in the same way as their ancestors did, or perhaps do not use it at all. Since we know that the olfactory organs are developed to an extent suggesting a moderate sense of smell, or even, in some species, a fairly good olfactory sense, it is of no importance to physiologists to deal with anatomical data. If the olfactory organ were not developed at all, we could hardly expect a sense of smell to exist. But on the other hand the occurrence of the anatomical substratum does not in the least ensure the presence of sensory perception. It is only by means of experiments that we are able to get any knowledge of the problem. As regards the purely anatomical aspect of the question I will therefore only point to the articles by ISHIHARA and by STRESEMANN. (*Vide* list of references at the end of this paper.) Of all the work done on the subject only the experiments of BAJANDUROW and LARIN were made by the method of conditioned reflexes. As this is the only entirely physiological method of investigating the existence of sensory perception, I judged it to be of importance to continue and extend the experiments made along these lines. Especially certain psychologists are of the opinion that the method of conditioned reflexes has many disadvantages; I therefore used, in addition, training experiments and free feeding experiments.

The animals used in these experiments were: pigeons (*Columba livia domestica*), domesticated ducks (*Anas sp.*), siskins (*Carduelis spinus*), and parakeets (*Melopsittacus sp.*). Part of the odorants chosen were the same as those used by earlier authors.

In the latter part of the investigations another method was also employed. In pigeons I recorded the electric potentials of the brain before, during and after the administration of odorants. Two needles introduced into the brain through the skull, at various depths and distances, were used as electrodes. The electro-encephalograms were much interfered with by the action-potentials of the muscles of the neck, the eyes and the eyelids. Indications were obtained that pure odorants do not affect the electro-encephalogram, whereas substances stimulating both olfactory and trigeminus nerve endings in man, cause alterations in the records. This might be interpreted to mean that the former substances are unable to arouse a sensory perception. I am of opinion that electro-encephalography may yield valuable information in this direction. Results will be communicated when the experiments are in a more advanced stage.

A remark must be made concerning terminology. When a reflex has been formed on a stimulus which did not originally produce this effect, the reflex is *conditioned*. The stimulus, however, is not conditioned, but served as an agent to condition the reflex; it is, therefore, a *conditioning* stimulus. Consequently, the stimulus that causes the reflex as an inborn reaction is the *non-conditioning* stimulus. As, moreover, the word unconditional, which was always used in the literature, has a different signification in colloquial English, it should be avoided.

Chapter I

Review of the literature.

As far as I was able to consult the original papers the physiological literature concerning the sense of smell in birds is here briefly reviewed in chronological order.

The earlier literature mainly treats of descriptions of observations to which the value of physiological experiments cannot be attached. For the greater part they were made on birds of prey. It was especially these birds that were credited with an acute sense of smell, since they may come from a great distance to carrion and smelly putrifying flesh.

AUDUBON has been generally quoted from his work "Ornithological Biography" (1834) (often moreover wrongly dated 1835). His paper was, however, read before the Natural History Society of Edinburgh in 1826 and subsequently published. In "Ornithological Biography" he reproduced the entire article. Only in this way can it be intelligible that DARWIN refers to AUDUBON in his diary of 1834.

From the way vultures seek their prey, AUDUBON had always doubted the deeply-rooted notion that these birds are able to find food by their sense of smell. He therefore staged some experiments, partly with black vultures (or carrion crows; *Cathartes jota = atratus*) and partly with turkey buzzards (= turkey vulture; *C. aura*). An entire deer skin was put out in the open. It had been thoroughly dried and was absolutely odourless. Nevertheless a turkey vulture at once noticed it, attacked and ripped up the skin, unaware that no flesh was inside. The corpse of a hog, which smelled awfully, was covered up so that it was invisible from above, whilst its bad smell was none the less perceptible. Large groups of vultures were in the air just above the carrion, but they did not pay it the least attention. A freshly killed pig was also hidden; the vultures did not perceive it, and only by following the trail of blood did they find it at last. AUDUBON held in captivity two wild vultures which had been accustomed to get food in their cage. Every time he carried the meat alongside the bars of the cage the birds became highly exited, but not the least reaction was to be seen so long as he held the meat behind the cage.

Having thus disproved the opinion that vultures have an acute sense of smell, AUDUBON tried to explain the origin of the belief from the keen sense of vision and the habit of these birds to follow their companions. When one bird of a flock perceives a prey, the others observe its behaviour and consequently also find it.

BEEBE characterized this as follows: "....Overhead the sky was quartered in every direction by dozens of others. Within a few minutes all these birds had come, each guided by the suggestive descent of some brother vulture, who in turn had well interpreted *his* neighbor's actions...."

The acuteness of the sense of vision has been expressed in figures by SCHMID. Peregrine falcons (*Falco peregrinus*) were able to see an artificial crow from a distance of 1660 metres although visibility was bad. The experimenter could not perceive the object with a 6x Zeiss spy-glass. Pigeons on the ground were seen from 1080 metres. A dog, on the other hand, is able to see at a distance of only 800 m, and recognizes objects at 100 metres at best.

AUDUBON expressed himself proud of "the breach" which he had "made upon a general and deeply rooted opinion" about the vultures' sense of smell, and felt assured of having dissolved it. How disappointed he would have been if he could have foreseen that more than a hundred years afterwards the question of the sense of smell in birds would still not be settled.

The experiments of AUDUBON did not inspire much confidence in America. He therefore induced his friend BACHMAN to confirm his results and he judged it necessary to have BACHMAN's experiments attended by some scientists of good reputation. Afterwards a certificate was signed by them. These observations were also made on *Cathartes aura* and *C. atratus*. Three freshly-killed animals and a carriage full of garbage were put under a large screen; the sides were open so that the scent of flesh was to be observed everywhere in the vicinity. Although the birds were in the neighbourhood in large numbers, they were not attracted by this abundance of delicacies. They were at once attracted, however, by a picture of a ripped up sheep, which they tried again and again to devour. Although the picture was put close to the flesh and garbage, the birds were only attracted by the sight of the sheep and not at all guided by the smell of the flesh. On another occasion a large quantity of meat, both fresh and tainted, was covered by a thin sheet of canvas spread over it. A few pieces were put on the top of the sheet; these were immediately found and devoured, whereas the birds did not discover the rest of the meat. One vulture starved to death in the midst of a large amount of flesh after having been blinded. It was a common belief that, after a deer had been killed, some vultures would be attracted by the smell of it and would warn other vultures, so that in less than no time large numbers of birds were present. BACHMAN, however, did not believe the vultures to be guided by their sense of smell, because they were on the spot so quickly that there was not yet any possibility of the meat smelling. This objection, however, is not valid in my opinion. If the birds have indeed a keen sense of smell, then it is possible that they perceive the odour of fresh meat which is practically inodorous to ourselves. BACHMAN's conclusion was that the birds are able to find their prey by the optical sense only.

DARWIN's diary relates the journey with the Beagle. When the Beagle was anchored within the mouth of the Santa Cruz, excursions were made starting from this point. On April 27 DARWIN shot a condor (*Gymnogyps gryphus*), and some remarks were made in connection with the event. One of the methods of the Chileno countrymen when catching condors was to put a carcass inside an enclosure. The birds were attracted and could not afterwards leave the enclosure, as there was not enough space to take a run, which the birds need to fly up. The Chilenos were apparently of opinion that the condors were guided by their sense of smell. The description of the conditions rather suggests, however, that it was the optical sense that guided the birds. DARWIN did not accept the Chileno opinion and made an experiment. A piece of meat was wrapped up in a paper, and this parcel was placed in the middle of a group of condors. The birds did not pay it the least attention. One condor looked at it for a moment but did not approach it. The parcel was pushed nearer and nearer to the birds, but it was all no use. No sooner was the parcel opened, however, than the birds went up to it and devoured the meat with great enthusiasm. "Under the same circumstances" DARWIN remarked, "it would have been quite impossible to have deceived a dog". DARWIN was sure that birds of prey have an extremely well developed sense of vision. He noticed, moreover, carrion-vultures (species of *Cathartes* or of *Coragyps?*) flying and hovering at such great heights, that it was hardly, if at all, possible to see them with the naked eye. It is highly improbable that anyone walking or riding on horseback would pay attention to the sky except for the part less than fifteen degrees above the horizon. One might stage an experiment and not be aware that the birds had already seen all the preparations.

NAUMANN is mentioned by SOUDEK as one of the great ornithologists who credit birds with an acute sense of smell. In his "Natural History of the birds of Germany", NAUMANN does not, either in the short anatomical description of the

sense organs of birds or in treating of the means by which they find their food, express such an opinion. Neither could I find any indication in favour of SOUDEK's comment in running through NAUMANN's twelve volumes.

RHOADS made a plea in favour of the birds' sense of smell. He observed turkey vultures (*Cathartes aura*) in New-Jersey. The carcases of a cow and a horse, which had been buried several years ago, were dug up. He could not perceive any smell, but large numbers of vultures arrived from a great distance. He draws the rather premature conclusion that the vultures possess a very acute sense of smell. He then refers to GOSSE's narrative to the effect that the bad odour of a piece of meat lying *in* a house attracted numberless vultures. When, on another occasion, a vulture coming from a great height took a piece of absolutely fresh meat, GOSSE ascribed this to the bird's sense of vision. In my opinion it is properly observed by RHOADS that the latter conclusion is not valid. Assuming that birds have an acute sense of smell they may perceive fresh meat by it as well. Moreover, RHOADS objects, against GOSSE, that in one species of birds there is never more than one well-developed sense organ. Irrespective of the validity of this presumption, RHOADS's conclusion, that birds of prey possess a poorly developed sense of vision because he once observed a behaviour that seemed to him to be in favour of the assumption that the sense of smell is very keen, is absolutely inadmissible.

REEKER communicated AUGSBURG's observation of birds eating food which he had strewn on the snow in his garden. In less than no time the whole meal had been consumed, but for one potato at which a cat had sniffed. None of the birds even came to try this potato. Yet AUGSBURG was positive about the fact that part of the birds were not yet present when the cat was abroad. He therefore assumes that the birds were prevented only by their sense of smell from pecking this potato. The visitors to his garden were: blackbirds (*Turdus* *merula*), starlings (*Sturnus vulgaris*), chaffinches (*Fringila coelebs*), titmice (*Parus sp.*), a wren (*Trochloditus trochloditus*), and sparrows (*Passer domesticus*). Only a year before, on the other hand, REEKER himself related that some birds are remarkably unaffected by bad smells. Wrens laid their eggs in evil-smelling ditches and in the corpse of a horseman. Blue titmice (*Parus coeruleus*) made a nest in the mouth of a hanged criminal. The fact that both these species were also mentioned in the above-cited communication casts a strange light on REEKER's conclusions.

RASPAIL attributes to birds a sense of smell as keen as the olfactory sense of a dog. Neither pheasants (*Phasianus*) nor partridges (*Perdrix*) will ever come under the wind of the hunter; only on the windward side do they approach him, providing he keeps very quiet. RASPAIL had a blind made on the edge of a glade where wood-pigeons (*Columba palumbus*) used to come. If he was in this shelter when the wind was from it to the pigeons, they would leave the spot and stay away for some time. If, however, the wind was in the opposite direction, the pigeons came near to his place of observation, although the tent was in a fairly exposed position. Breeding pheasants seldom leave their nests, but he observed them on dry days walking in a straight line for 180 metres to a water basin that had only just been filled. According to RASPAIL they must have been guided by the smell of the water. Partridges would walk in the snow from a great distance to the feeding place where grains of corn had been strewn, apparently attracted by the smell of the grains. A great titmouse (*Parus major*) removed a piece of Gruyère cheese from a mousetrap in the dark. Rooks (*Corvus frugilegus*), magpies (*Pica pica*), and blackbirds (*Turdus merula*) would pick larvea of *Melolontha* from the soil without ever mistaking the place of their prey. Turtle-doves (*Streptopelia turtur*) leave their eggs and do not return when the eggs have been touched by man. From all these facts RASPAIL draws his above

stated conclusion. Here again we have the drawback of mere observations without the possibility of obtaining unequivocal results. Since further checks were omitted one cannot exclude the possibility of the birds leaving the lee side of the hunter or the observer, warned by their acoustic sense. Partridges and pheasants accustomed to a feeding place may travel to it guided by their sense of vision and of orientation. It is far more probable that grubs are found by vision than by smell. The birds may discern the small movements of the soil which man is unable to see. To touch the eggs of the turtle-dove the author had to scare the bird away from its nest. Probably the bird was frightened for some time and later on perhaps judged the eggs too cold to sit on.

GILL kept a condor (*Gymnogyps gryphus*) in a cage under the open window of his working room. When he dissected a rabbit the condor, which could not see his actions, did not show any reaction so long as he was engaged with the head. The bird got excited, however, the moment he opened the abdomen.

ROUSE investigated the influence of various stimuli on the respiration of pigeons. According to the author emotional life in birds is more highly developed than in "other lower vertebrates, including dogs". Respiration is the most sensitive index to psychic reactions. The influence of some odorants was examined. Oil of bergamot and essence of lily of the valley exerted no influence. Asa foetida caused slight acceleration of respiration with a decrease in amplitude of the movements. Turpentine and ammonia accelerated respiration and increased the amplitude; sometimes a strong expiration was observed. The author himself emphasized that these reactions were probably due to the stimulating effects of these substances on the trigeminal nerve endings.

HILL was the first to make real experiments expressly designed to study the birds' sense of smell. Anatomical data failed to give him any solution of the problem; rather did they lead him astray. He rightly chose the only exact way, i.e. experiment. It is not the question whether the organ is developed or not which interests us, but whether or not there is an olfactory sense. He related the persistent myths that pigeon-fanciers let their animals find their way back to the pigeonries by greasing the latter with aniseed-oil, and that poachers lure pheasants with tincture of valerian. He staged experiments with a hen- and a cock-turkey (*Meleagris sp.*). In front of the gate of their cage two portions of seeds of the same appearance were placed. In orderless succession odorants were added to the left or the right-side one. The female always came outside first and went to the right-hand side irrespective of the position of the odorous seeds. The cock, therefore, always went to the left. Asa foetida, aniseed-oil, lavender oil, and valerianate of zinc were used as odorants. The birds never showed any difference in behaviour with regard to the odoriferous and the odourless seeds. Bread soaked in camphor solution was taken as willingly as ordinary bread. Grains of seeds were put on a sieve which was placed over odorants. At first, HILL used moderate strengths of odours, but gradually the quantities were raised until alarming amounts were given; 4 ounces of carbid in a saucer of water, bisulphide of carbon, chloroform (the hen was partially anaesthetized while eating), cyanide of potassium in diluted sulphuric acid (the prussic acid evolved was to be perceived far away in the surroundings, and the cock only just failed to die). No unusual behaviour was, however, observed towards either of these substances; the birds were not warned against the dangerous nature of any of these substances by their scent. Apart from these experiments HILL relates some observations: GUILLEMARD, in a verbal communication, gave as his opinion that vultures were not able to smell. When he had shot a wildebeest or some other game, he disembowelled it, and hid the carcase in the hole of an ant-bear. Here his game was absolutely safe from the voracity of the birds, which, however, had devoured the intestines in less than no time.

HILL does not attribute to birds any sense of smell. He makes, however, one exception. Both in view of the anatomical data and the terrestrial way of living of *Apteryx* he expects this animal to possess a well-developed sense of smell, and entertains hope that experiments may be made on this species.

The following year already BENHAM described such experiments, which he had induced R. HENRY to make on *Apteryx australis*. The food of this kiwi consists of earth-worms. It is nearly blind, and a hair-like feather tuft, moreover, prevents the bird from viewing the soil in front of its bill. Worms were put in trays filled with earth, 10 cm under the surface. The kiwi at once dug into the earth with its bill, making loud sniffling noises, so that, as BENHAM stated, it was impossible to the bird to hear the earth-worms (*sic.*). All the worms were found in a short time. Similar trays, without any worms, were not able to attract the kiwi's attention; earth that had contained worms the previous day had no attractive power either; but dead worms were sought and eaten as willingly as the live ones. From the moment the kiwi was used to eating pieces of meat, experiments with this food had the same result. Similar experiments with juice of pressed-out worms were not made. BENHAM sees sufficient indication that *Apteryx* has a sense of smell, but crucial experiments are needed.

SCHWARTZ made thorough investigations into the food preference of graminivorous singing birds. Many interesting details are given concerning the connection between food and the construction of the beak. Various kinds of seeds which might, according to shape, measurements, and breakableness, be considered as excellent food, were not taken, apparently owing to other properties. It is evident from SCHWARTZ' paper that, in deciding whether grains should be taken or not, the birds are often guided by their sense of vision. Experience (conditioned reflexes) and instinct should never be excluded. Several poisonous seeds that have neither smell nor taste to man were refused by all the birds experimented upon. Finally a group of seeds was dealt with having both scent and taste to us. Apart from the odour, the seeds he used always had either a bitter, sweet, "astringent", "acrid", or "warming" taste. This very interesting paper gives, therefore, no unequivocal results and is consequently of no use to us.

Following the literature in chronological order we come again to a description of observations rather than experiments. BEEBE first referred to the well-developed eyesight in vultures, probably representing the highest development of the power of vision of any living creature. According to this author, they find food by vision alone, and do not possess any sense of smell. Exception was made, however, for the smaller species, the black vulture (*Catharistes urubu* = *Coragyps atratus*) and the turkey vulture (*Cathartes aura septentrionalis*). Specimens of both sorts were held in captivity. After a few days' fasting a piece of tainted meat was placed under a box, while a pretence was made of placing something under two other boxes. The birds did not approach (!). Then a piece of meat was thrown on the bottom of the cage; after having eaten it the birds came to the box with the meat, attempting to find food. From this BEEBE concludes some faculty of smelling to be present in these two species. An experiment staged with so little precautions, however, arouses too much mistrust for us to agree with the conclusion drawn from it by BEEBE.

HESSE did not suppose that birds are able to get the scent of food or of their enemies ("Witterungsvermögen"), but that they are guided by their vision in their search for food. He explained this from the nature of the odorants which are all heavier than air, so that the birds do not come into contact with odorants for the greater part of their lives. This line of reasoning is rather strange; it is questionable, moreover,

whether HESSE's notion about the nature of odorants is valid (cp. NOLTE). HESSE saw a hobby (*Falco subbutio*) pecking repeatedly at a piece of sealing-wax. This was apparently mistaken for a piece of flesh; a fact which shows that the bird was guided by vision only.

STRONG was the first to make laboratory experiments, which do not suffer from the disadvantages of free field observations. In a detailed description of the habits and the behaviour of the herring gull (*Larus argentatus*), STRONG (1915) does not deal with our problem. In relating the taking of food and especially the refusal of putrid flesh, STRONG suggests, however, that this is only done by the aid of the senses of vision and taste. The publication of 1911 is the one that interests us. Useful anatomical data are given. The author is of opinion that merely observing the behaviour of birds that are offered odorants, instead of staging well-conceived experiments, is useless. He constructed a kind of maze from which the birds could go to four separate boxes. In one of these food with odorant was placed. The birds experimented upon were hybrids of white and blonde ring-doves (*Turtur alba* and *T. risorius*); the odorants used were animal-musk, violet-sachet powder, eau-de-Cologne, and oil of bergamot. When food without odorant was offered the animal went to each box in 25% of the cases, as was only to be expected. With eau-de-Cologne or with oil of bergamot the distribution of the choices was almost the same. The most promising results were obtained with violet-sachet powder; as these series, however, were too small, no value could be attached to them. In the series with oil of bergamot four pigeons were used; the box with the odorant was chosen in 37%, 31%, 36% and 47% of the cases, respectively. Although these figures go indeed beyond 25%, the conclusion drawn from them by STRONG is rather premature, for at the end of his paper he stated that experiments with ring-doves warrant the conclusion that, in some birds at least, behaviour is influenced by olfactory stimulation. In addition to his laboratory experiments STRONG gives the results of some observations. Although some simple experiments on turkey vultures (*Cathartes aura*) did not furnish any but negative results, he concludes from an open air observation that this animal is able to get the scent of its prey. Experiments with three specimens of *Apteryx mantelli*, on the other hand, yielded only negative results, although, if any sense of smell could be expected in birds, it should have been in the genus *Apteryx*. Oil of bergamot did not in the least affect two emeus (*Dromaeus*).

Feeding experiments with humming birds (*Archilochus colubris*), described by SHERMAN, do not furnish any indication in favour of a sense of smell. Solitary birds came at random to the flowers from which they obtain their nourishment or to the feeding trays, inasmuch as they were not conditioned on situations known to them. The majority of the birds, however, came to the feeding places because they were attracted by others already present. When choice was possible between molasses, molasses with vanilla, and molasses with extract of lemon, no preference was shown for either of these. No experiments were done in order to investigate the sense of smell; further conclusions cannot, therefore, be drawn.

Some remarks of O. and M. HEINROTH should be quoted here. In a chapter concerning the raven (*Corvax corax*) it was stated that the olfactory sense is not used in the search for food. It is by accident only that a piece of flesh hidden in the sand or behind obstacles, is found. But pieces of bread, or even bread-crumbs strewn between gravel or sand, are readily found, although absolutely invisible to us. In this pursuit the birds are guided only by their eyesight. Peregrine falcons (*Falco peregrinus*) accept putrid flesh as willingly as fresh. Only when in their beak is a rotten piece rejected. If a meal consisting of a mixture of fresh and tainted flesh

is offered, the falcons do not immediately swallow a morsel, as they are used to doing, but each piece is carefully examined. From the description this seems to be done rather by tasting the food than by smelling it.

It is difficult to interpret the article by NOLTE. It is known among hunters that, when duck-shooting, the bird should not be approached with the wind at the back, and this has given rise to the opinion that ducks are able to get the scent of man ("wittern"). In order to prevent this, keepers in "Vogelkojen" always take with them a pot of smouldering peat, which has been a deep-rooted custom for centuries. The fact that this custom is as old as the existence of the "Vogelkojen" is no evidence at all that it is well-founded, as the author believes. It is said that a catch without peat is impossible. In order to obtain further information on the subject the author procured admission into some "Kojen". A "Vogelkoje" consists of a pond with several curved ditches leading away from it. The banks of these ditches are planted with trees and shrubbery in order to mask the keeper (Kojemann). The far ends are fenced off with netting. The wild ducks are lured into the ditches with the aid of trained decoy-ducks whose wings have been paralysed.§) Smoking, both of cigars and pipes, is absolutely forbidden, as this is said to frighten the birds. (Why should ducks make any difference between peat and tobacco?). The author tried to obtain an answer to the following two questions: (1) Is it possible to make a catch without taking along a peat pot, and (2) is it possible when a pipe is smoked? During two visits to different "Kojen", the author walked through the "Koje", sometimes without the smouldering peat, and at other moments he smoked two different kinds of strongly smelling tobacco, either with or without taking along the pot of peat. No indications were obtained that the ducks got the scent either

§) It is interesting to note that both the German word "Vogelkoje", and the English word "decoy-duck" are derived from the Dutch "kooi".

of him or of the tobacco. The fact that the ducks in the pond all lie with their bill into the wind is only caused by the effect of the wind on their body and favoured by the triangular shape of the duck. This is, therefore, not an indication that they try to get a scent. Only once, during a third visit to still another "Koje", did the author observe that all the birds flew up at the moment that he increased the distance between himself and the keeper with the peat, thereby causing himself to be no longer shielded by the peat smoke. As far as the above-mentioned questions are concerned, an indication is, therefore, only obtained in answer to the first one. NOLTE attached much value to the fact that it was drizzling on that occasion, and brought this in relation with other observations. The decoy-ducks are fed on grains of barley cast into the water. The water in the pond is wholly opaque. (One gaines the impression that the author did not prove this fact by measurements of light-intensity at the bottom of the pond.) In finding their food the ducks, he asserts, would be guided only by chemical stimuli. Ducks are able immediately to find pieces of flesh under a 10 cm layer of snow. NOLTE is of opinion that ducks are able to perceive olfactory stimuli when the water vapour content in the air is high. On the other hand, he does not believe that the musk odour of the musk-duck (*Aromia* = *Cairina moschata*) serves as a signal to the sexual partner. NOLTE objects to HESSE's opinion that odorants are heavier than air and gives some convincing examples in support of his view. Nevertheless NOLTE does not accept the notion that birds of prey are guided in the search for food by their faculty of smelling. This is obvious, for instance, from the straight line along which the bird swoops down upon his prey. A trail of odour in the air always has a very fickle course. This is, in my opinion, also an objection to the conclusions of RASPAIL. NOLTE promised further experiments, but these have not yet been published.

An extreme view was expressed by SOUDEK who stated that

all birds are anosmatic. In experiments with pigeons not the least reaction could be observed when food with odorant was offered, as compared with their reaction to odourless food. He used alcohol, xylol, pyridine, scatol, and aniseed-oil. Only when the grains were wet with odorant would the pigeon refuse the food, and even in that case not until after having eaten some grains. Here, the sense of taste alone appears to govern the pigeon's behaviour. It proved to be possible to train pigeons to refuse seeds soaked in pyridine in favour of grains treated with aniseed-oil. In the checkings it appeared that training had been performed exclusively on optical stimuli. Experiments with drinking-water made on pigeons procured the same negative results. Choice was possible between two similar trays, one of which contained pure water and the other a 10% solution of ammonia. After a few choices the pigeon already began to hesitate and proved to have learned that there was a possibility of making a wrong choice. It was not warned, however, by any sense of smell; only by tasting the solution was the pigeon able to discern between the two trays. The odour of denatured alcohol did not prevent a pigeon from drinking it to such an amount that it died soon afterwards. Training proved to give immediate results when the ammonia was dyed with methylene blue. When, afterwards, the pure water was stained blue and the ammonia made colourless, the pigeons drank the latter solution and, again, were not warned by its odour.

A blinded young bird did not find its parents and died. A male was not aware of the female that was close by, but invisible to the male. Drinking-water experiments with partridges yielded the same results as with pigeons. Partridges did not perceive a dog, however close to them, as long as it remained invisible. Neither could any faculties of smelling be ascribed to the carrion crow (*Corvus corone*), rook (*C. frugilegus*), tawny owl (*Strix aluco*), long-eared owl (*Asio otus*), song-thrush (*Turdus philomelos*), linnet (*Acanthis* *cannabina*), goldfinch (*Carduelis carduelis*), northern bullfinch (*Pyrrhula pyrrhula*), chaffinch (*Fringilla coelebs*), and domesticated ducks (*Anas sp. domesticatus*).

A number of tainted dead fowl were hidden under grass in a place where vultures often came to eat. Although the vultures had immediately eaten all the flesh that had not been covered, they never found the fowl. Finally SOUDEK quoted the verbal communication of KARASEK to the effect that aquatic birds are not able to get the scent of food or man ("wittern").

PUSTET and BERGER concluded from their training experiments with pigeons that the results were due to the animals being guided by olfactory and gustatory stimuli, since optical differences between the two possible objects of choice were excluded. The training was performed on seeds of maize as such as against seeds soaked in diluted *tinctura spirituosa stramonii e semine*. As taste was not excluded and training, as the authors stated, was mainly established on position, the conclusion that the pigeons are able to smell the seeds is not valid.

TJUMJANZEW formed a conditioned reflex in a pigeon on a sound of 1000 vibrations per sec. The non-conditioning stimulus consisted of blowing *oleum pini* on the pigeon's face, causing it to shake its head. After 12 combinations had been given, the pigeon made the same head movements on the sound alone. It is rather questionable whether a conditioned reflex can be established in a pigeon with so small a number of combinations. But surely this has nothing to do with olfactory sense, since the same reaction would have been obtained if a current of pure air had been blown on the bird's face.

MARPLES, in investigating the factors controlling the behaviour of the ringed plover (*Charadrius hiaticula*) in respect to its eggs, found out that the bird recognizes its eggs chiefly by vision. Eggs put outside the nest and smeared with strongly smelling odorants were nevertheless taken back to

the nest by the bird, MARPLES assumes that the sense of smell is not present in this bird, or is at any rate of no importance in finding and recognizing the eggs.

In his book about birds GROEBBELS makes some remarks in connection with our problem. On page 332 he gives as his opinion that humming bird flowers are odourless, *which is to be understood from* the anosmy of their visitors. The line of reasoning is, of course, erroneous, but the author signifies that humming birds have no faculty of smelling, SCHWARZ' experiments, to which GROEBBELS refers, have already been cited from the original. On page 337 GROEBBELS gives a list of birds regularly eating various species of beetles and bugs that have a bad smell as judged by man. In my opinion this is not, however, an idication that these birds have no sense of smell. We can only conclude that, if these birds are able to perceive the odours, their appreciations are different from ours.

In a paper that is for the greater part anatomical and histological, ISHIHARA deals at some length with the physiology of the olfactory organs in birds. He repeated SOUDEK's experiments with pigeons relatively to their drinking, and obtained the same results. A parrot, moreover, that had become accustomed to drinking coffee, did not alter its behaviour when a large amount of pyridine was added. Respiration of pigeons was the same as usual after plugging up their nostrils. As it is questionable whether the inhaled air ever passes through the nasal chambers and as the birds' habit of swallowing their food does not suggest either that they smell it, the author is of the opinion that there is not much possibility of birds perceiving odours in their surroundings. He points to the possibility, however, that chemical stimuli furnished by the contents of the mouth or the gizzard may exert an influence upon the olfactory organs. Perhaps the duration of stay of the food in the gizzard is regulated with the aid of olfactory stimuli.

ZAHN obtained positive results by the method of training in various birds. Food with odorant as training stimulus was offered as against food without odorant, which had been made uneatable by quinine; on other occasions the birds were allowed to eat food without odorant, whilst they were prevented from eating of the odorous food by the quinine. (cp. Chapter 4 of the present paper in relation to the denaturation of seed). Although training failed in pigeons, jays (*Garrulus glandarius*) and a starling (*Sturnus vulgaris*), with the odorants aniseed-oil and essense of cloves, the author stated that these birds possess a sense of smell, and that the failure of training was due to the experimental arrangement. In view of my results obtained in similar experiments I suppose, on the contrary, that the positive results of ZAHN were due to the experimental arrangement and not to the sense of smell. Robins (*Erithacus rubecula*) and warblers (*Sylvia sp.*), which can smell very well, could not be trained. One may well wonder how the author was able to know that these birds have a faculty of smelling, since training on odorants failed.

Training yielded positive results in a blackbird (*Turdus merula*) on rose-oil and essence of cloves; in greenfinches (*Chloris chloris*) on the same substances; and in a blue titmouse (*Parus coeruleus*) on concentrated solution of scatol. Domesticated ducks, when trained on the odorant, walk alongside a row of six feeding boxes, only opening the box that contains food with odorant. If, however, the wind is from the boxes to the duck, it walks straight up to the correct box from a distance of $1\frac{1}{2}$ metres.

Not until 1935 was a solution of the question of the sense of smell in birds attempted with the aid of the method of conditioned reflexes. The publication of BAJANDUROW and LARIN was written in Russian, even without a summary in a western language. Since I had the opportunity of getting it translated (by Dr. A. N. DIAKONOW) I shall refer to it in

some detail. The problem posed was whether it would be possible to establish a conditioned reflex on odorants in birds, and whether an acquired reflex would remain after the removal of the hemispheres. The animal experimented upon was *Columba tartus* (?, probably a misprint for *turtur*). The bird was tied up in a jacket which was fixed to the ceiling of a small isolated room. One leg hung down freely; induction shocks applied to this leg caused retraction as a non-conditioned reflex. The extent of the leg movement served as a measure of the intensity of the reflex. As olfactory stimuli eau-de-Cologne, tincture of valerian, methyl salicylate, and oleum menthae were used. The head of the pigeon was intruduced into a glass dome into which a current of air was led. The experimenter was able to charge the air current with odorant at the moments of stimulation. The odorant was offered for 10 to 15 sec and 4 to 5 induction shocks were given during that time. This procedure was repeated 4 to 8 times a day. The odorant soon caused a reaction when offered without the pain stimuli. Before the experiment the olfactory stimulus was tested to see whether it did not give any reaction; none of the odorants used, initially caused any reaction. The reflex, having been established, met the requirements that it was extinguished unless continually seconded by the non-conditioning stimulus, and that it was soon re-established when the non-conditioning stimulus was again added; that it disappeared in alcohol anaesthesia; and that it could be differentiated. Apart from the odorant given as conditioning stimulus, a second odorant was offered during the same experimental time. This odorant was not, however, combined with the non-conditioning pain stimulus. At first the second odorant produced a conditioned reaction as readily as the first. But in the course of this experiment of differentiation the reaction to the second odorant gradually lessened, and finally only the original olfactory stimulus was followed by a conditioned leg movement. Differentiation was complete, since PAVLOW's requirement was fulfilled that the new stimulus applied at the beginning of an experimental day should not effect any reaction. The same held true, moreover, when the differentiating stimulus was given in the middle or at the end of a day; it was preceded, therefore, by a number of normal reactions to the conditioning stimulus. From the course of the formation of the conditioned reflex and the differentiation, two types of pigeons may be distinguished. In one type excitatory states predominate, in the other type inhibitions.

Pigeon No. 1 was conditioned on eau-de-Cologne. After 67 combinations the reaction was constantly obtained. When the non-conditioning stimulus was omitted for some time, the effect gradually decreased (extinction); but only a few combinations were sufficient to re-obtain the initial effect. Methyl salicylate was given as differentiation stimulus. At first it effected a reaction that equalled the reflex on eau-de-Cologne, but methyl salicylate having been given 10 times, no reaction followed. During the onset of differentiation the effect of eau-de-Cologne was deminished, but in the course of the experiment the original effect was again obtained. When afterwards other differentiating stimuli were given, they from the first gave no response. Checking experiments showed that the positive effect from the conditioning stimulus was not due either to sounds, stimulation of the conjunctiva, or such-like.

On pigeon No. 2 conditioning was effected with oleum menthae. The first conditioned reaction was already to be seen after the 20th combination, and the reflex was fixed after 25 combinations. The reflex was, therefore, established with a rather small number of combinations; differentiation, on the other hand, could only be brought about with great difficulty, and even then it was not fixed. In this pigeon checks also showed that the reflex occurred only on the olfactory stimulus.

Pigeon No. 1 is an example of the inhibited type; pigeon No. 2 of the excited or sanguine type. In 10 other pigeons conditioned reflexes were also established; they could also be classified in one or the other group.

In pigeons Nos. 1 and 2 both hemispheres were removed. Although their general state always was excellent, conditioned reflexes on olfactory stimuli could not be established any more.

Strange facts were related by SALVERDA TER LAAG from experiments with siskins (*Carduelis spinus*). Every day she gave the animals water for their bath. When the same water was given on two occasions, the siskins did not use it the second time; they did not even try it. When this refused water was filtered so that it appeared to us absolutely pure, the siskins accepted it as drinking water, but it was refused for their bathing. Staining the water did not prevent the siskins from taking a bath in it, although at first they hesitated. Solutions of scatol 1 : 4×10^5 and of pyridine 1 : 200 were accepted for drinking, but the far more diluted solutions of scatol 1 : 10^{11} and of pyridine 1 : 2×10^4 were rejected for bathing. These liquids were tasted by the siskins before they accepted or refused them for their washing. The authoress stated that the scatol and pyridine solutions are absolutely tasteless; according to her the siskins should be able to smell them. Their sense of smell, therefore, is said to be very acute.

According to WAGNER the robin (*Erithacus rubecula*) could be trained on odorants. After 4 to 6 combinations (*sic!*) the bird connects one out of two odours with a taste.

It is superfluous to deal with the literature on the subject of conditioned reflexes in birds. I will only point to the articles by TEN CATE and by BERITOW.

Chapter 2

Respiration and the sense of smell.

As is known, for instance, from ROUSE's paper respiration in birds may be altered readily by various influences. I wonder, by the way, whether or not the fact that a stimulus influences respiration can be considered as an indication that it is able to evoke a sensory perception. Small noises, movements of objects in proximity to the bird, are able slightly to increase or accelerate respiration while often no other effect on the bird is perceptible. Offering smelling substances, however, does not alter respiration, as may be seen from my experiments to be described anon, and as is stated by BAJANDUROW and LARIN. Better information about the

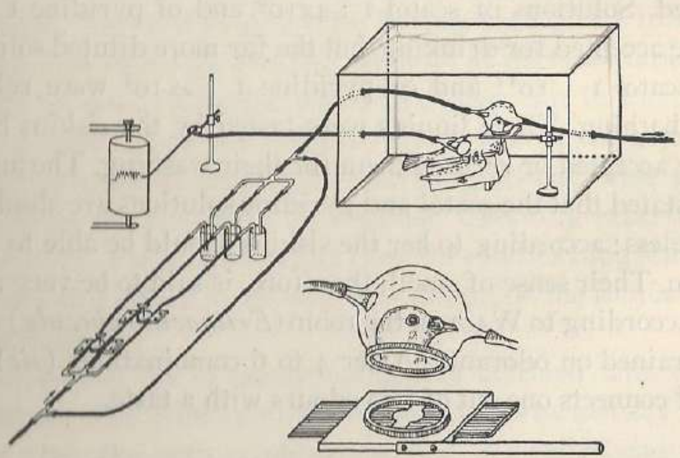

Fig. 1. Apparatus used in order to administer olfactory stimuli.

sense of smell in birds may be obtained from experiments upon the possibility of forming a conditioned reflex on an olfactory stimulus as conditioning agent. Although no adequate proof that a subject does not experience a sensory perception

on a given stimulus can possibly be furnished, yet it is highly probable that no sensory perceptibility ever exists without the possibility of forming a conditioned reflex to the stimulus.

Part of the apparatus used for administering olfactory stimuli was identical with that described by BAJANDUROW and LARIN. The devices described below were used in the greater part of my experiments (see fig. 1). The pigeon was fixed in a TRENDELENBURG-block and its head introduced into a glass dome which was fixed into a clamp. The dome was closed by brass slides adjustable around the bird's neck. The current of air flowing into the dome was directed to the back of the head, while the outflow tube was in front of the animal's face. The inflow tube was provided with a perforated tinned iron plate in order to smooth the current and disperse it throughout the dome. This current of air had to be charged with odorant at the moments of stimulation. Without special precautions this might, however, change the strength of the current and thus act as a stimulus. This was avoided as much as possible with the aid of the following device. Air from the laboratory pressure conduit was led into three tubes, each leading *via* a tap to a washing-bottle. Their outlets came together in a common final tube ending in the inflow tube of the dome. The centre bottle did on no occasion contain any odorant; during the whole experiment the current of air was conducted through this bottle, except at the moments of stimulation. Turning of one of the two taps would lead the current through one of the outer bottles, the air thus being charged with odorant which was put in either of them. In order to prevent an abrupt change in the air-current during the change-over of the circuits, these taps consisted of ebonite discs, the turning of which on an eccentric axis opened one tube to the same degree as it closed the other. Furthermore, an additional tube was shunted off the circuit before the taps and bottles, rejoining the circuit before the glass dome. Throughout an experimental session the pressure in the whole apparatus slightly exceeded the atmospheric pressure; the effect of this was that the odorant was taken up by the current without much delay, and could be smelled by the experimenter some two seconds after the tap had been turned. On the other hand the odour had faded away completely within three to five seconds after replacing the tap in its former position, again as estimated by the human olfactory sense.

Before studying the influence exerted by the odours on respiration, it was necessary to see whether the mere changing over of the circuit might affect respiration, although everything had been done to smooth the current of air as much as possible. Without the influence of external stimuli, the respiration rhythm shows slight variations; no appreciable change in this rhythm could be observed during the turning of the taps. I add figures of some experiments taken at random from the data obtained with pigeon No. 5, and which illustrate the effect of the change-over of the circuit from the centre bottle to one of the outer bottles, which did not, however, contain any odorous substance. The figures were obtained from countings of the records, respiration having been recorded by a Marey thoracograph and *tambour enrégistrateur* on a smoked drum; they represent the duration of each respiration in secs. (Table 1.)

In the same way respiration was recorded in pigeon No. 7, and the effect examined of leading the air-current for some time through one of the outer bottles, while before and afterwards the current flowed through the centre bottle, or viceversa. (Table 2.)

In most cases no variation exceeding the normal deviation is seen. These figures may serve as a background for the next experiments.

Now and then, however, an abrupt change-over could not be avoided. This was accompanied by some change in pressure. The pigeon would be somewhat scared, as was apparent

TABLE 1. Duration of 1 respiration in sec. Pigeon No. 5.

Before	During	After Change-Over
1.3—1.3—1.2—1.2—	—1.2———	—1.3—1.2—1.3
1.2—1.3—1.3—	—1.1—1.1—	—1.2—1.2—1.3
1.3—1.1—1.3—1.3—	—1.3———	—1.2—1.3—1.3—1.2
1.3—1.3—1.3—1.3—	—1.3———	—1.2—1.2
1.4—1.2—1.2—1.2—	—1.3———	—1.3—1.2—1.4
1.2—1.2—1.2—	—1.1—1.2—	—1.3—1.4
1.2—1.2—	—1.2———	—1.3—1.3—1.2—1.2
1.2—1.2—	—1.3—1.2	

TABLE 2. Duration of 5 respirations in sec. Pigeon No. 7.

Centre Bottle	Side Bottle	Centre Bottle
5.2—5.1—5.1—5.2—	—5.0—5.0—5.0—4.6—5.1—5.1—5.3—5.0—5.2—5.2———	—4.9—5.2—4.8—4.8
5.1—5.0—5.1—5.0—	—5.0—5.1—5.1—5.0—5.1—5.1—5.0—5.0—4.9—5.1—5.1—	—5.0—5.0—5.0
5.0—5.0—5.1—	—5.0—5.1—4.9—/ /—5.0—4.9—4.9—	—4.8—5.0—4.9

Side Bottle	Centre Bottle	Side Bottle
5.1—5.1—5.1—	—5.0—5.1—5.1—5.2—5.2—5.1—5.1—5.1—5.2————	—5.1—4.7—5.0—5.1
4.9—4.8—4.9—	—4.8—4.7—4.8—5.1—4.7—5.0—/ /—4.8—5.0—5.0—	—5.2—5.1—4.9—4.8
4.9—5.2—5.0—	—5.1—4.9—4.8—4.8—4.9—/ /—4.8—4.9—5.0—	—5.1—5.3—4.8

TABLE 3.

Pigeon No. 5. 18 Dec. 1936. Amyl acetate. Duration of 1 respiration in sec	
Before stimulation	1.3—1.5—1.4—1.4—1.5——
During do	——1.5—1.5—1.5—1.5—1.4—1.4—1.5—1.4—1.5—1.4—1.5—1.4—1.4—1.5—1.5——
After do	——1.4—1.4—1.5—1.4—1.6
Pigeon No. 5. 18 Dec. 1936. Amyl acetate. Duration of 3 respirations in sec	
Before stimulation	4·5—3·7—3·4—3·6—3·7—4·0—4·2—3·7——
During do	——3·8—3·6—3·7—3·8—3·9—3·6—/ /—4·3—4·3—3·7—3·8——
After do	——3·9—4·2
Before do	4·4—4·3—4·7—4·3—4·6——
During do	——4·7—4·4—4·3—4·3—4·7—4·5—4·6——
After do	——4·6—4·4—4·5—4·6—4·7
Pigeon No. 6. 15 Jan. 1937. Pyridine. Duration of 5 respirations in sec	
Before stimulation	4·9—5·2—5·2——
During do	——5·1—5·1—5·1—5·2—5·3—5·2—5·4—5·3——
After do	——5·3—5·3—5·3—5·4
Before do	5·3—5·3—5·4——
During do	——5·3—5·3—5·4—5·4—5·4—5·3—5·4——
After do	——5·3—5·3—5·4—5·4
Pigeon No. 6. 15 Jan. 1937. Amyl acetate.	
Before stimulation	5·1—5·1—5·3—5·3——
During do	——5·3—5·2—5·2—5·3—5·3—5·3—5·5—5·3——
After do	——5·5—5·5

Pigeon No. 6. 17 Jan. 1937. Pyridine.	
Before stimulation	6.5—6.6——
During do	——6.6—6.9—7.0—7.5—7.3—7.2—7.5—7.6——
After do	——7.3—7.3—7.3
Before do	5.9—6.1——
During do	——5.9—5.9—6.0—6.1—6.4—6.2—6.3—6.4——
After do	——6.5—6.4—6.4—6.5
Pigeon No. 7. 19 Jan. 1937. Amyl acetate.	
Before stimulation	4·3—4·2—4·3—4·2——
During do	——4·2—4·3—4·3—3·9—4·1—4·3—4·3—4·4—4·5—4·8—4·6—4·7—4·7—4·5—4·4——
After do	——4·5—4·5—4·8—4·7
Pigeon No. 7. 19 Jan. 1937. Pyridine.	
Before stimulation	4·9—4·9—5·1—5·3—5·4——
During do	——5·2—5·1—5·2—5·5—5·7—5·7——
After do	——5·4—5·3—5·3

TABLE 4.

Pigeon AE. 26 Oct. 1934. Pain stimulus on skin of the wing. Duration of 5 respirations in secs	
Before stimulation	4·2—4·2—4·0—3·8—3·8—3·7——
During do	——2·5—2·6—2·4—2·7—/ /—3·2—3·3—/ /—2·9—2·7—/ /—3·0—2·7——
After do	——3·5—4·1—4·1—4·3
Pigeon Q. 10 Sept. 1934. Pain stimulus on foot-sole.	
Before stimulation	7·2—7·6——
During do	——5·3—5·4——
After do	——6·9—7·7—7·3

from slightly frightened movements of the head, and respiration would be accelerated for some time. In order to obtain as adequate a check as possible on the variations of pressure, a KOENIG flame was placed in the circuit. A change of pressure sufficient to cause alterations in respiration brought about an appreciable movement of the flame. When the influence of odours on respiration was examined, all determinations during which flame movements were observed, were rejected, as being likely indications of stimulation by pressure change. Odorants used in this experiment were amyl acetate and pyridine, in amounts of from two to four drops on the bottom of one of the outer washing-bottles. In the individual experiments the intensity of the smell, as judged by the experimenter, varied over a rather wide range extending from clearly perceptible to strong. I could never observe any influence exerted by the odorants on respiration. Some figures are given in Table 3; other experiments yielded the same results, except for a few times where notable pressure differences were caused by an abrupt change-over of the circuits, as could be detected by movements of the flame.

As set forth above it was expected that, although no effect on respiration was obtained from olfactory stimuli, it should be possible to cause a conditioned change in the respiration rate by combining olfactory stimuli with such agents as might effect an alteration in respiration. Pain stimuli were applied, being most effective. A few examples of the influence of pain stimuli show this clearly enough. While respiration was recorded on the smoked drum, stimuli were applied to wings, back or feet with a needle or a pointed steel-wire. The strength of these pain stimuli was so small that no other reactions were perceptible. Yet a marked increase in respiration rate was obtained. (Table 4.)

As stimulation of the skin of the wing was most effective in the majority of cases, this was always employed in forming conditioned reflexes. The arrangement for the experiments was the same as in testing the influence exerted by olfactory stimuli on respiration, except that the KOENIG flame was now superfluous, as even variations in air pressure too small to be detected by flame movements might act as a conditioning stimulus, so that in case of succesful conditioning special attention would be necessary in that direction. As much care as possible was taken to avoid noises and other accidental stimuli, as these may all act as conditioning stimuli if repeated at each combination. This also holds true, for instance, for differences in the air current due to a change-over of the circuit. If the reflex is established, a check must therefore be taken by putting the odorant in another container and repeating the stimulus in order to ascertain whether the result was caused by the mere stimulus of alteration of the circuit or actually by the odour. In case of a positive result, moreover, the reflex should stand the check of differentiation, that is to say that, after the respiration has been conditioned on a given olfactory stimulus, another odorant having been given during the same period without non-conditioning stimulus, a reaction must be caused only by the former odorant.

Experiments were performed on pigeons Nos. 6 and 7; their conditioning stimuli were amyl acetate and pyridine, respectively. Fresh odorant was added before every experimental session in order always to attain the same strength of smell as nearly as possible as judged by the human sense of smell. Each animal had from 9 to 12 combinations a day, divided over two sessions. A session lasted from three to five quarters of an hour; in order to prevent the formation of a reflex on an experimental rhythm, the interval between two combinations was varied within a range of from 2 to 20 minutes. During these intervals only pure air flowed through the glass dome in which the pigeon's head was placed. At the moment of stimulation the tap was turned quickly but smoothly in order to prevent any change of pressure. In this way the odorant was added to the current of air, and flowed through the dome. Some 5 to 9 sec afterwards the pain stimulus was also administered, and the odorant was offered for another 20 to 30 sec, during which time the wing was pricked every now and then. After this both stimuli were stopped. In order to check the result of conditioning, a different method was followed on several occasions. The conditioning stimulus, i.e. the odour, was given for 30 to 40 sec without the pain stimulus; not until after these 40 sec was the pain stimulus given as well. Respiration was recorded before, during and after application of the odorant; the effect of conditioning was inferred from the respiration record during the time between the start of the olfactory stimulus and the delayed pain stimulus.

In pigeon No. 6 conditioning was tried on amyl acetate as odorant. The experiment was continued until 246 combinations had been administered in the course of 37 days, 27 of which were experimental days with 40 sessions. Until the 73rd combination, when the pain stimulus was delayed and respiration recorded, no influence was exerted on respiration by the olfactory stimulus. During the next period, however, when the result was checked in combinations 137, 149, 160, 161, 173, and 202, an increase of the rate of respiration was obtained each time before the start of the pain stimulus. Here it seemed that a conditioned reflex on the odorant had been established. It appeared, however, that a small leak had formed in the circuit of the amyl acetate-air mixture, so that a tiny little noise could be heard during the time when the amyl acetate was administered. The noise was so faint that it did not attract my attention until a rather advanced stage of the experiment. When it became clear to me that there was much chance that even this faint sound might act as a conditioning stimulus, the rubber tube was replaced by a fresh one, with the result that from that moment no noise was heard on leading the current of air through the

amyl acetate container. After this no acceleration or other alteration of respiration was any longer obtained. It should be borne in mind that throughout the entire duration of each session the air-current through the apparatus made a continuous and rather strong noise which was supposed to mask occasional sounds. Nevertheless the small alteration caused by the leaking tube was able to act as an acoustic stimulus, and to result in a conditioned acceleration of respiration. This fact demonstrates once more the facility with which conditioned reflexes may be formed in birds. As the acoustic stimulus was not intended, it is unknown in how many combinations it had been active. It is highly probable, however, that the leak was present only for a short time. It is the more remarkable that I never succeeded in establishing a reflex on an olfactory stimulus as conditioning agent. The repair having been effected, combinations Nos. 214, 222, 223, 224, 237, 244, and 246 were given with delayed pain stimulus, whilst respiration was recorded. In none of these any alteration could be observed. It proved to be impossible to form a conditioned reflex on respiration with odour as conditioning stimulus. The following table gives the figures of this experiment. From the records the durations of successive groups of 5 respirations were calculated in seconds. From the moment of the start of the pain stimulus respiration often became too irregular adequately to determine the durations; of these respirations, therefore, I have given the figures referring to a part of the combinations only. (Table 5.)

The surprises of the preceding experiment are absent in the results of conditioning pigeon No. 7 on pyridine. The conditioning stimulus, i.e. the odour, never produced any alteration of respiration, although conditioning was continued over a period of 37 days. Of these, 27 were experimental days, with 40 sessions and 242 combinations. In this case, too, I did not succeed in obtaining a reaction on the olfactory stimulus. Figures of some of the combinations in which the

TABLE 5. Pigeon No. 6. 29 Jan. - 8 March 1937. Conditioning stimulus amyl acetate; non-conditioning stimulus pain by pricking left wing. Duration of 5 respirations in sec.

Combination number	Before stimulation	Conditioning stimulus alone	Conditioning and non-conditioning stimulus together
73	6.7—6.8—7.0—6.7—	—6.9—6.8—6.8—6.7	
137	5.6—5.8—6.1—6.0—	—5.9—5.3—5.2—5.4—5.5—5.6 — — — — — — —	—4.1—3.8—3.8—4.1
149	5.7—5.8—6.1—6.1—	—5.4—5.4—5.3—5.4—5.5—5.6 — — — — — — —	—3.9—3.6—4.0—4.7— 4.4—4.6—4.7—4.8
160	6.1—6.2—6.3—6.1—6.2—	—6.4—5.6—5.0—5.6—6.1—6.0—5.9 — — — — — —	—4.4—3.8—4.4—4.7
161	5.2—5.3—5.2—5.1—	—5.1—4.4—4.4—4.5—4.6—4.7—4.9 — — — — — —	—4.2—3.3—4.1
167	5.0—5.0—5.1—5.0—	—5.1—5.1—4.9—4.9—4.8—5.2—5.1 — — — — — —	—3.8—4.0—3.5
173	6.7—7.1—6.8—	—6.4—6.1—5.7—5.6—5.4—5.3	
202	5.7—5.7—5.8—5.8—	—5.5—5.2—5.2—5.5—5.6—5.5	
	New tube (see text):		
214	3.3—3.3—3.5—3.5—	—3.4—3.4—3.3—3.4—3.3—3.3	
222	3.8—3.6—3.5—3.4—	—3.8—3.9—3.7—3.4—3.6—3.6—3.5—3.5	
223	3.8—3.9—3.8—	—3.9—3.9—3.8—3.7—3.7—3.8—4.1—3.9	
224	4.0—3.9—4.1—4.2—	—3.9—4.1—4.0—4.0—3.9—4.1—4.2—4.2—4.5	
237	4.4—4.6—4.7—4.6—	—4.3—4.1—4.1—4.2—4.2—4.2—4.2—3.8	
238	5.0—5.0—4.9—5.0—	—5.2—5.0—5.0—4.6—4.7—4.8—4.9—4.8	
239	4.6—4.9—4.9—5.0—	—4.9—4.9—4.8—4.3—4.6—4.4—4.6—4.8—4.7—4.4	
244	5.0—5.2—5.3—5.9—	—5.9—5.8—5.5—5.3—5.6—5.6	
246	4.1—4.1—4.1—4.3— —4.3—4.0—3.7—3.8—	—4.0—4.0—3.7—3.7—3.7—3.8—3.9—3.6—3.6— —4.2—3.9—3.8	

TABLE 5. (cont.)

In the following, last two checks, no pain stimulus was administered. Figures are given of respirations before, during, and after olfactory stimulus:

247	Before	4.3—4.1—4.1—4.2—4.0—3.9—3.9——
	During	——4.1—4.1—4.4—4.3—4.3—4.2—4.3—4.4—4.2—4.2—4.0—4.1——
	After	——4.2—4.0—4.8—4.1—4.2—4.4—4.7—4.5—4.2
248	Before	4.2—4.1—4.3—4.5—4.1—4.1——
	During	——4.4—4.5—4.7—4.6—4.4—4.7—4.7—4.1—4.3—4.4——
	After	——4.3—4.5—4.5—4.4—4.5—4.7—4.5

pain stimulus had been delayed and respiration had been recorded in order to check results, are given below.

TABLE 6. Pigeon No. 7. 29 Jan. - 6 March 1937. Conditioning stimulus pyridine; non-conditioning stimulus pain by pricking left wing. Durations of successive groups of 5 respirations in sec.

Combination number	Before stimulation	Conditioning stimulus alone	Conditioning and non-conditioning stimulus together
79	4.8—4.2—4.0—5.2—	—4.2—4.2—4.1—4.1—4.5—4.8—4.6	
146	3.7—3.6—4.0—4.0—4.0—	—4.0—4.2—4.2—4.2—3.9—4.0—4.0—4.1—	—3.3—3.1—2.9—3.2
157	4.2—4.3—4.2—4.0—	—4.1—4.1—4.1—4.2—4.1—4.3—4.3—4.0—4.1	
167	4.5—4.4—4.4—	—4.4—4.3—4.3—4.4—4.6—4.5—4.4—4.7	
220	4.1—4.1—3.7—4.1—	—4.1—4.1—4.2—4.1—4.4—4.6—4.4	
222	4.6—4.5—	—4.5—4.7—4.5—4.6—4.7—4.7—4.7	
237	3.7—3.6—3.7—	—3.7—3.7—3.6—3.8—3.6	
242	4.7—5.3—5.3—	—5.1—5.2—5.4—5.4—5.4	

Chapter 3

Conditioning of leg movements on olfactory stimuli.

It was something of a disappointment that I did not succeed in establishing a conditioned reflex on olfactory stimuli, for BAJANDUROW and LARIN did get positive results. I therefore altered my way of attack and arranged experiments in the same way as the Russian authors. The apparatus employed to administer conditioning stimuli and described in the preceding chapter could be used almost without any alterations. The only part requiring further provision was the fixation of the animal. The TRENDELENBURG-block could not be used, as one leg had to be free in order to be able to record its movements. The bird was therefore tied up in a sort of overall closed at the back, which left one or both legs free. With the strings that closed the jacket at the back the animal was fixed on a stout clamp; its head was then introduced into the glass dome. The non-conditioning stimulus consisted of a series of induction shocks applied to the skin of the leg. The best result was obtained when stimulating the tibial part of the leg after plucking the skin. Around the leg a ribbon of soft and flexible rubber was fixed by means of a small light clamp. The rubber was pierced by the U-shaped ends of two insulated copper wires; care was taken that the wires did not make contact although they were close together. The parts of the wires protruding from the inner surface were stripped of the insulation. The opposite ends of the wires were connected with the secondary coil of a DU BOIS-REYMOND inductorium. The primary circuit consisted of a 4 V accumulator, foot-switch, primary coil, and electro-magnetic signal marker. Make and break shocks were applied one immediately after another, so that both together could be considered as one stimulus. A second signal marker, with accumulator and foot-switch, indicated the duration of the olfactory stimulus. The reaction of the pigeon to each induction shock consisted of one, sometimes a few movements of the leg. This, hanging down freely at first, was quickly retracted. For the greater part these were short reactions, the leg at once regaining its former position. The strength of the stimulus was regulated each time as the need of the moment dictated. As the contact between the electrodes and the leg might easily vary at each leg movement, it is impossible to indicate the strength of stimulus in terms of coil distance. For each session the position of the secondary coil was chosen in such a way that each pair of make and break shocks just caused one leg movement. By a light ring round the foot and a fine silk thread, the leg was connected *via* a number of small pulleys with a lever which recorded the movements on a smoked drum. Each time the conditioning stimulus was first given alone for 6 to 10 sec; during the next 10 to 20 sec, 4 to 6 induction shocks were applied, the olfactory stimulus being continued.

The odorants employed were eau-de-Cologne and methyl salicylate, as BAJANDUROW and LARIN had obtained positive results with these substances after 25 combinations or, in the most unfavourable experiments, after 65 combinations.

Pigeon No. 9 received 88 times the combination of eau-de-Cologne and induction shock at the leg, in the course of 14 days, 11 of which were experimental days. Every day there was one session, in which the combination was offered 6 to 10 times. The duration of the intervals between two combinations was varied as much as possible. Starting with the 70th combination, the non-conditioning stimulus, viz., the induction shock was delayed on several occasions for from 30 to 60 sec in order to check the influence of the olfactory stimulus when applied alone. This was done either at the beginning, in the middle, or at the end of a session. The administration of eau-de-Cologne alone was never followed by a movement of the leg.

Pigeon No. 11 obtained methyl salicylate as conditioning stimulus, combined with induction shocks at the leg during 11 experimental days, distributed over 16 days, with 92 combinations. Neither was any result obtained in this experiment. Nevertheless, in both series of experiments conditioning was continued far longer than necessary according to the statements of the Russian authors.

A similar experiment was performed with a duck. Ducks are supposed to have an even better sense of smell than pigeons. If so, it ought to be comparatively easy to form a conditioned reflex on an odour. The arrangement of devices was nearly the same as in the experiments with pigeons, but for the chamber in which the head was to be enclosed. The glass dome used in the experiments with pigeons was too small for ducks. It was difficult to make a similar device for ducks owing to the large measurements that would be needed. Enclosing the head in an apparatus entirely made of metal would meet with the difficulty that the animal, being in the dark for the time of an experimental session (amounting from 60 to 110 minutes), would fall asleep. To avoid this inconvenience, part of the apparatus was made of glass, while the part with which the duck's bill could come into contact was made of brass. As in the case of the pigeons, the current of air was led in behind the duck's head and allowed to leave the container in front of the head. The inflow tube was again provided with a perforated tinned iron plate to divide and smooth out the current. If judged by the human sense of smell, the odour is at full strength in front of the duck's head 6 to 8 sec after changing over, and fades away 7 to 10 sec after the flowing through of pure air. Applying induction shocks as a pain stimulus did not give good results. I therefore resorted to pinching the web of the foot with a surgical forceps. Movements of the leg were recorded on the smoked drum. One duck which I intended to employ for these experiments made leg movements continually and was therefore of no use for this purpose. This was not a reaction to the olfactory stimulus, as might be supposed, since the movements were equally frequent before, during, and after stimulation. Duck No. 2, on the contrary, was always very quiet and only retracted its leg on being pinched. This animal received 102 combinations of methyl salicylate and pain stimulus during 9 experimental days with 14 sessions distributed over 11 days. The animal had already had 27 combinations, but then the experiment had to be interrupted for 10 days; those 27 combinations have, therefore, been left out of consideration. Although more combinations were given than would be expected to be necessary according to the statements of BAJANDUROW and LARIN, I could never obtain any leg movements when the odorant was administered without pain stimulus; briefly, I did not succeed in forming a conditioned reflex on olfactory stimuli.

According to NOLTE, birds should be able to perceive odours better in moist than in dry air. In order to check this statement I repeated the experiments with pigeons in which it was tried to obtain a conditioned reflex on olfactory stimuli by combining them with induction shocks. The apparatus was the same as that described in the beginning of the present chapter. In addition to it there was a device for saturating the air with water vapour. In order to obtain this the air of the laboratory pressure conduit was conducted through a tube branching into six pipes, each provided with an aquarium-stone and enclosed in a water basin. Saturation was nearly 100%. The moist air flowing out of the basin was led through the rest of the apparatus.

Pigeon No. 12 was conditioned on pyridine in moist air. In the course of 24 days, 15 of which were experimental days, the animal received 128 combinations in 20 sessions.

Pigeon No. 13 got 129 combinations of methyl salicylate in moist air, and pain stimulus. 20 sessions were distributed over 23 days, 16 of which were experimental days. In neither case did conditioning have any result. Never was the olfactory stimulus alone followed by any leg movement.

Chapter 4

Training experiments.

In addition to the method of conditioned reflexes, I also made use of training experiments in investigating the problem of the sense of smell in birds. Although a study of the literature on the subject of conditioned reflexes does not give any foundation to any such criticism, yet many people are of opinion that this essentially physiological way of investigating the possibilities of sensory perception does not enable the animal to unfold all its faculties in this direction. Nevertheless, the literature shows that merely observing birds in their natural conditions and surroundings does not bring us much further. One is compelled to interfere experimentally with the course of events. Although the above-mentioned objections are unfounded in my opinion, I staged the training experiments in the daily surroundings of the birds (albeit these do not represent their natural environment), instead of in the situation used in investigating conditioned reflexes.

Feeding-training experiments were performed on two parakeets and three siskins; in the course of the experiments there was now and then an opportunity for incidental feeding experiments as with the ducks.

The feeding place was connected with a roomy living-cage. It consisted of two perfectly similar compartments; their entrances were of exactly the same appearance as seen from the cage. They were situated one beside the other, along one of the short walls of the cage, symmetrically with regard to the centre of that wall, and could be reached in similar ways. Both feeding compartments were covered by a glass plate, in order to enable the experimenter to observe the behaviour of the birds. He was, however, invisible to the birds as long

as they remained in the main cage, as a large triplex screen had been made between the cage and the feeding rooms. The experimenter took the utmost care not to be heard by the birds either. Communication between the cage and feeding compartments could be made and broken by pulling up and lowering small sliding doors.

The bird was allowed to find in each compartment, every time it was let in, a tray with a few grains of seed, the amount of which was adjusted to the appetite of each object, as experience had taught. The fact that birds are always hungry was of great help in these experiments. Thus, one was able to hold two sessions each day, during which food was offered six to eight times with varying intervals. At the day's end the rest of the daily ration was put in the feeding tray, which had always been cleared by next morning, so that the birds were hungry enough again for a new experimental session to be started. The feeding-trays consisted of small crystallizing-glasses, 6 cm in diameter and 2 cm in height, on the rim of which a brass ring with 1 mm-mesh wire-netting was fitted. The grains were put on the netting. On the bottom of the tray a piece of filter-paper was placed, with a few drops of either liquid paraffin or paraffin-odorant mixture. To human judgment both trays had the same appearance. A mark was made on the odorous tray for the use of the experimenter, but in such a way as to be invisible to the bird. In order not to obtain optical training, both trays were, moreover, replaced every now and then by fresh ones.

To scare the bird away from the "wrong" tray, i.e. the odourless one, it proved of no use to mix up the food with quinine, which was the method employed by Zahn. On the one hand it was impossible to imitate the grains mixed with quinine. This would be necessary to avoid optical training, but the "right" tray must not be spoiled. On the other hand it proved, rather to my astonishment, that the birds could not possibly be deterred even by alarming amounts of quinine.

Both parakeets and siskins would eat from the grains spoiled by quinine as if nothing whatever was wrong with them. Grains were soaked in saturated solution of quinine hydrochloride and then dried. Food was even mixed with dry quinine in large quantities. In both cases the result was the same. Thus, it was necessary to shoo a bird away every time it came in the "wrong" box. After the bird had pecked two or three grains of seed from the "wrong" feeding tray, the experimenter tapped on the glass cover at a point over the bird's head. The bird had had an opportunity of perceiving the odour, and, with that, the difference between the right and wrong tray. One should not think this too drastic an interference; the punishment was regulated in such a way that without much manifestation of fear the bird turned round and left the box. After the first day of training the animals were already accustomed to choose again immediately after having been shooed off; and in the case of a right choice they would eat quite at ease. The feeding trays were changed in irregular succession in order to avoid training on sequence of experiment or on position; on the whole, however, both sides were used the same number of times for the right tray.

It is obvious that after some time of training the compartments are no longer completely inodorous, as the tray with odorant has been on both sides. True, the boxes were ventilated as much and as often as possible, so that there was at most a very faint scent to the human sense of smell. The training, therefore, if successful, would only be relative. The difference in strength of scent, however, was so great, again as judged by the human sense of smell, that it could hardly have any disturbing effect upon the experiments. Generally speaking we have to consider three possibilities. (1) The animals experimented upon possess no sense of smell. Then no difference in concentration will be of any importance. (2) They can smell moderately acutely. In this case an odour

hardly perceptible to man cannot be an effective stimulus. (3) The animals experimented upon have a well-developed sense of smell. It must then be possible to train on the difference in concentration offered. Anyhow, a positive result will be evidence of a sense of smell, provided it be out of the question that other stimuli could have caused the result. Negative findings will, on the other hand, be a strong support to the opinion that the animals do not have any sensory perception from olfactory stimuli.

Assuming birds to have a sense of smell, our expectations of training may be twofold. Firstly, the animals may already perceive from a distance, in this case from the main cage, on which side the source of the odour is situated. Then, after training, the bird can be expected immediately to choose the correct tray. Secondly, it might be presumed that the bird is only able to smell the odour when it is near the feeding tray provided with the odorous substance. Then, in case it has chosen the wrong tray, it will depart from the box after having eaten some grains, and get into the other compartment, in order to find the feeding tray with the odour on which training has been performed.

The results of the training experiments follow here. Siskin No. 1 was trained on lavender-oil and on aniseed-oil; siskin No. 2 on pyridine in low concentration, on avoiding pyridine, and on avoiding scatol; siskin No. 3 on avoiding pyridine. Both parakeets were trained on jessamine-essence, and on essence of cloves.

Training of siskin No. 1 on lavender-oil was continued during 23 days, 16 of which were experimental days, during which food was offered 180 times in conjunction with odour in the way described above. After the last day of training the feeding trays were put in the feeding compartments without any grains of seed, and the animal was allowed to choose. Without delay it entered one of the compartments, but it showed no preference for the odoriferous side at all. When the trays with seeds were put one beside the other in one feeding box, the siskin would go in and eat from the odorous tray as willingly as from the odourless one. Nor did the animal show any preference for one of the feeding trays during normal training and offering of food.

From a total of 180 possibilities of choice, the olfactory stimulus was offered 92 times on the left- and 88 on the right-hand side. Each time food was offered, the first choice was recorded. A choice was judged to be right not only when the siskin at once took the side of the odorous feeding tray, but also if, after having eaten two or three grains from the wrong tray, the animal turned round voluntarily and got into the right box. Judged in this way the siskin went 83 times into the left-, and 97 times into the right-hand compartment; out of these, 87 choices were right, and 93 wrong. In the last ten days of this experiment the choice was correct 25 times, and 31 times wrong. Spontaneous change-over from the wrong into the right box was sometimes observed; for the first time it was seen on the third day of experimenting, after 55 combinations had been administered. That we cannot consider this as a perception of olfactory stimuli by the bird was proved by the fact that the bird would go from the right into the wrong box as well. It was also often seen that the siskin left the compartment, be it either the right or the wrong one, after having eaten some grains, and returned at once to the same box. This gave the impression that the animal was accustomed to being shooed off in half the number of cases, but that it did not perceive the olfactory stimulus. Whereas training on a perceptible stimulus brings this stimulus into prominence to the animal experimented upon, it being repeated each time on the correct side only, while casual stimuli, on the other hand, are scattered both over right and wrong sides, an imperceptible stimulus will confuse the animal. This is also known from the study of

conditioned reflexes; for instance, in attempts to differentiate between stimuli with too small a difference in strength to give any discrimination in the sensory perceptions. While the circumstances seem to be the same to the animal, yet one time it is allowed to eat, but another time it is shooed off. The animal may thereby become excited and nervous. It was thus with our siskin which was often uneasy when making its first choice. Expressing the bird's actions in terms of human behaviour one would say that the siskin had only learned that the experimenter was very inconsistent, allowing it to eat as often as he forbade it. Being acquainted with the fickleness of the experimenter, the animal would go into the compartment and eat without fear; but it had learned to go to the other side every time it was shooed off. The odour proved to be no signal to the bird to find the side on which it was allowed to eat without disturbance. In fact, it went to the wrong side as often as to the right; nearly as often into the left- as into the right-hand box.

The training on lavender oil having thus been finished with, a feeding tray was offered with some drops of pyridine on the bottom, the amount of which was chosen so that it gave an unbearably bad smell to man. Nevertheless the siskin ate as quietly and undisturbedly from this tray as under normal conditions; so pyridine did not give the bird an unpleasant sensation, and probably no sensation at all.

After this *intermezzo* the siskin was fed for some days from trays provided with aniseed-oil to accustom it to this new olfactory stimulus. Then training on this smell was started, and continued during nearly two months with 30 experimental days and in total 182 combinations. Here again, the result was absolutely negative; 70 right choices as against 112 wrong ones. One should not conclude to an aversion of the siskin against aniseed-oil; the far greater number of wrong choices was caused by a temporary, obstinate preference of the bird for one side of the feeding boxes. During the first nine experimental days the siskin went 9 times to the left- and 68 times to the right-hand side, the olfactory stimulus having been on the left 46 times and on the right 31 times. Later on this preference became inverted; in the last seven days the stimulus was on the left 15 times and on the right 22 times, the siskin, however, chose the left- 31 times and the right-hand side 6 times. A similar temporary preference for one side was also observed now and then in subsequent experiments.

During the whole of this experiment the siskin made 70 right and 112 wrong choices; aniseed-oil was offered 92 times on the left- and 90 times on the right-hand side; the bird went 80 times to the left and 102 to the right. During the last seven days its choice was right 19 times and wrong 18, the olfactory stimulus having been given 15 times in the left- and 22 times in the right-hand compartment; the left-hand side was chosen first 31 times, as against 6 times for the right-hand side.

Work with the parakeets was carried out in the same way as with the siskin. At the outset both parakeets lived in one cage; during this time training was performed on jessamine essence.

Almost always it was the female which entered the feeding compartment first. Sometimes the male was driven away by the female; in most cases, however, it followed its wife submissively. For this reason those choices only were recorded that were made independently. In this series most numbers are, therefore, obtained from the female. As in the experiments with the siskin, we see again a certain preference for one side, but no results from training. In 15 sessions during 22 days the combination food-odorous substance was offered 149 times. Of this, the male let pass 3 opportunities, so that it had 146 combinations. Subtracting therefrom the choices not made independently, we get for ♀ 139; and

for ♂ 73 possibilities of choice. From the numbers it is apparent that the female had the leading part in choosing and entering the feeding compartments. Out of 139 independent choices it had 63 right and 76 wrong ones. It is evident from these numbers that training on the olfactory stimulus had failed. ♀ went 89 times to the left- and 50 times to the right-hand side. Now and then preference is shown for one side; for instance, on the 7th experimental day, ♀ went to the left box in all of the 13 combinations, although this was wrong 7 times. The bird had soon learned to go into the other box after being shooed off when the first choice was wrong. Nevertheless it now and then had remarkable fits of obstinacy. In the 26th combination, for instance, the parakeet entered the wrong box 25 times in succession and picked two or three grains of seed, although it was as often induced to go away. It seemed as if positive results were obtained on the 11th experimental day. 7 out of 8 choices were correct, the odorous tray being 4 times on the left- and as often on the right-hand side. The trays were thereupon substituted by fresh ones and these promising results were not again obtained. During these last experimental days the feeding tray with jessamine essence was put on the left side 9 times and on the right-hand side 13 times. The parakeet went to the left 16 times and to the right 6 times, making 13 mistakes and 9 right choices. The apparently positive result of the 11th day was either only accidental, as may occur with such small numbers as our daily amount of combinations, or a reaction to minute visual stimuli. Anyhow, there was, over the whole of the experiment, no question of right choosing induced by the olfactory stimulus.

As far as the male is concerned, figures are rather low, as 73 out of the total of 146 combinations had to be dropped, ♂ having entered the feeding compartment after ♀, so that one cannot be certain that this was not mere passive following. Of the other 73 the parakeet went only 9 times to the left-, and 64 times to the right-hand side. The training stimulus having been 44 times left and 29 right, the bird had made 41 wrong choices as against 32 right ones. In the male there is no indication of any result either.

The attempt at training having thus been ended, the odour was replaced by pyridine, in order to observe the behaviour of the birds. If both feeding trays were provided with pyridine, then the birds conducted themselves in quite a normal way. Although the amount of pyridine used (4 drops) not only gave a very disagreeable smell to man but even strongly irritated the mucous membranes, the birds took their food as if nothing had been altered in their daily feeding conditions. If, on the other hand, it was possible to choose between one tray provided with pyridine and another with the former training stimulus, *viz.*, jessamine essence there was a slight preference to be observed for the latter. From the results both of the training experiments and the above-mentioned feeding with two pyridine trays it is obvious that this preference is not caused by the smelling power of the jessamine but rather by its appearance. The jessamine essence was mixed with liquid paraffin just as in the training experiments immediately preceding these tests; pyridine, however, was pipetted undiluted on the filter paper on the bottom of the glass tray.

Training on essence of cloves was continued during an appreciably long time, as it seemed every now and then that training would give positive results, and I wanted to follow up every possible trail. As has already been set forth one is only justified in concluding that training has had a positive result when it is out of the question that other stimuli than the intended ones can have caused the effect. Moreover, successful training on olfactory stimuli must meet the requirement that the result is negative immediately after the olfactory nerves have been transected. It will be shown that the present experiments could not stand this test.

During the start of these experiments both parakeets lived in the same cage, as in former ones; later on they were separated. Thus, part of the results are not completely reliable, but this has been provided for by considering only those choices that were made independently. Induced choices occurred especially in the male, which at first waited for the female to make its choice, and then followed it. Later on it was often seen that the male was afraid to go into the box occupied by the female and, if it did so, it was chased away.

581 combinations were given to the female out of which it made 511 choices independently. It was observed, not explained, however, that out of the 70 induced choices the decision "right-hand side correct choice" was made after the example of the male 56 times, whilst the female made 125 independent correct choices on the right-hand side. During the whole of the experimenting time of 90 days and 54 sessions, and after deducting the 70 choices which were perhaps induced, ♀ went 331 times to the right tray and 180 to the wrong one; the odorous tray was put on the left side 252 and on the right side 259 times; ♀ went to the left-340 times and to the right-hand side 171 times. Results were more favourable during a later period of the experiment, as may be seen from the figures obtained from the 39th session to the 48th inclusive. Then 81 correct choices were obtained as against 41 wrong ones. The odorous tray was offered on the left 71 times and on the right 51 times; ♀ went 92 times to the left- and 30 times to the right-hand tray.

During the last 6 experimental days, being sessions 49 to 54 inclusive, the male was removed from the cage during the experiments. All choices made by the female were therefore independent and could be relied upon. In this period 71 correct choices were made, against only 16 wrong ones. The essence of cloves tray was put on the left 44 times and on the right 43 times; the animal went to the left- 36 times and to the right-hand side 51 times.

At the 59th combination already the ♀ spontaneously corrected a wrong choice for the first time. Later on this often happened, but as often she spoiled the right decision by leaving the tray provided with essence of cloves and entering the wrong box. Especially during the first period of this experiment the bird had a marked preference for the left side. In the first 15 sessions it went to the left 92 times, and only 18 to the right-hand side; 56 of these were correct and 54 wrong choices, whilst the training stimulus was in the left box 50 times and in the right-hand one 60 times.

After having obtained an apparently favourable result in the last six sessions, the next step was to transect the olfactory nerve fibres on both sides. A difficulty was the minuteness of the material. There is a small distance only between the nasal mucous membrane and the anterior pole of the fore-brain. Moreover, the olfactory nerve is covered in this species by a rather thick layer of pneumatised spongiosa. As the useful range is very narrow in birds greatest care must be taken in applying anaesthesia, lest this experimental animal, having become very valuable by the long time of training, should die during the operation. The brain was not injured.

The surprising fact was obtained that the result was not altered in the least. The female operated upon was offered 82 times the combination of food and essence of cloves, during 13 days with 9 sessions. The result, 75 right and 7 wrong, was nothing less than astonishing. The odorous tray was put on the left 51 times and on the right 31; the parakeet went to the left side 52 times and to the right-hand side 30 times.

These results were considered as an indication that the transection was incomplete. It was therefore repeated with the utmost care. During the next 5 days, with 5 sessions, results were 37 right as against 6 wrong choices. The olfactory stimulus was put on the left 22 times and on the right 21 times; the parakeet went into the left box 24, and into the right-hand one 19 times.

28 days later the parakeet was killed and the head introduced into a solution of formalin. Dissection and examination with the aid of a binocular microscope showed that the olfactory nerves had been thoroughly transected.

It is evident that training on the olfactory stimulus had failed; that there was, however, a positive result; that unintended differences between the odorous and odourless trays must therefore have caused this result. As such we have to consider in the first place stimulation of the trigeminus nerve fibre endings on the nasal mucous membranes or the conjunctiva. According to VON SKRAMLIK, the highest authority on this point, essence of cloves does not stimulate trigeminus nerve endings in man. Assuming that the same holds true for birds this assumption must be dropped. In the second place the possibility of optical discrimination is not to be excluded. Although the trays were now and then replaced with fresh ones, yet there remains the possible difference between the appearance of pure paraffin and the paraffin — essence of cloves mixture; a difference not visible to man. I do not see any other possibilities, unless there are factors beyond human imagination that may help birds to discriminate.

Out of 618 chances offered the male parakeet made 194 decisions possibly induced by the female. Training remained without any result. Out of 424 combinations offered in 66 sessions distributed over 128 days, the tray with essence of cloves was given on the left 182 and on the right 242 times. ♂ made 244 right and 180 wrong choices. It went to the left 64 times and to the right-hand side 360 times. Here again an obstinate preference for one side is seen. The male often entered the right-hand side apparently irrespectively of the situation of the odoriferous tray. Thus, the female, in choosing the right-hand side, often came too late to consider the choice to have been made independently. That notwithstanding the high number of right-hand side choices the male made as many as 244 correct choices is explained by the fact that the essence of cloves tray was put on the right-hand side more often than on the left (242 as against 182 times). The stimulus has been equally distributed over left and right sides, but while the male had only 33 correct choices to the left made independently, 107 left-hand choices were induced by the female. The results did not improve during training, as may be seen from the 37th to 48th session incl. The stimulus was on the left 51 times and on the right 92; the parakeet, going to the left 22 times and to the right-hand side 121, made 82 right and 61 wrong choices. From the 49th session to the 56th incl., the results were 34 correct and 14 wrong choices; but the stimulus had been on the left 12 times and on the right side 36 times. The animal went to the left 8 times and to the right-hand side 40 times. During the last days of training the parakeet made nearly as many right as wrong choices; session 57 to 66 inclusive: 46 correct as against 51 wrong. The odorous tray had been on the right side 37 and on the left 60 times; the animal went to the left feeding tray 17, and to the right-hand one 80 times.

After these training experiments some tests were made with other smelling substances. As only dissection could reveal whether the olfactory nerves had really been transected, the ♀ was also used in these tests. As stated above, the five days following the operation were the last days of training. Immediately after the last training day, feeding trays were offered to the female, but without any smelling substance. Now, one would expect, if training had been effective, that the animal would hesitate or even refuse to eat from trays unlike the one on which training had been performed. In point of fact the female tried both feeding trays for some time, but refused to eat from them. We may conclude from this how much care should be exercised in interpreting "positive" results: the animal could not possibly smell, as

both olfactory nerves proved, on post-mortem examination, to have been completely severed.

Evidently other factors than olfactory ones were active here. Eventually some smelling substances were offered alternately in one of the feeding trays, while the other had been treated in the usual way with essence of cloves. Should these substances give an olfactory sensation, then there was the chance that this would be reflected in the behaviour of the birds. Both male and female reacted in quite the same way, which gives us an opportunity to deal with them both together, although tests were done with the animals separately. The substances used were: aniseed-oil (strong smell), citral (strong), lavender oil (strong); phenol (str.), xylol (str.), toluene (str.), benzene (very faint). The quantities administered were such as to cause a sensation in man as stated between brackets. The series is divided into two parts; the former consisting of substances of which it is known that they stimulate only the olfactory nerve endings in man, the latter stimulating the trigeminus nerve endings also. No departure from the former behaviour could be observed with either group. Whether the test substance was chosen or the essence of cloves depended upon individual preference for left- or right-hand side. If the new substance was selected, then the bird would eat as if the situation had not altered in the least. An effect was observed, on the other hand, when ether, chloroform, or benzene (all in moderate quantities) were used. Either at once, on entering the feeding compartment, or while eating the first grain of seed, the bird was noticeably alarmed, would make frightened movements with its head, ruffled its feathers, and would leave the box to enter the other compartment and quietly eat the seeds lying over the essence of cloves. Then the bird sometimes tried once more to eat from the tray it had first rejected, but only with a similar result as the first time. On benzene especially this reaction was to be observed, this being the more remarkable as it was offered in a concentration which was not at all disagreeable to man, and which, moreover, gave absolutely the same impression to man as toluene, both as regards its reaction on the olfactory nerve and on the n. trigeminus. Now we have seen that toluene gave no reaction at all, either in the normal male, or in the female with transected olfactory nerves. From the fact that reactions were absolutely the same in the sound male and in the female operated upon, and from the nature of the substances used (those giving a positive result stimulating both olfactory and trigeminus nerve endings in man), it follows that the reactions observed in some cases are due only to stimulating effects to the trigeminus endings. Finally I would point once more to the remarkable facts, first, that pyridine, which causes so strong a sensation in man, causes no reaction whatever either in the siskin or in the parakeets, and secondly that, whereas to man there is hardly a difference, if at all, in the sensations obtained from toluene and benzene, yet the former gives no reaction whatever in the birds.

As we have already seen when reviewing the literature upon the subject, SALVERDA TER LAAG, in her investigations into the drinking and washing habits of birds, came to the opinion that siskins are very fastidious in the choice of their washing water. Although solutions of 0.5% pyridine and 2.5×10^{-5}% scatol in water were accepted for drinking use, the birds refused far more diluted solutions (5×10^{-3}% pyridine, and 10^{-9}% scatol) for washing. The discernment of those very low concentrations, going beyond the discrimination of odours in man, presumes a highly developed sense of smell in birds. It appeared to me of great importance to apply the same substances in the training experiments. For this purpose the same species of bird was employed as used by SALVERDA TER LAAG, *viz.*, siskins. After the birds had learned to come and find their food on the

feeding trays in the feeding compartments, one of the trays was filled with 10 cc pyridine solution, the other being filled with the same amount of pure water. Both siskins would eat on either side with the same appetite, not showing the least confusion or aversion against the pyridine odour.

In siskin No. 2 training was performed in such a way that the animal was allowed to choose food over a 1 : 100,000 pyridine solution, but was shooed off on the side of the pure water after having eaten one or two grains of seed. Again the feeding trays were changed every now and then in an irregular way. In less then a day the bird had learned to leave the wrong box at once after being shooed off, when trying to eat from the grains over pure water, and to go immediately into the other box, in order to eat the grains lying over the training stimulus. In the course of this experimental series the direct way from the cage to the feeding tray was blocked by small screens so that the bird could not see the trays from a distance. It could only reach them by making a detour around the screen. All this was done in order to prevent the bird as much as possible from choosing by means of optical discrimination. It was amazing in how short a time the bird had learned to find its food, although this could not be seen. Siskins are marvellous objects for training experiments, as they are able to acquire a habit in a very short time, and evidently on all sorts of stimuli. This should be borne in mind in view of the negative results of training on olfactory stimuli.

Training was performed during 18 days, 14 of which were experimental days with 21 sessions. In 214 combinations the smelling tray was placed on the right-hand side 107 times, and as often on the left. The result, 112 correct choices as against 102 wrong ones, shows the absolute failure of the training. As we have already seen before in other birds, the siskin, too, showed a clear preference for one side irrespective of the site of the training stimulus. The bird went to the left 77 times and to the right-hand side 137 times. The figures for the last five experimental days run as follows: 114 combinations, with the training stimulus on the right 58, and on the left 56 times. The bird made 59 correct choices and 55 wrong ones, going to the left side 35, and to the right-hand side 79 times.

This training having failed, the set-up was altered in such a way that the animal was forbidden to eat from grains of seed lying over a 1 : 1000 pyridine solution, whilst it was allowed to eat at the other side from a tray with grains over pure water. If I did not shoo it off, the siskin would eat with undisturbed appetite from the food over the rather high concentration of smelling substance and without any sign of being startled. This fact is in amazing discordance with the observations of SALVERDA TER LAAG. The bird was, however, chased away every time it tried to eat here and it had already learned in the previous experiment to go at once into the opposite box. Over a period of 15 days with 16 sessions in 12 experimenting days, training was performed with 193 combinations. The odourless tray was placed on the left 96 times and on the right 97 times. The bird went to the right-hand side 60 times and no less than 133 times to the left. It should be borne in mind that in the previous experimental series the same animal showed an avowed preference for the *right*-hand side. It is not supposed that this has anything to do with smell. In another bird, siskin No. 1, a similar change-over of its preference was seen during one and the same experiment. I am at a loss to account for this peculiar behaviour. Again the result of the training was negative, for as against 91 correct choices there were 102 wrong ones. Nor could any improvement be observed during the last five days, when the results were: 41 correct choices as against 42 wrong ones. The training stimulus was put on the right 41, and on the left 42 times; the animal went to the right-hand side 21, and to the left 62 times.

Finally, this bird was trained to avoid food over 1 : 1000 scatol solution §). As in the case with pyridine the bird did not show any hesitation in eating food over a scatol solution. Neither could training make the bird discriminate between the scatol and the odourless tray. Training was continued during 12 experimental days (13 days) with 15 sessions and 134 combinations. The distribution of the odourless food over right and left sides was 69 to 65, respectively. 62 choices out of a total of 134 were correct. The animal went to the right-hand side 77, and to the left 57 times. Results did not improve during training; during the last five days 23 out of 56 choices were correct.

Siskin No. 3 was trained to avoid food combined with a 1 : 1000 pyridine solution, the alternative being grains of seed offered over pure water. Eating from the latter was regarded as the correct choice, while the bird was chased off if it tried to eat from the odoriferous tray. As in the other experiments training remained without any result, the numbers of correct and wrong choices being hardly different. In a period of 11 days (10 experimental days with 16 sessions), 136 combinations were offered. The odourless tray, being the training stimulus, had been on the left 69 and on the right side 67 times. 73 were correct choices, as against 63 wrong ones; the siskin went to the left 58, and to the right-hand side 78 times. For the last 5 experimental days with 8 sessions the figures were 44 correct and 31 wrong choices. The training stimulus was on the right 36, and on the left 39 times, while the siskin came to the left- and right-hand sides 22 and 53 times, respectively.

The data obtained in training experiment with siskins and parakeets are tabulated below.

§) The scatol experiment with siskin No 2 was performed in our laboratory by Miss C. OUWEHAND.

TABLE 7

Bird	Training stimulus	TOTAL Number of choices	Stimulus L	Stimulus R	Choice L	Choice R	Correct	%	Wrong	%	LAST DAYS Number of choices	Stimulus L	Stimulus R	Choice L	Choice R	Correct	%	Wrong	%
Siskin No. 1	Lavender-oil	180	92	88	83	97	87	48	93	52	56	28	28	33	23	25	45	31	55
	Aniseed-oil	182	92	90	80	102	70	38	112	62	37	15	22	31	6	19	51	18	49
		see text																	
Siskin No. 2	Pyridine 1 : 100,000	214	107	107	77	137	112	52	102	48	114	56	58	35	79	59	52	55	48
	Avoiding pyridine 1 : 1000	193	97	96	133	60	91	47	102	53	83	42	41	62	21	41	49	42	51
	Avoiding scatol 1 : 1000	134	65	69	57	77	62	46	72	54	56	25	31	26	30	23	41	33	59
Siskin No. 3	Avoiding pyridine 1 : 1000	136	69	67	58	78	73	54	63	46	75	39	36	22	53	44	59	31	41
Parakeet ♀	Jessamine essence	139	65	74	89	50	63	45	76	55	22	9	13	16	6	9	41	13	59
Parakeet ♂	Jessamine essence	73	44	29	9	64	32	44	41	56	18	13	5	2	17	7	39	11	61
Parakeet ♀	Essence of cloves	511 } see text																	
Parakeet ♂	Essence of cloves	424 }																	

Chapter 5

Feeding experiments with odorant food.

Besides investigating conditioned reflexes and the effect of training I made observations on ducks during feeding. As I used odorous food, it could be expected that after some time the birds would be guided by the odour in their attempts to find their food. There is but little difference between this method and the training, since both methods are based on learning. The main difference lies in the fact that no choice can be made in the feeding experiments. Also in the formation of a conditioned reflex learning is the principal factor; when using this method the experimenter is able to control conditions better than with the other ones. As, on the other hand, many psychologists are of the opinion that it is not correct to study the reactions of an animal in the unnatural conditions of the laboratory experiment, I have used the other methods as well, even though, in my opinion, the objections raised by these psychologists carry but little weight. The results of these investigations may be found in the previous and the present chapter.

Two ducks had been fed with fish-meal during a long time. This food has a strong scent, clearly perceptible to man at a few yards' distance, especially when mixed with hot water. After this had been their only food for ten days, both ducks were blindfolded with sticking plaster. In the beginning the animals were much annoyed by the bandage, but after half an hour or so they had got accustomed to it and would walk round in search of their food, for they were very hungry. They had been placed in a room at some distance from a tray with their ordinary food, *viz.*, the strongly smelling fish-meal. Their behaviour showed clearly that the ani-

mals were extremely hungry. Nevertheless they did not succeed in finding the feeding tray. They searched and felt about the floor with their bill, their necks stretched and their heads protruding. Not the least influence was exerted by the tray of food. Even when it was placed close to the ducks they did not pay the least attention to it. Nor did either animal eat from the fish-meal when the tray was placed under its very head. But no sooner did I touch the duck's bill with the edge of the tray than the animal started eating gluttonously. When it had been eating for some moments the tray was taken away. The duck at once tried to find the food, walking round and making gobbling movements everywhere, and groping about on the floor with its bill. The fact that the searching was not at all guided by the olfactory sense was most clear when the duck went in the direction of the feeding tray and, whilst seeking and feeling about, walked past the food without paying it the slightest attention. Feeding with this smelling food was continued during two months without any other food being given; but after this period the result of similar checks was absolutely negative.

From these tests the conclusion may be drawn that the animal needs its vision in its search for food, and that olfactory stimuli are of no importance. The smelling food had always been given in a white enamelled tray. When I entered the duck-park with this tray at the usual feeding-time, the ducks came in my direction and stood waiting at a distance to come up to the food when I should withdraw. They acted in quite the same way when the usual tray was filled with sand and water, this mixture having the same appearance as the fish-meal. Even the empty tray had the same attraction for the ducks. If, however, the tray was covered for the greater part with paper or boards, in order to make it invisible while the scent of the food was perceptible as well as ever, the animals did not pay the least attention to the food. The same was observed when food was put in an unusual tray. I employed a black tray of an uncommon shape and an orange tray of the normal shape. It was not until a few days afterwards that the ducks found out that such a strange tray might contain the normal food. It was probably by investigating ever attainable object that food was found at last. Nor was it immediately after coming up to the tray that the ducks discovered the food. Only by picking accidentally at the edge of the tray did they find it. It was enough to put the usual white tray in the park to attract the ducks immediately, irrespective of whether it was filled with food or not. If empty, they went away at once after having looked at what was offered. If the tray was filled with sand and water the ducks tried to eat at several repetitions, apparently attracted by the visual similarity of this stuff and their ordinary food. These observations also indicate that food is found mainly by optical discrimination, and that the olfactory sense does not play any part.

In order totally to exclude this optical orientation and to give a fair chance to any possible olfactory discrimination, the eyes were removed. In duck No. 2 both eyeballs were completely removed in deep ether anaesthesia, which was continued with an ether and alcohol mixture. The eyelids were sewn together and a pressure bandage was applied. In duck No. 1 the cornea was removed at both sides and the eyeball spooned clean. Here, too, the eyelids were sewn and a pressure bandage fixed. Some hours after the operation the ducks were walking in the cage feeling their way with the end of their bill. During the first time following the operation they were extremely nervous and behaved as if in great rage every time someone came in their neighbourhood. For the greater part of the time the ducks were sitting quietly in their cage. Apparently when the animals were hungry, they walked cautiously to and fro, their necks stretched out and their heads protruding. When touching an obstacle with their bill the ducks would withdraw and

remain motionless for some time, afterwards to resume their searching walk. In many cases touching an obstacle would be followed by eating movements and groping around the object, under continuous gobbling movements.

Immediately after the operation both ducks were fed once a day with a mixture of fish-meal and barley in warm water. Food was offered in an enamelled tray about 20 cm in diameter, which was covered for one-half by a board with filter paper in such a way that the filter paper was just in front of the nostrils if the duck put its bill into the tray. The filter paper was provided with a large amount of odorant. Both ducks were fed in this way during two months. Duck No. 1 was fed with pyridine on the tray and duck No. 2 got amyl acetate as an odorant. Judged by the human sense of smell, the odour was very strong at a distance of two yards, and still perceptible at two or three times that distance. One might expect, that, if the odour could be perceived by the animals every time they ate from their daily food, they would be guided by the odorant in finding the food, the more so as, apart from the general cutaneous sense which is not of much use in this case, the possible sense of smell was the only way of finding the food, the sense of vision having been eliminated. During the latter half of the experiment food was given now and then in small amounts in order that the animal should be very hungry the next day and anxious to get its food. Each duck was then placed in a separate room where it started immediately to seek food. Then the feeding tray with the odorant was placed on the floor, where air currents caused a sufficient spreading of the odorant for it to become perceptible throughout the whole room. The scent was, however, not uniform through the whole space. Introducing the odoriferous tray into the room did not affect the duck's behaviour in the least. It continued its random walking and searching for food, not paying the least attention to the strong scent. The blind duck would rarely walk a long stretch in a straight line. Thus, it was observed now and then that the animal walked for some moments in the direction of the odour, but it always changed its direction before reaching the tray. On several occasions a duck passed hard by the tray, which, however, had no attraction for the animal. It was not even any use to bring the tray directly under the animal's head. Only when a duck accidentally touched the edge of the tray, be it in the course of its peregrinations or because I put the tray against the animal's bill or chest, it would at once start eating with so much fervour that it was obvious that the duck was very hungry and anxious to get its food. Even after 44 days (with 44 experimental days) no reaction was obtained.

Once both ducks were fed from a tray provided with methyl salicylate instead of the odorant to which they were used. The odour of methyl salicylate differs so much from both pyridine and amyl acetate to the human sense of smell that it is hardly plausible that any animal able to smell would get the same perception from both. One would expect that, assuming the duck to be able to smell the odour daily offered with its food, the animal would at least be confused if food was given with so different an odorant. This was not so; the ducks ate from the food with methyl salicylate as normally as always and did not show in the least a behaviour that could be interpreted as a reaction to olfactory perception.

All these feeding experiments did not furnish a single argument for crediting the birds with any sense of smell.

Chapter 6

Conditioned gastric juice secretion in ducks.

In five ducks with a fistula in the pars glandularis of the stomach or *proventriculus*, I tried to condition the gastric juice secretion on olfactory stimuli. A silver cannula was introduced into the left side of the *proventriculus*, slightly ventrally. The inner and outer flanges of the cannula were adjusted to the shape of the stomach and the body wall. From the inner flange a small sector was removed in order to be able to insert the cannula into as small an opening in the gastric wall as possible. The cannula was fixed with a tobacco-pouch suture and a final stitch through the serosa. Its distal end was fixed between the last rib and the last but one, slightly ventrally to the joint between the vertebral and sternal parts. A piece of rubber was put between the skin and the outer flange in order to prevent irritation of the skin. The opening was closed with a small cork; it was necessary to cut off the protruding part, because of the attempts of the duck to pull it out with its bill.

Owing to the necessity of combining the odour serving as a conditioning stimulus with the non-conditioning stimulus of eating, the apparatus employed in the experiments described in Chapters 2 and 3 could not be applied. The head had to be free in order to enable the duck to eat; but at the same time a current of air charged with odorant had to be directed to the nostrils. As a sudden current of air would give a stimulus which might set up a conditioned gastric juice secretion, it was necessary to expose the animal to a constant current of pure air, to which at the moments of stimulation the odorous substance was added. Instead of to the dome into which the animal's head was introduced, the current was led through a small funnel to the duck's face. The outer end of the funnel was provided with a small-mesh wire netting in order to smooth the current. Over the duck's head a large funnel was fixed, connected with a suction pump to remove the odour from the surroundings as much as possible. The relatively small effect of this procedure was of no importance to the experiments, as the air-current was directed straight into the duck's face, so that, immediately after stopping the administration of the odorant, fresh air was given in large quantities. §)

The duck was fixed in a kind of overall, tied up at the back and leaving the opening of the cannula free. This jacket was fixed in a clamp. In some experiments a box, consisting of two compartments, one on top of the other, was used. In the upper compartment the duck was placed in an almost natural sitting posture. The neck and head protruded through an opening made in one of the short sides, which was bevelled in order to leave the head free. A small tube fastened into the opening of the cannula during the experimental session and provided with a dripping top led into the lower part, where the dripping could be observed. In this way, however, it was often very difficult to observe the falling drops of gastric juice, owing to the animal's movements. This method was, therefore, soon abandoned.

One can never avoid some unnaturalness in the position of an experimental animal when it has to be fixed. This holds true especially in birds, which may move away not only in the horizontal plane but have also the third dimension at their disposal for escape; they must, therefore, be fixed

§) Originally it was planned to destroy the odorous substance by ultra-violet rays as described by ZWAARDEMAKER. This, however, proved of no effect. A small drop of pyridine on the bottom of a large glass aquarium was irradiated during a quarter of an hour, but afterwards the odour of pyridine was as strong as in the beginning. Although, according to ZWAARDEMAKER, pyridine would in this way be destroyed and made inodorous very quickly, this procedure was therefore of no use to us.

very well. Thus, it is admitted that the position of the animal in my experiments is not that of a duck eating its food in the open air. Yet, apparently, this fact is not of great importance. Every day during an experimental session, the animal is in the same position again and again; thus, a habituation will result and this fact cannot be held responsible for a failure of conditioning on olfactory stimuli. This is proved, moreover, in the experiments with other conditioning stimuli where positive results, not at all inhibited by the way of fixing the animal, were obtained.

In all experiments the bird was separated from the observer by a triplex screen, so that the only thing the animal could see was the observer's hand with the feeding tray when the non-conditioning stimulus was given. No special precautions were taken to avoid extraneous noises, which, in consequence, "masked" any sound caused by the experimental procedure.

A serious difficulty was encountered in the registration of the gastric juice secretion. It was impossible to construct a device reacting fast enough to record each drop. The dripping top made the drops extremely small. In moments of augmented secretion the rate of dripping would be too high to obtain a separate recording of each drop. The alternative was an electro-magnetic recorder operated by the observer. Each time a drop fell the observer pressed a key. As he had to keep both his hands free in order to be able to administer the food and to regulate the kymograph, the key was arranged as a foot-switch. After a short training it was possible to record every drop accurately.

I will first describe the experiments in which it was attempted to condition the gastric juice secretion on olfactory stimuli, and then proceed to the subject of conditioning on other stimuli.

One month after the operation in which the cannula was fixed into the *proventriculus*, duck No. 4 was placed daily in the experimental position and fed every now and then during one or two hours. It had its total daily amount of food in this way in order to establish as quickly as possible a habituation to the situation. This having been achieved, the experiment proper was started. Some dry scatol was put on the bottom of one of the outer washing-bottles. The smell of the outflowing air was very strong, as judged by the observer. It was the more remarkable that even the first time of administration there was not the least orientation reaction to be seen in the duck. Every experimental day the animal was fixed in the apparatus and left alone for 15 to 35 minutes. During a further $\frac{1}{2}$ - $1\frac{1}{2}$ hours six combinations were given at irregular intervals. Each time the conditioning stimulus was first administered alone during 10 to 15 sec; the following 10 to 20 sec food was given; during this time of feeding the administration of odorant was continued. To give an idea of the daily routine the data of the 15th experimental day are shown in Table 8.

The experimental series was continued during 36 experimental days, distributed over 46 days, and with 181 combinations.

About once a week, the gastric secretion was recorded. The conditioning stimulus was given alone, without feeding. Before, during, and after stimulation each drop falling out of the cannula was marked on the smoked drum. The cannula was opened some time before the beginning of the registration and provided with the dripping top.

Already after a few days' experimenting, conditioned gastric juice secretion was obtained on showing food. The record of 26 Nov. gives the results after the 16th experimental day and after a total of 87 combinations (fig. 2). Signal c d denotes the period of 45 sec during which food was shown in the same way as usual, the only difference being that the duck was prevented from eating of it. A

TABLE 8. Fixation of the animal 11.30 a.m.

Combination number	Time	Conditioning stimulus alone, during	Conditioning and non-conditioning stimulus together, during
77	11,50 a.m.	10 sec	15 sec
78	11,58	10	25
79	12,12 p.m.	15	15
80	12,25	10	20
81	12,28	10	20
82	12,32	10	40 till apparent satiation

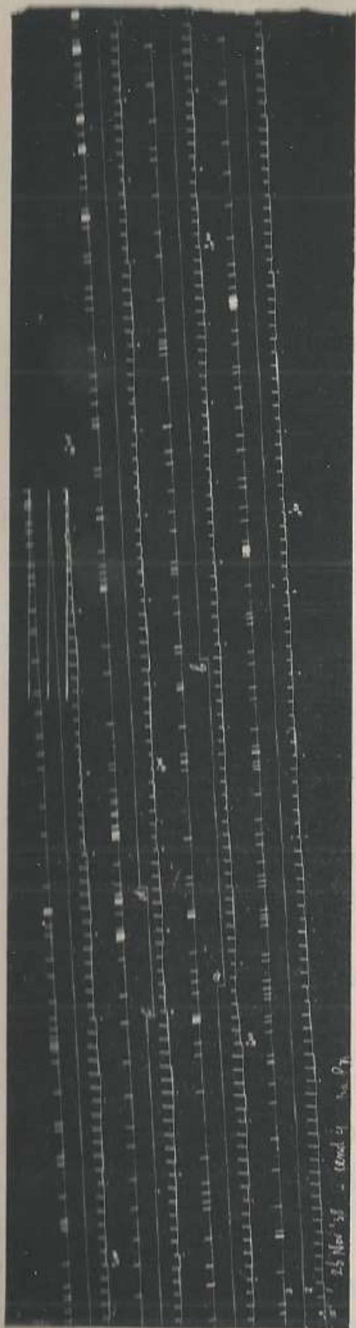

Fig. 2. Records are to be read from left to right and from bottom to top. 1. Time in 5 sec. 2. Signal of stimulus. 3. Gastric juice secretion. Duck No. 4; gastric secretion after 87 combinations of odorant and food, *a b* olfactory stimulus; no reaction, *c d* showing food; increased secretion.

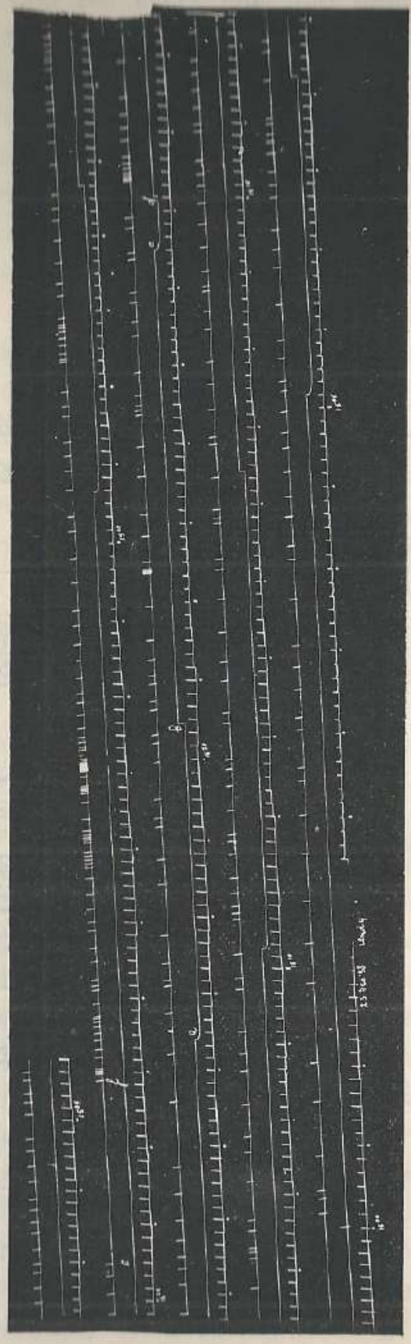

Fig. 3. Duck No. 4 after 181 combinations. Signal without figures denotes the olfactory stimulus. *a b, c d,* and *e f* showing food. Cp. text and caption of fig. 2.

marked conditioned secretion was already observed 25 sec after the beginning of the conditioning stimulus (showing of food). Table 9 gives the number of drops in each period of 30 sec. The increased secretion on this optical stimulus, continuing for several minutes, is shown both in the table and in the record. On the other hand, gastric juice secretion on the scatol stimulus was observed on seven days distributed regularly over the whole experimental series. On no occasion was a definite increase of secretion observed, although conditioning was continued during 181 combinations.

The results of some of the recordings will now be given. 23 Dec. was the last experimental day (fig. 3). As shown by the signal in the record, scatol was given at 3,5 p.m. and again at 3,10 p.m. No increase of continuous gastric secretion is seen at either time. A slight reaction is seen upon food being shown at some distance, under a glass plate. But to feed the animal in the normal way, the experimenter had to leave his recording apparatus. Thus, when food was shown in the normal way at 3,25 p.m., the recording was interrupted for 70 sec. A very distinct conditioned secretion resulted. But when scatol was again given five minutes afterwards no reaction was obtained at all. The occurrence of a conditioned reflex on the optical stimuli proves that conditioned gastric juice secretion can be developed in birds. Nevertheless no reaction could be obtained on the scent of scatol, not even after 181 combinations. So, one is forced to conclude that this olfactory stimulus, however strong to man, does not arouse any sensory perception in the duck.

Another example is reproduced in fig. 4, recorded after the 22nd experimental day, when 111 combinations had been administered. The bird was fixed at 9,40 a.m. and the cannula opened. Secretion was recorded from 10,25 till 10,40 a.m. At 10,31 scatol was offered for 120 sec (ab). No alteration in the amount of gastric juice secreted could be observed.

Fig. 4. Duck No. 4. Gastric secretion after 111 combinations. Scatol stimulus during *a b*.

Fig. 5. Gastric secretion in duck No. 7 after 79 combinations of pyridine and food. Olfactory stimulus during signal (12,23 until 12,27).

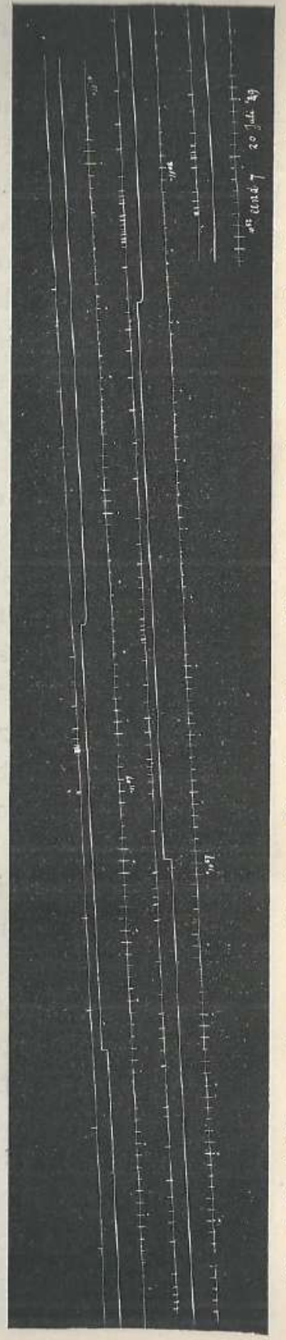

Fig. 6. Duck No. 7; after 212 combinations. Elevation of the 2nd line denotes the time during which pyridine was administered.

In duck No. 7 conditioning was started a month and a half after the cannula had been introduced into the *proventriculus*. During conditioning, and in the experiments in which the influence of the conditioning stimulus was tested and the number of drops registered, the animal was placed in the box as described above. It goes without saying that the bird was put in the experimental position about half an hour before beginning each experiment, in order to ensure accommodation to the surroundings. It is often seen that the quantity of gastric juice secreted on various days is not the same for the same length of time. But as the quantities per minute in each separate experiment are compared before, during, and after stimulation, this fact is of no importance.

In this duck I tried to form a conditioned reflex on the smell of pyridine. 50 cc pyridine solution 1 : 1000 was put in one of the outer washing-bottles. The bottle in the centre contained 50 cc pure water. The experiment was continued during 32 experimental days; the number of combinations of feeding and olfactory stimulus of pyridine was 244. In the test following the last day of conditioning there was no increase of the amount of gastric juice per min when pyridine odour was given for 240 sec. In the course of this experiment gastric secretion was apparently somewhat inhibited, as the amount of gastric juice per min was rather small. On the other hand it was observed on several occasions that an effective stimulus, such as an acoustical or optical one, is able to cause abundant secretion in such a case. The failure of pyridine to bring about increased secretion is, therefore, an indication that the pyridine did not act as a conditioning stimulus. The same results were obtained, moreover, after 10 experimental days, with 79 combinations (fig. 5), and 27 sessions with 212 combinations (fig. 6), respectively. In both tests the average number of drops of gastric juice was not altered during and after the administration of pyridine, as compared with before.

Toluene was applied as stimulus in conditioning ducks Nos. 8 and 10. An amount of 10 cc toluene, together with 40 cc water, was put in one of the outer washing bottles. Toluene does not mix with water; but when the air-current is directed through the toluene container, the air first bubbles through the water, and after that through the toluene; thus, the air flowing out of the funnel in front of the duck's face is charged with toluene, and has a strong smell, again as judged by man.

Duck No. 8 obtained, during 27 experimental days, 202 combinations in all. Each day 6 combinations of toluene scent and feeding were given in the course of approximately one hour. The intervals between feeding times were varied as much as possible, in order to avoid the animal getting accustomed to a fixed regularity. Even after 202 combinations had been administered no increase of gastric secretion could be seen when toluene odour was given without the non-conditioning stimulus, as is shown in table 9 (see fig. 7).

Neither did the experiment with duck No. 10 give more than a negative result. Conditioning on the scent of toluene was tried in 331 combinations of feeding and odour. Often two groups of six combinations were given in one day. Thus, during 33 experimental days, the experiments were performed in 52 sessions. Records of gastric secretion and tabulations show that there is no change in the amount of drops secreted during and after the administration of the odour, not even after conditioning had been continued during more than 300 combinations (see figs. 8 and 9).

In duck No. 9 I endeavoured to form a conditioned reflex of the gastric juice secretion on the scent of aniseed-oil. Ten days after the cannula had been introduced into the stomach the experiments were started. Every day some drops of aniseed-oil were added to the water in one of the outer washing bottles. The quantity of oil was regulated so that

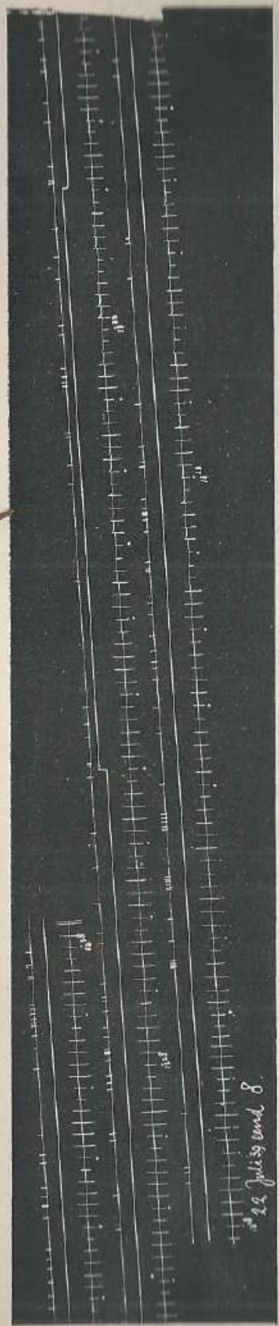

Fig. 7. Duck No. 8; after 202 combinations. During signal toluene was given.

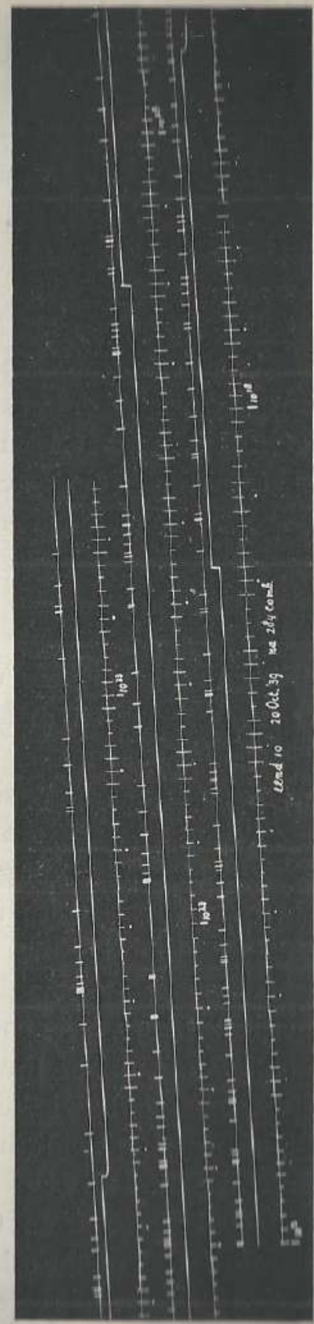

Fig. 8. Gastric secretion in duck No. 10. After 284 combinations of toluene and food.

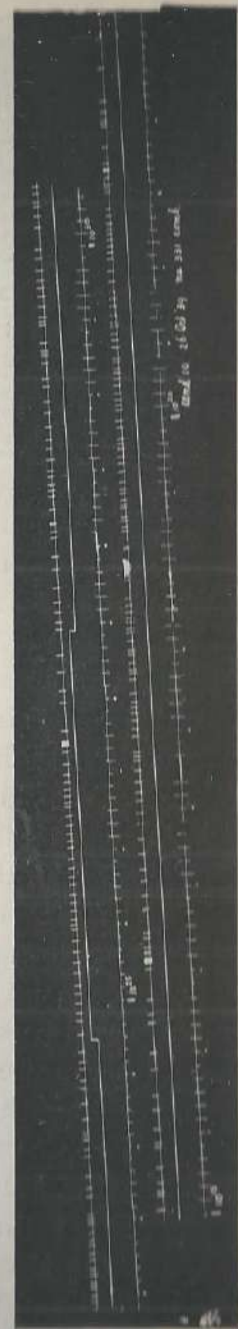

Fig. 9. Duck No. 10. After 331 combinations.

the air charged with aniseed-oil had a strong smell to the experimenter. Twice a day an experimental session was held with six combinations. In all, the duck got 331 combinations in 55 sessions. Under the heading of "sham stimulus" in table 9, the effect is given of the change-over from pure air to pure air, where the conditioning stimulus was not given at all. As is apparent from the data given, there might be some indication of a slight reaction. In a few cases it appeared as if the application of odorant caused conditioned secretion. It was found, however, that application of odorant was followed by an increase in secretion only when the change-over was effected somewhat abruptly; so that it is probable that the change-over as such acted as stimulus in these cases. No effect was ever obtained in those cases where an abrupt change in the air current could be avoided (see figs. 10 and 11).

In the experiments with ducks there was never any increase of gastric juice secretion on olfactory stimuli, exceeding the normal variation.

The fact that it is by no means impossible to bring about conditioned gastric secretion may be seen from the positive results with other stimuli as conditioning agents.

I shall not deal at great length with the results of conditioning to non-olfactory stimuli, since this subject is not germane to the principal issue; only some experiments on duck No. 3 will be communicated here. The conditioning stimuli used here were the optical stimuli of the ordinary feeding tray, both with and without food, and the acoustic stimulus of an electric bell. Before starting conditioning the influence of the acoustic stimulus was tested. It proved not to affect gastric secretion, as may be seen from the data given in table 9 (13 May). Showing food, on the other hand, produced a marked and prolonged increase of secretion. This animal was rather new to the experimental conditions; nevertheless

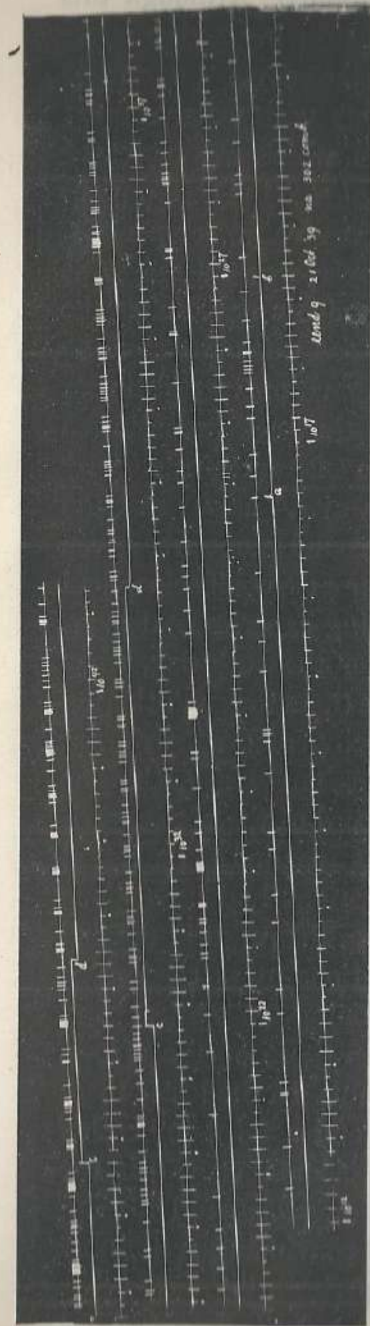

Fig. 10. Duck No. 9. Gastric secretion after 302 combinations of aniseed-oil and food. *a b* sham stimulus (see text); *c d* olfactory stimulus.

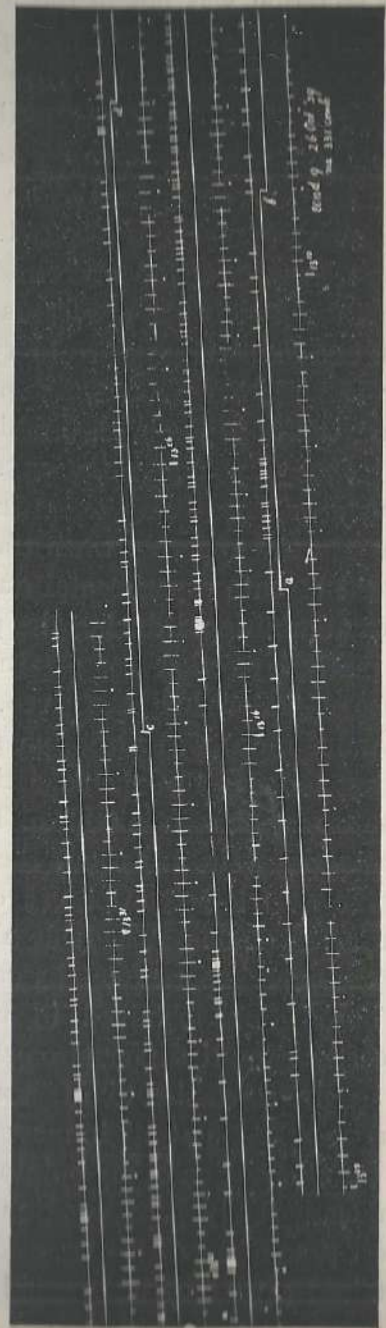

Fig. 11. Duck No. 9. After 331 combinations. *a b* sham stimulus; *c d* aniseed-oil. Recording was interrupted from 1.14½ p.m. until 1.16.

the secretion was not in the least inhibited. Although this animal had been fed in the apparatus during a short time only, conditioning not having been started yet, the optical stimulus of the feeding tray filled only with water exerted a marked influence upon the secretion, which was increased to about the same extent as on showing food. Table 9 gives the numbers of drops secreted in successive 30 sec periods. Some days later the experiment proper was started. The duck was fed in the apparatus nearly every day. After the bell had been rung for 10 to 15 sec, food was offered while the ringing was continued. This combination was given six times daily; at the sixth combination the duck was allowed to eat until apparent satiation, so as to ensure the total daily amount of food being taken in this way. A slight reaction was already apparent when the bell sound alone was given on the seventh experimental day, after 31 combinations had been administered during the preceding experimental days. A marked reaction was obtained after the 20th day, when 99 combinations had been given. Three times the conditioning stimulus alone was given, no food being offered, in order to test the effect of the conditioning stimulus as such. The results may be seen in table 9. The record of the 24th experimental day (fig. 12) shows the stormy reaction to the sound of the electric bell after 115 combinations had been given during 23 sessions. The table also gives the result at the end of the experiment after 165 combinations in 34 sessions.

The figures obtained in conditioning on optical and acoustic stimuli differ strongly from those of the efforts to acquire a reaction to olfactory stimuli. In the latter there was no reaction at all in most cases, and a faint indication in the others, due in my opinion to accidental causes; in the former a fairly good reaction is already observed after a short time of conditioning, and most convincing results are obtained after a normal period of experimenting.

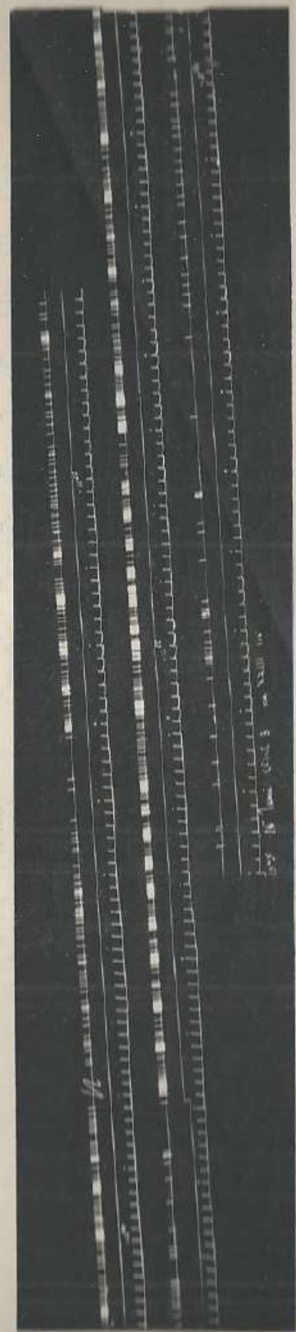

Fig. 12. Duck No. 3. Gastric juice secretion on a conditioning acoustic stimulus after 115 combinations of this stimulus and food.

TABLE 9. Gastric juice secretion in drops per 30 sec

Duck No. 4 26 November 1938 compare record	10,15—10,20 a.m.	6— 3— 3— 6— 7— 8— 6— 7— 5—16—	
	10,20—10,25	5— 4—19— 3— 2— 3— 4— 4— 3— 2—	
	10,25—10,30	11— 8— 4— 4— 8— 5— 4— 4— 7— 2— ↑ scatol a-b ↓	
	10,30—10,35	2— 3— 3— 2— 3— 3— 3—13—12—19— ↑ c-d ↓	during c-d showing food
	10,35—10,40	3— 2— 9— 4— 7— 3—12—18—19—18—	
	10,40—10,45	6— 4— 8— 4— 9— 2— 5— 3— 6— 8—	
Duck No. 4 3 December 1938	10,25—10,30 a.m.	2— 2— 3— 3— 3— 3— 4— 4—10— 6—	
	10,30—10,35	3— 2— 3— 4— 3— 3— 2— 4— 5— 4— ↑ scatol a-b ↓	
	10,35—10,40	2— 4— 2— 2— 3— 2— 4— 4— 4— 2—	
Duck No. 4 23 December 1938 compare record	3,0 — 3,5 p.m.	4— 1— 1— 2— 2— 3— 4— 2— 4— 4—	
	3,5 — 3,10	4— 3— 4— 6— 3— 3— 5— 3— 3— 3— ↑ scatol ↓	
	3,10— 3,15	4— 4— 4— 4— 2— 5— 3— 3— 4— 4— ↑ scatol ↓	
	3,15— 3,20	5— 4— 2— 5— 2— 1— 2— 4— 2— 4— ↑ showing food a-b ↓	
	3,20— 3,25	5— 4— 7— 3— 5— 4— 5—10— 4— 3— ↑ c-d ↓	during c-d showing food
	3,25— 3,30	— — — — —14— 7— 8—14—20— 5— 3— ↑ showing ↓ food e-f	
	3,30— 3,35	4— 5— 9— 4— 4— 5— 7— 5— 6— 4— ↑ scatol ↓	
Duck No. 7 1 July 1939 compare record	12,18—12,23 p.m.	4— 4— 6— 5— 2— 6— 6— 6— 3— 2—	
	12,23—12,28	5— 3— 1— 4— 0— 6— 0— 1— 0—10— ↑ pyridine ↓	
	12,28—12,32	0— 5— 2— 0— 6— 1— 0—10—	
Duck No. 7 20 July 1939 compare record	10,52—10,57 a.m.	7— 8— 2— 4— 3— 4— 3— 4— 3— 4—	
	10,57—11,2	2— 6— 4— 9— 5— 2— 2— 3— 3—15— ↑ pyridine ↓	
	11,2 —11,7	3— 1— 1— 1— 0— 1— 1— 0— 1— 1— ↑ pyri-	
	11,7 —11,12	8— 2— 0— 0— 1— 1— 0— 1— 0— 0— dine ↓	
Duck No. 8 22 July 1939 compare record	1,18— 1,23 p.m.	3— 1— 0— 6— 8— 6— 2— 6— 6— 9—	
	1,23— 1,28	3— 1— 1— 1— 0— 2— 2— 1— 2— 4—	
	1,28— 1,33	11— 3— 2— 2— 5— 0— 1— 1— 3— 6— ↑ toluene	
	1,33— 1,38	2— 2— 5— 3— 5— 5— 6— 2— 7— 7— ↓	
Duck No. 10 20 October 1939 compare record	10,13—10,18 a.m.	6—10— 9— 8— 7— 7— 6— 4— 4— 5— ↑ to-	
	10,18—10,23	2— 7— 5— 3— 7— 6— 5— 9— 6— 4— luene ↓	
	10,23—10,28	7— 3— 2— 2— 8— 3— 3— 7— 6— 2— ↑ to-	
	10,28—10,33	2— 1— 6— 2— 1— 2—11— 1— 4— 2— luene ↓	
	10,33—10,34	1— 5—	

TABLE 9 (cont.)

Duck No. 10 26 October 1939 compare record	10,15—10,20 a.m.	8— 5— 4—15— 6— 8—12—10—13—11—
	10,20—10,25	11—10— 9—12— 4— 7—12— 7— 7— 7—
	10,25—10,30	8— 8—11— 9— 4— 6— 9— 7— 9— 8—
		↑ toluene ↓
Duck No. 9 21 October 1939 compare record	10,12—10,17 a.m.	2— 3— 2— 1— 3— 1— 4— 3— 1— 3—
		↑ sham
	10,17—10,22	5— 6— 2— 3— 2— 1— 3— 3— 1— 1—
		stimulus ↓
	10,22—10,27	4— 9—15—10—12— 5— 3— 5— 1— 5—
	10,27—10,32	6—10— 6— 6— 5—10—11—13— 7—10—
		↑ anis-
	10,32—10,37	13—11—10—10—13—12—12—14—20— 9—
		eed-oil ↓
	10,37—10,42	6— 5—27—21—13—16—13—13—20—20—
		↑ aniseed-oil ↓
		13
Duck No. 9 26 October 1939 compare record	1,5 — 1,10 p.m.	3— 4— 2— 3— 3— 3— 4—12— 3— 4—
		↑ sham stimu-
	1,10—1,14½	2— 4— 4— 4—16— 2— 3—17— 2—
		lus ↓
	1,16— 1,21	3—17— 9— 8— 9— 8— 8—12—11—10—
	1,21— 1,26	8— 9— 8— 5— 6— 6— 4— 7— 6— 4—
		↑ anis-
	1,26— 1,31	8— 6— 4— 6— 4— 5—10—12—12— 7—
		eed-oil ↓
	1,31— 1,33	7— 6— 7— 5—
Duck No. 3 12 May 1938	11,55—12,0 a.m.	9— 3— 8— 5—16— 6— 8— 8—11— 7—
	12,0 —12,5 p.m.	9— 6— 3— 7—11—13—12— 7— 7— 2—
		↑ bell ↓
	12,5 —12,10	6— 9— 8— 9—10— 7— 6— 8—10— 6—
	12,10—12,15	10— 4— 2— 3—10— 8— 5—65—61—30—
		↑ showing food ↓
	12,15—12,20	34—21—20—23—27—32—18—16—20—14—
	12,20—12,25	16—10—11—14—27—26—18— 9—13—16—
Duck No. 3 13 May 1938	12,10—12,15 p.m.	1— 2— 5— 2—19— 6— 1— 8— 1— 3—
	12,15—12,20	9—24— 4—12— 4— 3— 9— 3— 2— 9—
		↑ bell ↓
	12,20—12,25	6—19— 3— 3— 7— 1— 2— 6—18— 1—
		↑ do ↓
	12,25—12,30	13— 0— 4— 4— 7—23— 9—17—28—12— § showing feeding tray filled with water
		↑ § ↓
	12,30—12,35	46—38—55—60—50—61—50—58—73—50—
	12,35—12,40	61—30—36—52—49—25—35—10—32—
Duck No. 3 11 June 1938	10,35—10,40 a.m.	14— 2— 7— 3— 7— 4— 4— 3— 7— 8—
	10,40—10,45	13—11—14—13— 4— 3—12— 5— 8— 5—
	10,45—10,50	4—14—13—14—12—15— 7—31—20—13—
		↑ bell ↓
	10,50—10,55	7— 3— 7— 9— 9—10— 9—14— 8—30—
	10,55—11,0	10—31—18—13—20—18—20—23— 7— 9—
		↑ bell ↓
	11,0 —11,5	18—12—10— 8—15—10—15—24—13— 7—
	11,5 —11,10	15— 8—11—15—11—27—52— 9—36—12—
		↑ bell ↓
	11,10—11,15	9—10— 1— 7—14—21— 9—28—15—21—
	11,15—11,20	27—17— 7—12— 6—13—13—21—13—13—
Duck No. 3 29 June 1938	12,30—12,35 p.m.	5— 6— 4— 5— 8— 4— 6— 8— 6— 8—
	12,35—12,40	16—12—14— 7— 9— 4— 3—57—42—54—
		↑ bell ↓
	12,40—12,45	42—53—30—46—43—51—37—25—26—29—

Commentary.

All the experiments yielded negative results in that it was not possible either to condition any reaction on olfactory stimuli or to train birds on these stimuli. Nevertheless earlier authors obtained positive results with both methods. BAJANDUROW and LARIN were able to condition *Columba turtur* on various odorants which I used in my experiments with *Columba livia domestica*. They had positive results, whereas I could not obtain any conditioned reaction. Domesticated pigeons were used in the experiments of TJUMJANZEW and those of ISHIHARA, in which the authors obtained positive results. ZAHN was able to train domesticated ducks on odorants; in my experiments no reactions were obtained either in conditioning, or in training and free feeding experiments with these animals. The difference in the issues is not due, therefore, to the fact that domesticated animals were employed. Neither did training give any better results in my experiments with siskins, whereas other authors obtained reactions on odorants from these birds. In my opinion the results of earlier authors should be interpreted as reactions to other than olfactory stimuli. My experiments have shown that stimuli, which, in our opinion, are almost imperceptible, may even exert an influence, and, therefore, be responsible for the effect. The power of vision in birds goes far beyond our imagination; especially in training experiments, optical stimuli may cause effects ascribed to olfactory stimuli. There is one common criticism of all authors who have obtained positive results. Not one of them transected the olfactory nerves in order to examine whether the reaction would disappear at once, which would prove that the effect had been caused by olfactory stimuli.

I am forced to the conclusion that the animals I have used in the experiments do not possess the faculty of smelling. In order to gather a more general notion about the sense of smell in birds experiments must also be carried out on other species. It is absolutely necessary to obviate any possibility of non-olfactory stimuli interfering with the experiments. If apparently positive results are obtained they should meet with the requirement of being unobtainable immediately after transection of the olfactory nerves.

The fact that birds have a fairly well-developed "olfactory" organ is not an *a priori* proof that they possess the faculty of smelling; a self-evident truth, which has too often been forgotten. As no facts are known which can serve to answer the question of whether these organs have any other function than that of perception of gaseous chemical stimuli, or whether they have no function at all, speculation about this problem had better be omitted and discussion postponed until foundational data are available.

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*) The date 1840 in the 5th volume is a misprint.

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Summary.

The literature concerning the problem of the sense of smell in birds has been surveyed in Chapter 1, from which it is evident that the opinions of various authors differ widely. Birds are supposed by some of them to possess an excellent sense of smell, whilst others do not attribute to these animals any olfactory power; a third group of authors, finally, consider birds as microsmates.

Some experiments were arranged in order to investigate the matter.

Chapter 2 deals with the influence exerted by odorants on respiration. No reaction could be observed, but it was tried to obtain a conditioned acceleration of respiration by combining the olfactory stimulus with pain. Pigeon No. 6 got 246 combinations of amyl acetate and pain stimulus; pigeon No. 7 was given pyridine in 242 combinations. Neither series was successful; but in pigeon No. 6 a conditioned reflex on acoustic stimulation was easily formed.

In Chapter 3 conditioning of leg movements on olfactory stimuli is described. Pigeon No. 9 was given 88 combinations of eau-de-Cologne and pain stimulus; pigeon No. 11 got 92 combinations with methyl salicylate. The same procedure was followed with duck No. 2 in 102 combinations of methyl salicylate and pain stimulus. Pigeon No. 12 was conditioned on pyridine in moist air (128 combinations) and pigeon No. 13 on methyl salicylate in moist air (129 combinations). Without exception these series had negative results. No conditioned reflex could be established on odours as conditioning stimuli.

Training experiments with siskins and parakeets are described in Chapter 4. The birds were allowed to eat from

feeding trays provided with odorant, and forbidden to take their food from inodorous trays offered simultaneously. The table at the end of Chapter 4 gives the results of these series; it will be seen from it that neither training resulted in correct choice due to the birds being guided by the odorants.

Chapter 5. With two ducks, feeding experiments were performed, food with an inherent strong scent being used. Later on odorants were added. The ducks were not able to find the food when blindfolded, even when they had been fed in this way during more than two months. The eyeballs were then removed in order to accustom the animals to finding food without the guidance of the eye-sight. One and a half months afterwards they were still unable to find food on olfactory stimuli.

Finally (Chapter 6) I endeavoured to condition a vegetative reaction to olfactory stimuli. In five ducks with gastric fistulae attempts were made to condition gastric juice secretion on scatol (181 combinations), pyridine (244), toluene (202), aniseed-oil (331), and toluene (331), respectively. In none of these experiments was any result obtained. Conditioned gastric juice secretion was easily established on visual and acoustic stimuli.

All these experiments failed to provide any support to the view that birds are able to smell.

STELLINGEN.

I

De longontwikkeling bij de Reptielen geschiedt in centrifugale richting.

II

In het rechter atrium van het foetale zoogdierhart wordt het bloed, komende uit de vena cava superior, niet gemengd met dat uit de v. cava inferior.

III

De term „forma" wordt door WARREN in zijn „Monograph of the genus *Erebia*" verkeerd toegepast.

IV

De opvatting van HECHT, dat *Natrix natrix* (L) van het eiland Bornholm als subspecies *scutata* PALLAS onderscheiden moet worden van de ringslangen van het overige Denemarken, is onhoudbaar.

V

Daar de turgorbewegingen in de bladgewrichten niet geheel kunnen worden verklaard uit osmotische, noch uit permeabiliteitsveranderingen in de cellen van de gewrichten, verdient het aanbeveling de mogelijkheid van een actieve wateropneming en afscheiding in overweging te nemen.

VI

De opvatting dat het chromosoom bestaat uit een spiraal met een matrix verdient de voorkeur boven de meening dat het chromosoom zou ontstaan door condensatie van een netwerk.

VII

Vogels kunnen niet ruiken.

VIII

De meening dat de temperatuurzin van Visschen is gelocaliseerd in de zijlijnen is onjuist.

IX

Het ganglion stellare van de Cephalopoda heeft zoowel de functie van een reflexcentrum als van een automatisch centrum.

X

De veronderstelling van SPERBER, dat gistphosphatase en -phosphatese voor aneurinepyrophosphaat identiek zijn, is onjuist.

XI

De geleidingssnelheden der impulsen in de afzonderlijke vezels van een zenuw zijn recht evenredig afhankelijk van den vezeldiameter.

XII

De opvatting dat de alpha-golven van het electroencephalogram uitsluitend ontstaan in de schors der groote hersenen is niet juist.