

The Peck of the Pigeon: Free for All

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There seem to be four discernible areas of conflict between behaviourism, especially the experimental analysis variety, and other scientific schools of behavioural studies. I would like to discuss these briefly before introducing some factual information that hopefully will illustrate how I conceive a free-for-all analysis of behaviour. It is inevitable that I shall need to set up straw men to deal with these initial generalities. The diversity of stand-points among individual representatives of the various traditions is great and has doubtlessly increased recently. An eclectic attitude, for which I shall be pleading, seems to be spreading. Gradations rather than divisions of opinion are the rule. Schools of thought are no longer as monolithic as they once were. Other branches of the natural sciences appear to have gone through a similar dissolution of factions as the volume of positive knowledge they could command increased.

One of the areas of conflict has to do with the range of behaviours that the various schools study. I consider that for an ambitious general account of behaviour, the "experimental analysis" school of behaviourism studies a too restricted range of phenomena. We have been told that a botanising of behaviour is not needed but it would seem that this can no longer be taken for granted. What is, for example, the experimental behaviour analysis account of the sexual behaviour of the female rat or the singing behaviour of song birds? One should in principle be able to deduce from lever-pressing rats and key-pecking pigeons, but can one? The account offered by behavioural endocrinologists for the first case and by neuroethologists for the second is likely to be closer to the truth by any definition than one behaviourists could offer. It might be argued that the demand is unfair but

consider even such a classical experimental analysis item as concurrent schedule responding for food. I am not sure if the account offered by behavioural ecologists is not by now similarly superior. At the very least, the optimal foraging based approach has made the schedule literature a lot less arid than it used to be.

The next area of conflict is one that has gradually receded into history but at one time it caused much acrimony between ethologists and behaviourists. It is the age old nature versus nurture dispute where even only a decade or two ago one could still take a theoretical stand one way or another without being appreciably constrained by facts. Meanwhile the field of behaviour ontogeny has been flooded by evidence that supports an interactionist mode of behaviour development, and more fundamentally of neural development. The plurality and complexity of the interactions between genetic and environmental factors that have been revealed meantime dwarf all the conceptions that classical ethologists and behaviourists had about the ontogeny of behaviour. This new position also agrees well with the theoretical reasoning that derives from first principles of molecular biology. Together they constitute a knowledge network that cannot any longer be reasonably ignored, not even by psychologists.

More recently the dispute between behaviourism and ethology has shifted to the issue of the adaptedness of learning versus the general laws of learning. I hope that nobody doubts that the neural structures and processes that are the basis of the learning phenomena we study are the product of the historical process that started several billion years ago with the emergence of the first replicating molecules. Learning phenomena have repeatedly been shown to be critically dependent on the modern versions of these molecules, the genes. Biological evolution thus cannot be ignored when discussing conditioning. It is also an undeniable fact that we know a great deal about the processes underlying biological evolution. For example, it inherently tends towards fitness maximisation. There are no reasonable grounds for believing that learning is exempt from the consequences of this principle. It follows that the ways different organisms learn must on the whole match the ecological demands that they face.

That does not contravene the assumption that there are general principles underlying learning. For one thing we apply the term "learning" to a set of phenomena that exhibit certain similarities. It is likely that only a restricted set of causal processes is capable of yielding phenomena that fit this particular semantic category. Also, all animals whose learning we study live on the same macrohabitat, Earth, and that makes for evolutionary convergence. Not least, all species very probably have a common ancestry which together with phylogenetic inertia, another inherent trait of

evolution, makes for similarities.

A fourth area of dispute is not concerned primarily with ethology. Rather the conflict is with both cognitive behaviourism and physiological psychology. It stems from a tradition among behaviourists that studiously, if not stubbornly, avoids getting too involved with the processes within the organism that intervene between stimuli and responses. But a full account of behaviour must obviously include a description of these processes. Two approaches have proven eminently viable in studying intervening processes, among other areas in biology and engineering: inferential deduction from input-output analysis and direct-access identification and measurement. I see modern cognitive psychology doing the first, and behavioural neuroscience doing the second, and both as having accumulated a large amount of firm complementary knowledge. One can no longer reasonably ignore that the nervous system with its associated systems transduces, transmits, processes, and, particularly, stores and reproduces information in the course of behaviour production. The ways in which it does so incontrovertibly affect the relationships between stimuli and responses that behaviourists are interested in.

Summarising after a fashion, an ideally complete account of any behaviour has to include descriptions of its phylogeny, its ontogeny, and its physiogeny. The latter term is a neologism introduced here to replace the more common but cumbersome formulations "short-term causation" or "physiology in the wider sense" with which the triad is usually completed. These three elements of such a "complete" account are, however, hierarchically dependent simply because any behaviour we look at is necessarily the historical end-product of its phylogeny, ontogeny and physiogeny in that order. An account of the ontogeny of an organism's behaviour must square up with the evolutionary past of that organism. Similarly the description of the physiogeny of a behaviour must be in agreement with its developmental history. Behaviour is a biological phenomenon and the central fact of biology is evolution. Any "true" theory about behaviour must in a certain way always be a subset of evolutionary theory.

Rather than continuing with abstract assertions I now present a summary of some research on the behaviour of the pigeon (*Columba livia*), a classical subject of both the behaviourist and the ethological traditions. Our work has, however, been conducted with no particular regard for either position. It is motivated by an eclectic curiosity, a desire to "understand" the behavioural phenomena at hand, and is conceived as a contribution towards some future, all-embracing biology of the pigeon (Abs, 1983). It should demonstrate that an interdisciplinary approach can be enlightening, or if not that, entertaining.

CONSTRAINTS ON A DISCRIMINATION

First I deal with an issue that has already been touched upon. It concerns the fact that a given stimulus class is often effective in controlling responses in certain conditioning situations but not in others. I came upon this problem in a rather oblique way in connection with a neurophysiological experiment I was involved with while spending a year at the department of neurosciences at the University of California, San Diego. Anne Biederman-Thorson was recording the activity of single neurones in the main telencephalic auditory projection of birds, the so-called area L of the neostriatum caudale (Biederman-Thorson, 1970). In ring doves (*Streptopelia risoria*) she occasionally found neurones that appeared to respond specifically to particular species-specific vocalisations. As one test for specificity she played the tape recording of the relevant dove calls backwards and found, disappointingly, that the neurones were often also activated by these stimuli, thus making it doubtful whether they really were call-specific detectors. But we had to be certain that ring doves could behaviourally distinguish between forward and backward species-typical vocalisations.

We set up a successive instrumental discrimination experiment in which forward and backward played "bow-coo" calls were the conditional cues for the ring doves to peck either the right or the left key of a Skinner-box for food reward. In spite of extensive training and various methodological improvements the ring doves did not learn the discrimination that, to the human ear at least, seemed easy enough. About the same time Krasnegor (1971) had, in spite of an even more intensive and expert application of behavioural technology, found that pigeons would not discriminate two temporal tone patterns in an instrumental food reinforced situation. If I remember correctly my conclusions and those of Krasnegor's supervisor (William Hodos) regarding these analogous negative results differed markedly at the time. While Hodos was inclined to believe that these birds were fundamentally incapable of such discriminations I, based on admittedly weak collateral ethological evidence, was convinced that both doves and pigeons could distinguish between forward and backward auditory patterns but that the conditioning procedures that we had used were not adequate to demonstrate this.

On return to the department of psychology at Durham, England, I requested the cooperation of Roger Tarpy, a visiting fellow. His summary opinion was that recalcitrant conditioning debilities were always best resolved by the use of aversive reinforcers! And indeed, within a few days he had pigeons discriminating tones differing in pitch by only small frequency differences using an aversive classical heart rate differentiation procedure. I took over his method and quickly accumulated data showing

that pigeons have indeed no difficulty discriminating between the same tone pattern played forward and backward (Delius & Tarry, 1974). Subsequently, evidence was obtained that a proportion of avian area L neurones are also capable of the corresponding discriminations (Leppelsack, 1978).

When, however, my collaborator Jacky Emmerton attempted to apply the apparently so efficient Tarry method to the psychophysical measurement of the wavelength discrimination function of pigeons (Emmerton & Delius, 1980) she obtained results that seemed to indicate that pigeons were colour-blind! Of course they are not, as is well known from many appetitive instrumental key-pecking hue discrimination experiments. On the contrary, pigeons have exceptionally sophisticated colour vision capabilities (Emmerton, 1983b). In a formal experiment we then confirmed these asymmetric stimulus control results. The same pigeons were trained to discriminate both two different colours and two different tones, each in an appetitive conditional successive instrumental discrimination paradigm and an aversive classical successive heart rate-differentiation procedure. The results showed that the colours came to control the key pecking in the appetitive instrumental paradigm but not the heart rate in the aversive classical procedure and that the tones yielded control of tachycardia in the aversive classical but not of key pecking in the appetitive instrumental procedure (Fig. 5.1, Delius & Emmerton 1978).

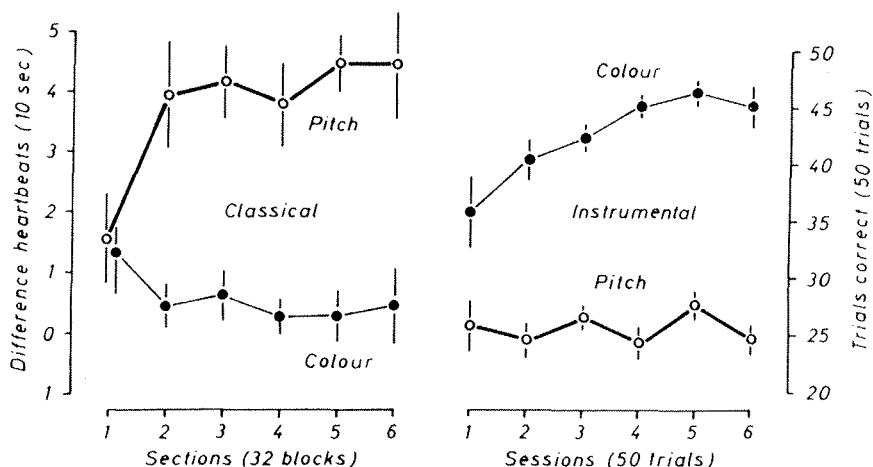


FIG. 5.1. Mean learning curves of pigeons on different tasks. The same subjects ($N = 4$) had to discriminate two diffuse lights differing in hue and two tones differing in pitch. In an instrumental, food-reinforced, successive conditional key pecking paradigm the pigeons easily discriminated the lights but not the tones. In a classical, shock-reinforced heart-rate conditioning paradigm they easily discriminated the tones but not the lights (Delius & Emmerton, 1978).

Taking into account other evidence (LoLordo & Furrow, 1976) showing that the relative control exerted by the light or the tone component of a compound stimulus in an instrumental treadle pressing conditioning situation switched according to whether food delivery or shock avoidance was used as a reinforcer, we surmised that the important factor for the asymmetry observed in our experiment was the aversive (shock)–appetitive (food) disparity. Also, a survey of the literature indicated that what auditory psychophysical investigations demanding fine discriminations had been done using pigeons, had almost exclusively used shock reinforcement. On the other hand, research on colour vision of pigeons as already remarked, had almost exclusively employed food reinforcement. That the classical cardiac conditioning per se is not responsible for the absence of colour discrimination was established in a recent heart rate–conditioning experiment employing an appetitive unconditional stimulus (water) (UCS) (Klinkenberg, Delius & Emmerton, 1984). Colours yielded good stimulus control, provided that the water reinforcement yielded a cardioaccelerative unconditional response (UCR), which in some birds it did not.

We interpreted these stimulus-reinforcement compatibilities-incompatibilities in terms of a constraint of learning of phylogenetic origin. In the normal environment of pigeons, sounds are unlikely predictors of food (grains are mostly silent) whereas tones are likely predictors of pain (predators are often noisy). Pigeons with only two millilitres of brain, compared with, for example, humans with 1200 ml, are bound to be too short of neuronal structures to be able to relate and store all the possible associations between the multitude of events they can perceive. It is inevitable that natural selection will apportion such memory space as is available to the registration of contingencies that are particularly conducive to fitness promotion. Thus bird species that feed on noisy prey should differ from pigeons in auditory-alimentary conditionability and indeed in at least one instance we know that it is so. Barn owls (*Tyto alba*) are exceedingly proficient at learning fine auditory discriminations with food reward (Konishi, 1973, & personal communication).

An incidental observation, auditory evoked potentials recorded from the frontal forebrain of a pigeon, made during an electrophysiological study of the somatosensory forebrain projections of pigeons (Delius & Benetto, 1972), eventually somewhat upset our conception. When we recently re-investigated these potentials, we found that they originated from the nucleus basalis telencephali or its immediate neighbourhood, and had a very short latency (5–8 msec, Fig. 5.2) as compared with the latencies of auditory potentials in the more orthodox acoustic projection in area L (12–14 msec, Delius, Runge & Oeckinghaus, 1979). This was already known (Naumov & Iljitschew, 1964) but it had been disregarded by later authors because of their inability at that time to find an anatomical correlate, an auditory

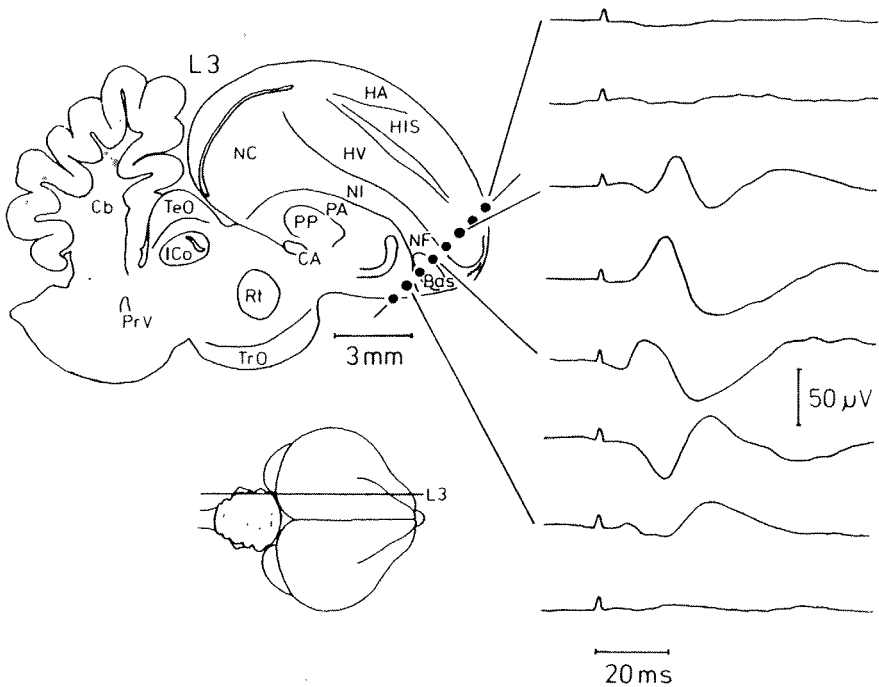


FIG. 5.2. Averaged auditory evoked potentials from the nucleus basalis of the pigeon. The anterior forebrain of anaesthetised pigeons was explored with a bipolar recording electrode for electroencephalographic responses to a click-tone. Short latency potentials were recorded in the neighbourhood of the nucleus basalis (Bas). Other abbreviations: Cb cerebellum, CA commissura anterior, HA hyperstriatum accessorium, HIS h. intercalatus superior, HV h. ventrale; ICo nucleus intercollicularis, NC neostriatum caudale, NI n. intermedium, NF n. frontale, PA paleostriatum augmentatum, PP p. primitivum, PrV nucleus principalis nervus quintus, Rt n. rotundus, TeO tectum opticum, TrO tractus opticus. (Modified from Delius, Runge, & Oeckinghas, 1979).

pathway to the nucleus basalis (Karten, 1968). This nucleus, which is an avian speciality, was only known to receive fast somatosensory afferences from the beak and face via the trigeminal nerve and the quinto-frontal tract with a synaptic relay in the medulla (Wallenberg 1903; Witkowsky, Zeigler & Silver, 1973). The auditory pathway reaching the basalis, we now know (Kirsch, personal communication; Schall, Güntürkün & Delius, 1985), has its origin in the nucleus of the lateral lemniscus, which itself receives direct input from the medular auditory nuclei (Karten, 1968).

The nucleus basalis has been implicated in the motivational/motor control of feeding in birds (Zeigler, 1976). It is at the head of a descending neural pathway consisting of the tractus fronto-archistriaticus that reaches the archistriatum mediale (as well as the overlying neostriatum caudale)

and the tractus occipito-mesencephalicus that from thence reaches various diencephalic, mesencephalic, and rhombencephalic structures (Fig. 5.3). The evidence for the involvement of the nucleus basalis in feeding behaviour stems from comparative studies showing that bird species with complex feeding behaviour have a large basalis complex (Stingelin, 1962), from a study in which lesions of the nucleus itself and structures of its efferent pathway affect food intake (Zeigler, Green & Karten, 1969; Levine & Zeigler, 1981) even though some of this evidence is in dispute (Martin Ramirez, 1979), and from a study in which electrical stimulation of the nucleus basalis and neighbouring structures yielded feeding related behaviour in herring gulls (*Larus argentatus*, Delius, 1971). We shall be commenting upon the role of the nucleus basalis later in this paper.

The fact that auditory information reaches a forebrain "centre" implicated in the control of feeding with an exceptionally short conduction-time

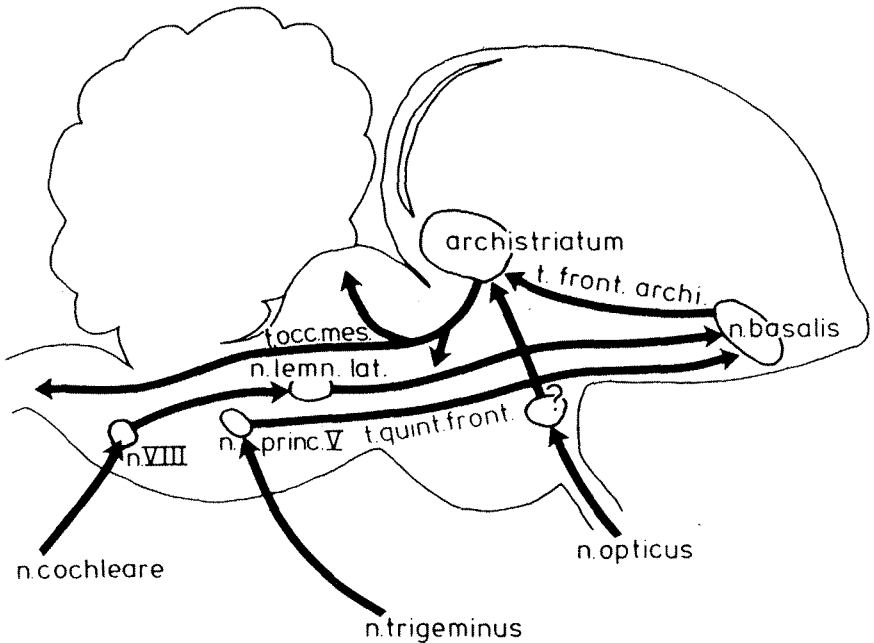


FIG. 5.3. Neural structures related to the nucleus basalis. Somatosensory afferences from the beak (trigeminal nerve) reach the nucleus basalis via the quintofrontal tract after synaptic relay in the principal sensory nucleus of the trigeminal (fifth) nerve. Auditory afferences (cochlear nerve) reach the nucleus basalis after relays in the medular nuclei of the eighth nerve and the nucleus of the lateral lemniscus. Efferences of the nucleus basalis reach the antero-dorsal archistriatum via the frontoarchistriatal tract. This area also receives visual input via the optic nerve through an unidentified relay nucleus. The occipito-mesencephalic tract that originates the archistriatum descends to various di-, mes-, and rhombencephalic structures and also reaches the upper spinal levels.

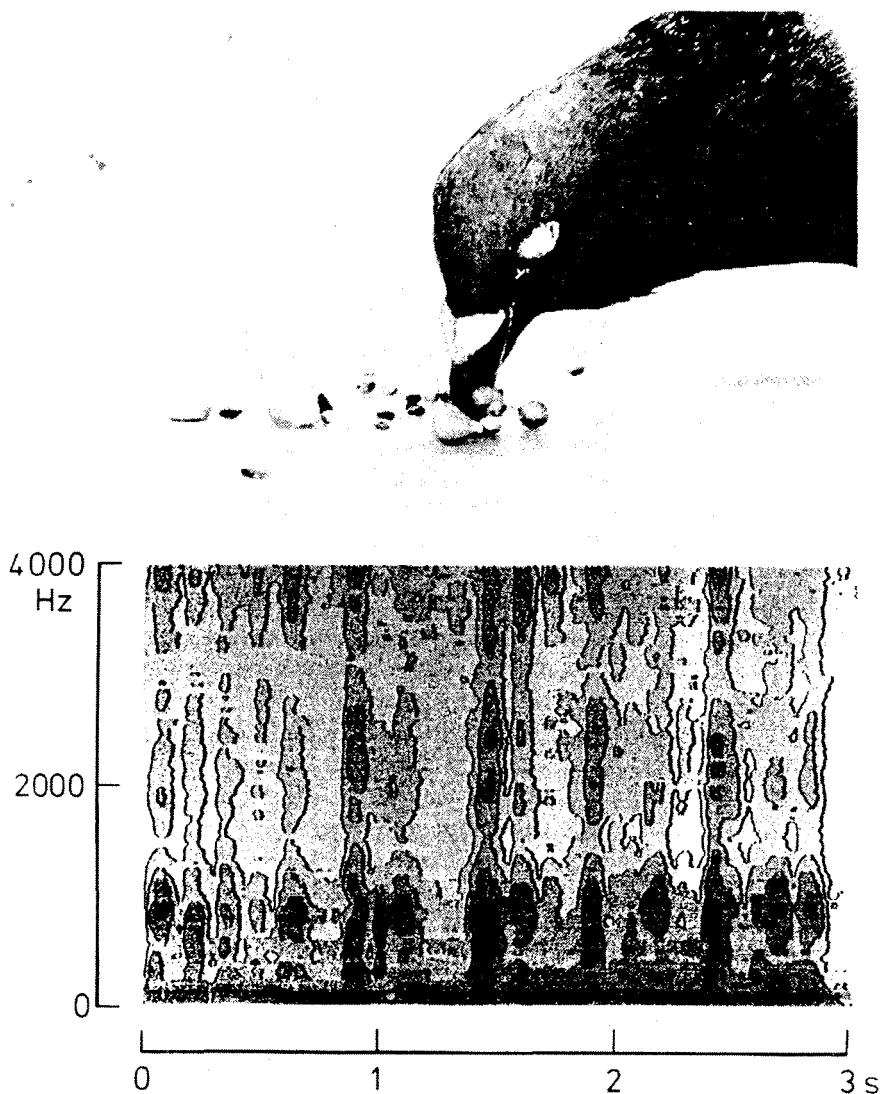


FIG. 5.4. Sonogram of noise produced by a pigeon as it pecked for grains among grit. Note that pigeons close their eyes in the terminal phases of pecking (courtesy of H. J. Jahnke).

clearly runs counter to our earlier argument that sounds are not important for feeding in pigeons. A brief reconsideration reveals that, though grains are silent by themselves, they generate a good deal of noise when they are pecked at. Figure 5.4 shows a sonogram of sounds recorded while a pigeon pecked at a heap of grains and sand. Notice that, as already described for

key-pecking by Hodos, Leibowitz, and Bonbright (1976), the animal has closed its eye in the final stages of the peck. They habitually do so, presumably as protection against back-scattering particles. A peck that reaches its target yields massive acoustic feedback. Part of this feedback is mediated by bone-conducted sound. The avian skull is especially suited for such bone-transmission as the jaw bones, the osseous elements of the beak, link up with the middle-ear bones that support the eardrums (Schall & Delius, 1985).

This auditory feedback could steer the grasping and mandibulation of food items, and possibly further pecking. If the latter were so it should be feasible to devise a food reinforced conditioning paradigm that yields efficient tone control over pecking. And that is just what we have done. The subjects had to discriminate between a brief tone (90 ms) and an even briefer tone (10 ms). In a two-key Skinner box, within a trial, each pecking response on a given key immediately yielded an S+ tone, while pecks on the other key always triggered S- tones. A fixed number (FR 16) of consecutive responses on the S+ key yielded reinforcement. Responses on the S- key never yielded reinforcement (EXT) and reset the FR count of correct responses to zero. After a reinforcement the allocation of S+ and S- to the two keys was determined according to a quasi-random sequence.

In one control condition the two tones were triggered by the programming equipment independently of the subject's pecking responses. In another control condition, the discriminative tones were still triggered by the key-pecks but with a delay of 600 msec. Pigeons only learned the discrimination when the tones followed directly upon the pecks, much as natural auditory feedback does, but not otherwise (Delius & Gebauer, 1985). Incidentally, Kinchla (1970), searching for an efficient method for auditory psychophysics in the pigeon, had devised a procedure which is similar to that reported here.

We conclude that if the tone stimuli to be discriminated are presented to the pigeons in a way that resembles the natural situation they are easily associated with pecking and food. Note that the conditioning procedure that was effective is not optimal in the sense that the noise the animal generated upon hitting the keys with its beak is likely to have interfered with the perception of the discriminative tones produced by the loudspeakers. Notice also that an analogous discrimination of light-flashes is unlikely to succeed with this paradigm as pigeons have their eyes closed at the relevant instant. But pigeons are quite efficient at discriminating the duration of light-flashes in a more conventional food rewarded discrimination procedure as Servièrè (1979), for example, has shown. Interestingly the same author (personal communication) could not obtain even gross tone duration discrimination using the same conventional procedure in spite of very extended training.

There is a further anomaly. Lab-lore has it that hungry pigeons become excited on hearing the noises of food handling and feeding equipment. On the basis of casual experimentation I believe that the observation is correct and that pigeons are acutely discriminating in this situation. It suggests that pigeons can associate auditory stimuli with food in a quite conventional conditioning context. Indeed, I believe that this has been demonstrated by Leyland (1977) and Nairn and Rescorla (1981) who showed that tones can act as mediators (conditioned reinforcers) in second order classical conditioning of pecking to a light CS with food as UCS even though tone stimuli as CS do not yield pecking as CR (Boe & Winokour, 1979). To put it in another way, if the response measured in classical conditioning of pigeons was motor restlessness and not the conventional key-pecking, tones may prove quite effective as first order CS. I also risk the opinion that if this response was made the operant in an instrumental discrimination of tones, pigeons will turn out to be well capable of fine auditory stimulus distinction under food reinforcement. This can easily be reconciled with normal foraging behaviour of pigeons. They are highly social feeders and it is apparent that the behaviour of other pigeons is used as a distant cue for food finding (Murton, Coombs & Thearle, 1972). Food-lucky pigeons generate both visual and auditory stimuli. In hungry conspecifics however these cues elicit approach rather than pecking.

PHYSIOLOGY OF AN OPERANT

Although our interest in responses has ranged more widely (Sieland, Delius, Rautenberg & May, 1981; Mallin & Delius, 1983) for present purposes I concentrate on pecking. Pigeons have their hands in the face, the "limb" capable of the finest manipulative motions being the beak. Zweers (1982b) has described in detail pecking as it is most frequently used by pigeons, for grasping grains. His description deals principally with late stages of this motion but it can be supplemented with accounts of the earlier stages by others (Friedman, 1975; Zeigler, Levitt & Levine, 1980; Goodale, 1983; Jahnke, 1984). Not all pecking acts seen in the context of feeding terminate individually in the swallowing of food (appetitive or search pecking, scattering [Timberlake, 1983], "begging"), and some may serve other unknown functions (adjunctive behaviour; Palya & Zacny, 1980). Also note that besides feeding-related pecking there are other kinds of pecking such as that employed in intra- and interspecific fighting (Martin Ramirez & Delius, 1979), in courtship, in preening, and in what ethologists have called displacement activity contexts. There is finally a pecking-like motion, beak-dipping, that subserves drinking (Zweers, 1982a). It seems

clear that when behaviourists get pigeons to peck manipulanda, most often a key, they are not really dealing with arbitrary behaviour. Rather it is a derivative of one of the various kinds of pecking that we have mentioned. This is best documented for the different forms of key-pecking that arise with food and water reinforcement: a grasping and a dipping peck (Jenkins & Moore, 1973). We have recently observed that pigeons may also activate a suitably designed manipulandum, a rubber bulb connected to pressure transducer with an action that is suspiciously similar to aggressive, wide-gape biting. This is particularly the case if a partial schedule of reinforcement is used suggesting that schedule-induced, frustrative aggression (Staddon, 1977) may be involved.

Our interest, however, has been in elucidating the neural bases of pecking. The starting point was a psychopharmacological approach developed in collaboration with Pierre Deviche, of the University of Liège. The drug apomorphine, a potent dopamine receptor agonist, is known to elicit persistent fits of pecking in pigeons when injected peripherally (Amsler, 1923; Brunelli, Magni, Morruzi & Musumeci, 1975). The drug-induced pecking is facilitated and guided by external stimuli, the pigeons preferring to peck contrasting, small-sized features (Fig. 5.5, Deviche, 1985). That this pecking is at least partly related to the operant pecking studied in instrumental conditioning situations is suggested by the fact that food reinforcement induced responding can sometimes be augmented with apomorphine injections (Graeff & Oliveira, 1975). But it is common for individual pigeons to develop idiosyncratic pecking stereotypies that do not always coincide with key-pecking and in fact can markedly interfere with it (own observations, Abelson & Woods, 1980). Even though the drug promotes pecking it does not facilitate feeding. Apomorphine-treated pigeons eat less, but do not drink less, than saline-injected controls. Interestingly this suppression is greater in the afternoon than in the morning. The food intake suppression occurs even with doses of apomorphine that do not induce pecking (e.g., 50 μg subject; Deviche, 1984). Intracerebroventricular injections of apomorphine do not yield pecking, however, suggesting that the site of action relating to this behaviour is not situated close to the ventricles (Deviche, 1983).

This issue is being investigated with the (^{14}C)-2-deoxyglucose autoradiography technique in collaboration with H. Scheich, at the Technical University of Darmstadt. Glucose is the prime energy source for neurones. 2-deoxyglucose, a chemically denatured glucose, is taken up by cells in the same way as glucose is but it cannot be metabolised further. It accumulates selectively in highly active neurones that normally would utilise more glucose than average. As apomorphine triggers fits of pecking, the population of neurones that controls this motor act should be activated and selectively take up 2-deoxyglucose. Pigeons were thus injected with both 0.5 mg apomorphine and 70 μCi radioactively labelled deoxyglucose. After

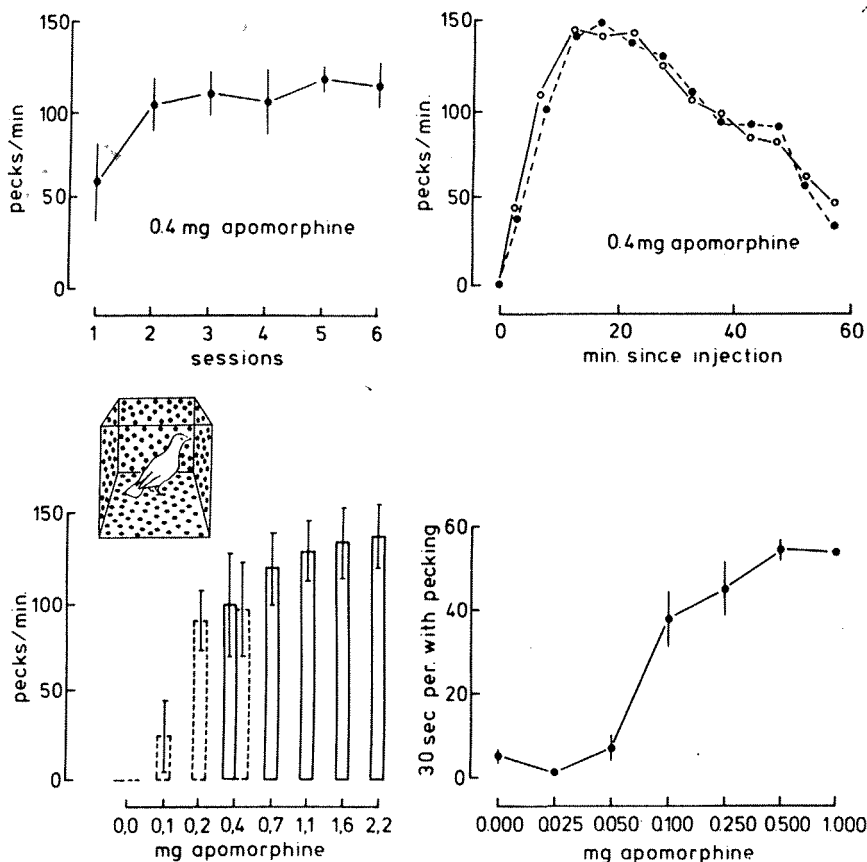


FIG. 5.5. Systemic injections of the dopaminereceptor agonist drug apomorphine elicit pecking in pigeons. The response is facilitated by providing a profusion of suitable targets. Top left: There is a sensitisation effect with repeated daily drug administration ($N = 6$). Top right: The pecking persists at high rates for over an hour; repeated experiments ($N = 6$). Bottom left: Dose-response curves; two separate experiments (doses mg/kg, $N = 6$). Bottom right: Alternative dose-response curve (doses mg/subject, $N = 9$). (Basten-Kreff & Delius unpublished; Deviche, 1985).

they had exhibited frantic pecking for one hour they were sacrificed and their brains were extracted from the skull, rapidly frozen and sectioned at $30\ \mu\text{m}$. The dry-mounted tissue sections were pressed against photographic film and kept in the dark for 14 days. The brain sites that have accumulated the radioactive deoxyglucose expose the film locally, this becoming visible on development. The autoradiographs can be matched up with the corresponding, conventionally stained brain sections.

We find that several different brain areas are marked in animals that have

been treated with apomorphine and have shown pecking as compared with saline treated controls, among them also the nucleus basalis (Fig. 5.6, Delius & Scheich, 1985). One cannot automatically conclude that all differentially marked structures are involved in the control of pecking since

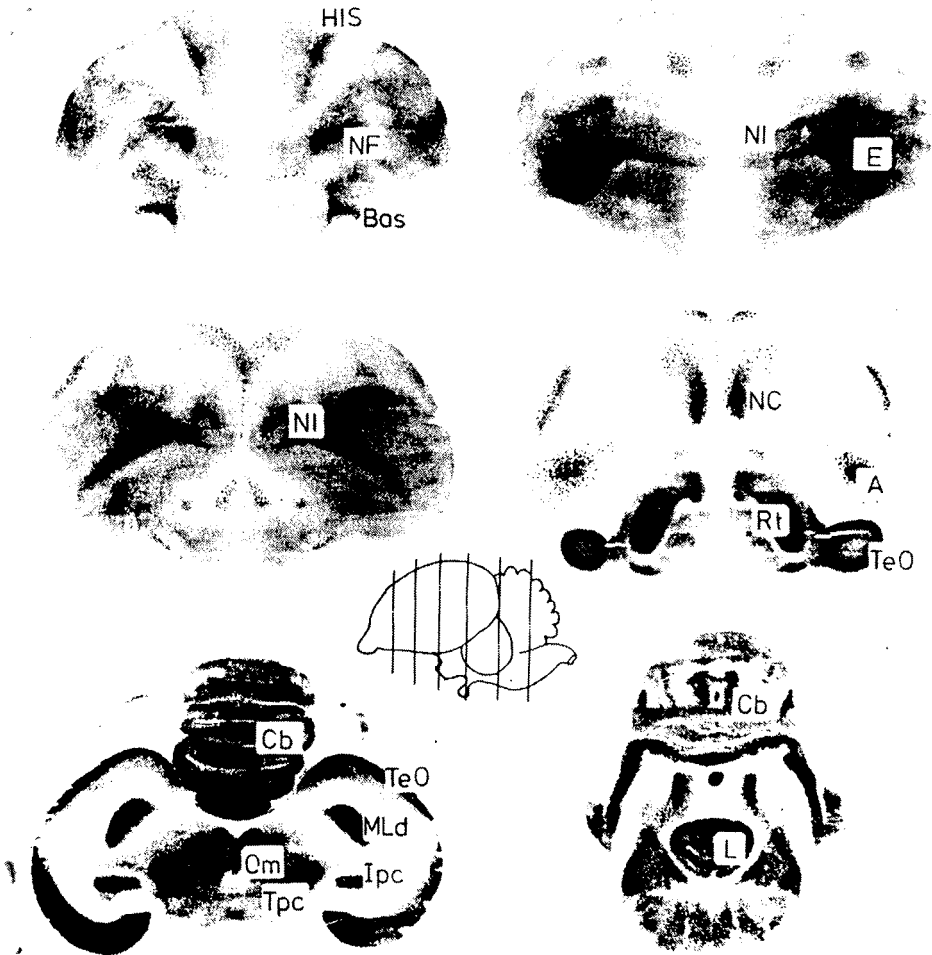


FIG. 5.6. Some examples of pigeon brain autoradiographs after apomorphine and radioactive deoxyglucose injections. Darker areas indicate above average, lighter areas below average uptake of glucose, an indication of the level of neuronal activity. Through comparison with brain autoradiographs of pigeons not injected with apomorphine it can be shown that a number of different brain structures are activated by the pecking-inducing drug, among them the nucleus basalis area (Bas; Delius & Scheich, 1985, retouched). Other abbreviations as in Fig. 5.2 and: A architectriatum, E ectostriatum, Ipc nucleus isthmi parvocellularis, L lingula, Tpc nucleus tegmenti peduncularis pontinus, MLd n. mesencephalicus lateralis dorsalis, Om nucleus nervi oculomotorii.

it is possible that apomorphine also activates subliminally other neural systems. It also remains uncertain whether a structure is marked because of direct excitation by apomorphine or because it is indirectly activated by another dopaminoceptive structure or even because it receives reafferent tactile, auditory or visual sensory input generated by the act of pecking. Visual stimulation can be avoided by carrying out the procedure in the absolute dark, as pigeons will continue to peck under this condition. Auditory feedback can be prevented by surgical removal of the cochleae, tactile afferences by sectioning the trigeminal nerve branches innervating the beak but we have not yet completed these experiments. Even so all the structures marked can be initially considered candidates for involvement in the control of pecking.

To check out more precisely the role of the various candidate brain sites, one can now proceed to inject into them micro-quantities of apomorphine. If the relevant structures are involved in the control of pecking such injections should elicit this response. This is exactly what happens in the case of the nucleus basalis (Lindenblatt, 1985). Pigeons were stereotaxically implanted with guide cannulae through which we then injected $2 \mu\text{l}$ of drug solution into the nucleus basalis. The effective dose of apomorphine is below $20 \mu\text{g}$, about 1/10 of the standard systemic dose necessary to elicit pecking. As suggested by the apomorphine/deoxyglucose autoradiography, other brain structures probably also yield pecking upon such microinjections but our work has not yet defined them sufficiently enough to make comment on them worthwhile. Goodman and Stitzel (1977), however, have described that such injections in the paleostriatum reliably elicit pecking. It is clear though, that, even with respect to dopaminoceptive neurones alone, the neural substrate of pecking is a distributed control system.

If, as it seems, apomorphine activates specific brain areas while eliciting pecking then one should be able to demonstrate an electrophysiological activation concomitant with pecking. With chronically implanted bipolar electrodes and a head-mounted preamplifier we have been able to show that while the animal pecks under the influence of the drug the electrocephalogram recorded from the nucleus basalis and its neighbourhood shows quite obvious changes in activity consisting of waves that apparently have the same rhythm as the pecks. Several other telencephalic locations that have so far been checked do not show such obvious peck-related activation.

Because of the difficulty of obtaining an accurate timing of the apomorphine induced pecks that could be cross-correlated with these local brain potentials, and with the intention of comparing the pharmacologically induced pecking with conditioned pecking we autoshaped the pigeons to peck a key providing a convenient signal. Although this kind of analysis has

not yet proceeded very far it is clear that nucleus basalis related locations do indeed often yield a rhythmic electroencephalographic activity that is phase related to the pecks. Of course, since pecking elicits auditory and tactile stimuli we can expect evoked potentials following these. But it seems likely that some loci show activation preceding these responses, indicating that it may be involved in the neuronal initiation of pecking commands (Delius, unpublished).

If that is so, electrical brain stimulation through electrodes implanted in such sites should elicit pecking. And indeed, even though head shaking, beak scratching and retching are the most common responses evoked, presumably due to trigeminal hallucinations, occasional locations are found that yield stimulus-bound pecking upon low current stimulation. As far as we can tell at present, such pecking is similar to apomorphine induced pecking insofar as it is not particularly directed at food. The nucleus basalis may thus be on the one hand the source of neuronal motor command components for pecking while at the same time it receives auditory and tactile afferences that are relevant for the control of pecking.

To this it must be added that, as discovered by Zeigler, Hollard, Wild and Webster (1978), electrical stimulation of the nucleus basalis, among other structures, has reinforcing properties. Delius, Williams and Wootton (1976) had previously found that the tracti quinto-frontalis and fronto-archistriaticus, both as described earlier associated with the nucleus basalis, supported brain self-stimulation (Fig. 5.7). Delius and Pellander (1982) noted an association between dopaminergic structures and self-stimulation sites in the pigeon, much as it has been reported in mammals. The dopamine agonist apomorphine is obviously capable of activating the nucleus basalis and histochemical investigations indicate that this, and other structures that support self-stimulation, are naturally rich in dopamine (Minelli, 1970; Brauth, Ferguson & Kitt, 1978). However, the coincidence of reinforcement pathways, sensory afferences and motor efferences in this area seems suggestive that this area may be directly involved in conditioning processes associated with pecking.

The pecking of pigeons, pursuing this line of thought, is undoubtedly under close and very plastic, in the sense of conditionable, control of visual stimuli. Where if at all, could visual information enter the presumed peck-steering nucleus basalis related system? I once speculated, simply on grounds of neighbourhood, that it did so via the optic thalamofugal projection reaching the fronto-dorsal telencephalon, the hyperstriatum or Wulst, a probable homologue of the mammalian visual cortex (Delius, 1971). But that is probably not so since large bilateral lesions in this area do not produce appreciable deficits in visually conditioned discriminative key-pecking (Parker & Delius, 1980) nor in visually guided unconditioned pecking (Parker, unpublished experiments). The fact that unilateral Wulst

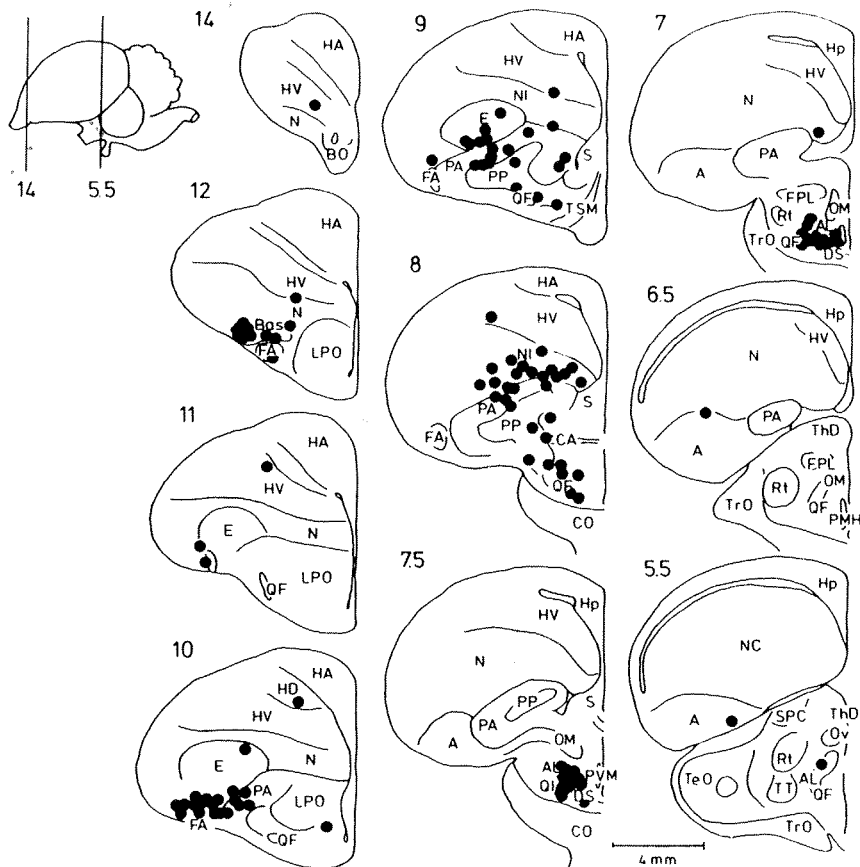


FIG. 5.7. Brain sites that have yielded instrumental electrical self-stimulation in pigeons. Note that among other structures the nucleus basalis (Bas) yields reinforcement effects (compilation, modified after Delius & Pellander, 1982). Abbreviations as in Figs. 5.2 and 5.6 and: BO bulbus olfactorius, CO chiasma opticum, DS decussatio supraoptica, FA tractus fronto-archistriaticus, FPL fasciculus prosencephali lateralis, Hp hippocampus, LPO lobus paraolfactorius, N neostriatum, OM tractus occipitomesencephalicus, Ov n. ovoidalis, PMH n. medialis hypothalami posterioris, PVM n. periventricularis magnocellularis, QF tractus quintofrontalis, S septum, SPC n. superficialis parvocellularis, ThD thalamus dorsalis, TSM tractus septomesencephalicus, TT tractus tectothalamicus.

lesions can affect monocularly guided instrumental pecking (Nau & Delius, 1981) does not alter this assessment since the imbalance so created is likely to have this effect by mediating a dysfunction at lower visual centres through descending pathways.

Rather we have found that lesions of the lateral forebrain markedly impair visual hue, intensity and pattern discriminations both proactively

and retroactively in an instrumental food rewarded pecking paradigm (Delius, Jäger & Friesel, 1984). Ritchie (1979) has reported that the post-erolateral aspect of the telencephalon of the pigeon receives secondary visual projections from the Wulst and the ectostriatum. Furthermore, a visual evoked potential study done in our laboratory confirmed and extended to pigeons findings by Phillips (1966) who had described short latency flash evoked responses in the archistriatum of chickens (*Gallus gallus*). Using animals with chronic implanted electrodes Güntürkün (1984) found in our laboratory that visual evoked potentials of short latency (15–18 msec) could be recorded from the archistriatum mediale/neostriatum caudale border suggesting a direct input from di- or mesencephalic visual nuclei. This is just where the tractus fronto-archistriaticus coming from the nucleus basalis terminates (Fig. 5.3). It is possible that the visual information that controls pecking may enter the network at the archistriatal level.

In this context we have become aware that in the pigeon, as has been known for some time to be the case in the domestic chicken (Rogers, 1982; Andrew, Mench & Rainey, 1982), the visual control of pecking is lateralised such that the right eye and left brain play a dominant role (the optic nerve is totally crossed in birds). The effect of unilateral lesions is accordingly markedly non-symmetrical when pigeons are allowed the use of only one or the other eye (Güntürkün, 1985). This applies also to the lesions of the lateral telencephalon to which I have just referred (Jäger, 1985).

COGNITION CONTROLLED RESPONDING

We now concentrate on the control exerted by complex visual stimuli over the pecking of pigeons. First, however, I would like to remind readers of the fact that the vision of pigeons has some remarkable features: a sensitivity spectrum extending from the near-ultraviolet (300 nm) to the deep-red (700 nm), detection of the polarisation plane of light, an at least tetrachromatic colour vision system, and a division of the retina into two histologically different areas possibly associated with two different kinds of vision (Delius & Emmerton, 1979; Emmerton & Delius, 1980; Delius, Jahnke-Funk & Hawker, 1980; Emmerton, 1983a, 1983b, 1983c; Emmerton & Remy, 1983).

Here, however, we will deal with the visual pattern recognition capabilities of pigeons. An object in the environment can, depending on its relative distance and orientation with respect to the observer, cast very different retinal images. Differing lighting conditions will also yield different images. The image of a given object may on different occasions fall on

sections of the retina that have different transducing properties. Also such an object may cast an image on both retinae or on only one as the pigeons' binocular field is of restricted extent while the monocular fields are nearly panoramic (Jahnke, 1985). The effective information about the retinal image that is transmitted to the brain further varies due to the previous stimulation history of the retina (adaptation phenomena).

In spite of this it seems probable that the pigeon's central visual system can recognise such variable information as it receives through the optic nerves as belonging to one and the same object or to different objects. It is capable of what is known as invariance of object recognition. The information processing operations that bring this about are by no means trivial as we know from engineers who attempt to furnish artificial vision systems with similar performance. We have begun to systematically explore pigeons' capabilities in this respect. First we needed a flexible method. In the matching-to-sample paradigm a pigeon is presented first with a visual stimulus on the centre key of a Skinner box which it has to peck for two comparison stimuli to appear on side keys. The pigeon has to choose the comparison stimulus identical to the sample in order to be reinforced. The problem was that we needed to be sure that the animals would do so on the basis of a general same/different principle and not, as some authors have argued, by having learned a collection of stimulus specific rules (Carter & Werner, 1978). We reasoned that if the number of stimuli involved in training the matching-to-sample, or rather the converse oddity from sample, performance was large, then a stimulus-by-stimulus solution would be impractical for pigeons and the application of a concept-like rule would be promoted. To test for the existence of such a general rule we used transfer trials under extinction conditions involving new stimuli. An above chance performance in these test trials indicates that, since pigeons could not apply stimulus specific rules as the stimuli were unknown to them, they must have used a general rule (Fig. 5.8, Lombardi, Fachinelli & Delius, 1983).

This concept-like same-different principle used by pigeons gives us the possibility of investigating the invariance of pattern recognition. For example, will pigeons recognise the identity of a given visual form when it is shown in different sizes, that is will they evince size invariance of pattern recognition? In current work at our laboratory Celia Lombardi has been looking at this. She trained the pigeons on the oddity-from-sample task using patterns of the different sizes but in any given trial both the sample and the comparison stimuli were of the same size. In test trials the pigeons were faced with instances where the comparison stimuli were larger or smaller than the sample stimulus by a scale factor of about two. When the comparison stimuli were small the performance of the pigeons was excellent showing that they recognised the equivalence/non-

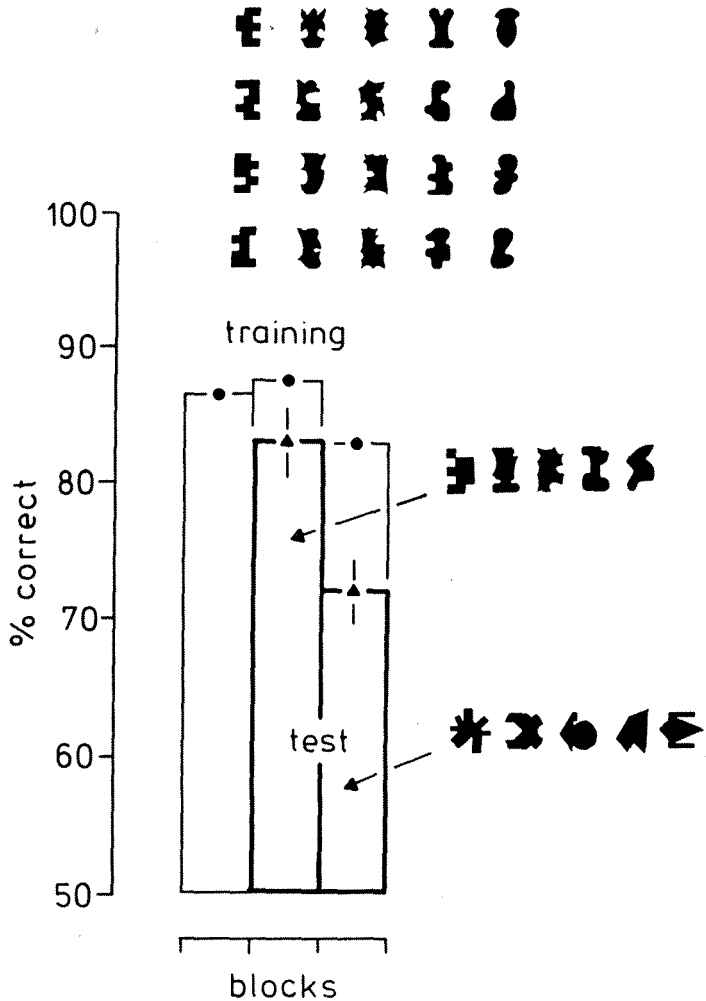


FIG. 5.8. Generalised oddity-from-sample performance of pigeons. The subjects ($N = 5$) learned the task with 160 three-stimulus configurations based on the 20 pattern (training, top). They were then tested for transfer of performance to totally new patterns in interspersed extinction trials using 40 configurations based first on the top five patterns, and then on the bottom five patterns (modified from Lombardi, Fachinelli & Delius, 1983).

equivalence of shapes in spite of size differences. When the comparison stimuli were large the discrimination of the subjects, though still above chance, was less good. At present we entertain two hypotheses about this latter result. Either pigeons are reluctant to peck at large stimuli and this interferes with discriminative behaviour or they only have a small visual-angle field of attention within which they can recognize a shape as a whole (Fig. 5.9).

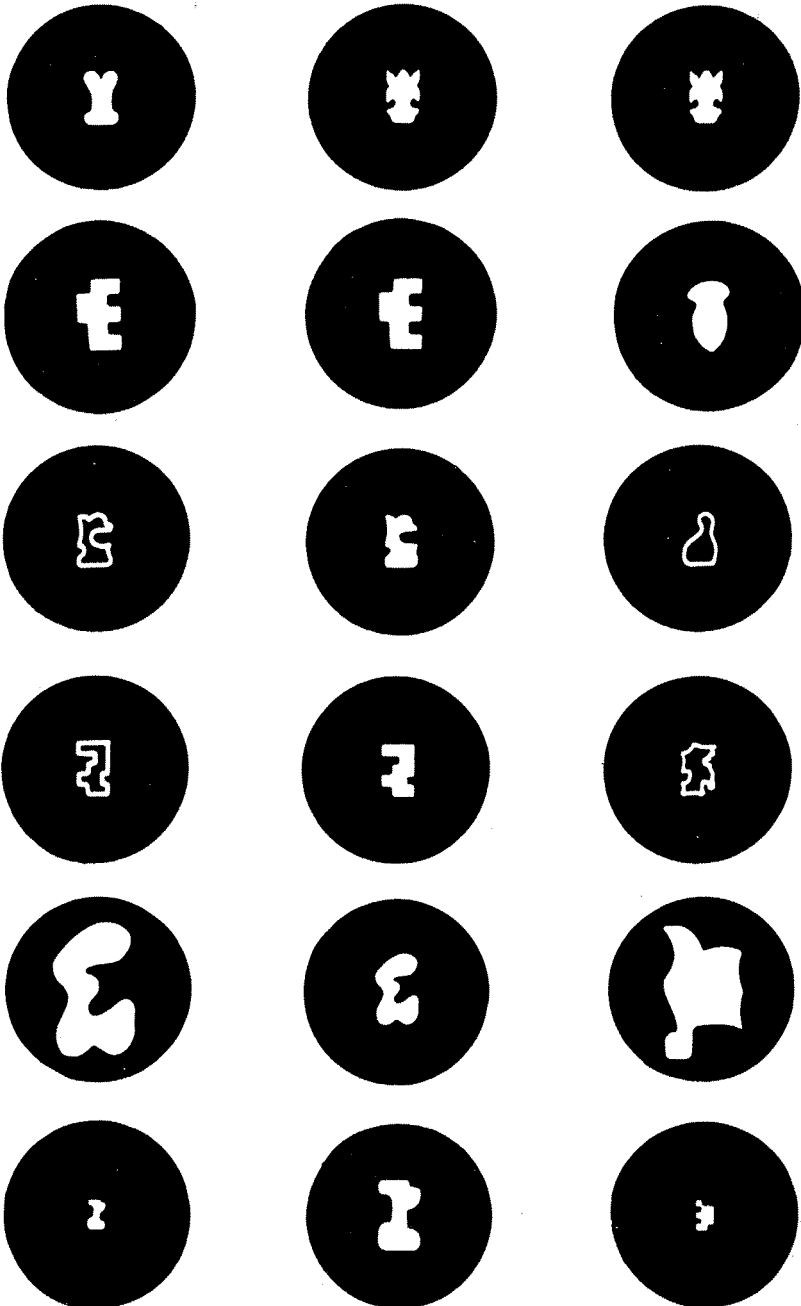


FIG. 5.9. Examples of oddity-from-sample stimulus configurations to study shape recognition invariance. Top: training configurations, middle: outline invariance, bottom: size invariance, test configurations (from Lombardi, unpublished; Lombardi and Delius, 1985).

Another invariance-of-pattern-recognition feat of which pigeons are quite capable is that of identifying the equivalence/non-equivalence of shapes and their outlines. That is what we do when we recognise objects represented in line-drawings. Since in nature such invariance is probably rarely in demand it is remarkable that pigeons should show this capacity. We suppose that as artificial vision designers (Duff, 1983) have found out, the extraction of the information equivalent to that of a line drawing from a visual scene is an almost essential basis for later scene interpretation, because it implies a considerable reduction of redundancy. There is good evidence that the mammalian visual system performs such outline extraction (Marr, 1982; Creutzfeldt & Nothdurft, 1978). Our evidence is that the avian visual system, though anatomically quite differently organised in being midbrain, optic tectum rather than forebrain, visual cortex based, does the same (but see Cerella, 1982).

A further instance of perceptual invariance performance by pigeons is of some interest because it is one that humans have difficulties with. R. N. Shepard and collaborators found that if humans were asked to decide whether two visual shapes are the same or different when the different shape is a mirror image of the original shape, the reaction times increase as a function of the orientation misalignment of the forms to be compared. Later research has revealed that the slope of this "mental rotation" function of a person correlates with his visuo-spatial abilities score measured by standard intelligence tests. The subjective impression while doing this task is that to solve the more difficult instances one has to think hard. There is more objective evidence that serial processing of information is involved where the number of successive steps until solution is greater when the angle of the orientation disparity between shapes is larger (Shepard & Cooper, 1982). We have looked at how pigeons deal with this task (Hollard & Delius, 1982). Using the matching-to-sample technique as described earlier the subjects were confronted on each trial with a sample geometrical form and subsequently with two comparison forms, one identical to sample, the other a mirror image of it. In the "mental rotation" tests the comparison patterns were rotated in the frontal plane by various amounts from 0 to 180 degrees against the sample shape that was always presented in a standard orientation. The animals showed better than chance performance on these tests and, importantly, showed no sign, either with respect to the error rates or the reaction times, that they found the increasing angular misalignments of samples and comparison shapes more difficult. Humans tested with the same shapes and apparatus showed a strong effect, reaction times in particular lengthening markedly with increasing angular mismatches (Fig. 5.10, Delius, 1985).

Pigeons thus performed better on this invariance task than intelligent humans. It seems obvious that pigeons do not utilise a serial mode of information processing as humans do but a parallel one. Humans can do

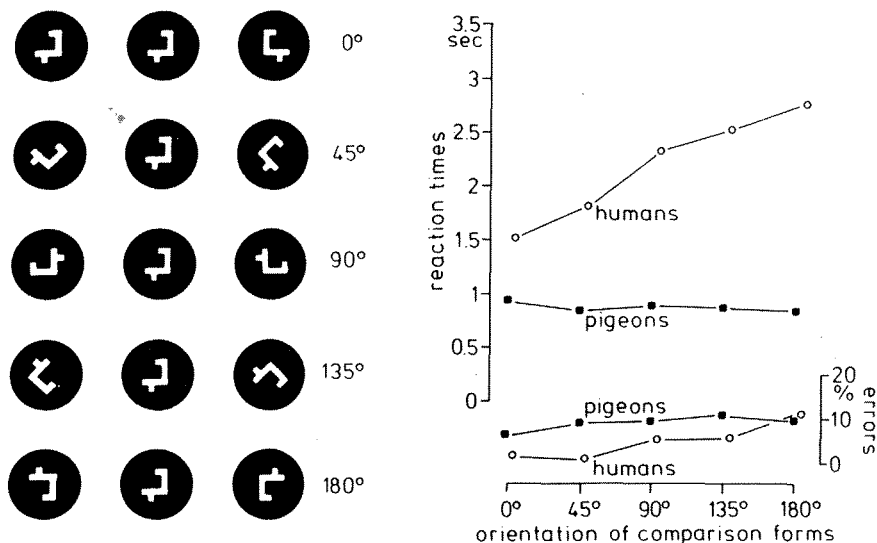


FIG. 5.10. Performance of pigeons and humans in a task involving the rotational invariance of shape recognition (right: examples). Humans ($N = 22$) yielded a typical "mental rotation" performance (longer reaction times with increasing orientation disparities), pigeons ($N = 9$) did not show such effect (modified from Hollard & Delius, 1982).

that too but only when the rotation invariance tasks involve arbitrarily different shapes rather than mirror image shapes. It is known that mirror image shapes are peculiarly difficult for humans to discriminate (Corballis & Beale, 1976). An explanation could be that pigeons find mirror image shapes just as easy as arbitrarily different patterns to distinguish and thus do not need to resort to the time consuming serial processing to which humans seem to be forced. Recent work of ours shows this not to be likely. Pigeons were taught to discriminate several pairs of visual patterns with a successive free operant method. Half of the pairs were mirror images, the other half were arbitrarily different shapes. The pigeons' performance was markedly worse on the mirror images (Lohmann, Delius, Hollard & Friesel, 1985). The other explanation that we offered is that pigeons may tend to store information about visual patterns in an orientation free mode because, differently from humans, they operate visually predominantly on the horizontal rather than the vertical plane. Whereas in the latter plane objects and observers usually have definite orientations with respect to gravity and the horizon, in the former neither objects nor observers have any preferred orientations. But how are we to imagine an orientation-free engram? Certain complex mathematical transformations of spatial patterns are said to yield this property (Hord, 1982). Perhaps the pigeon's brain is making use of such image information conversions.

Beyond the fact that a given object can cast different images on the retina it can also change its appearance by itself, particularly if it is a live organism. We know that pigeons are at a premium to recognise such objects in spite of their variable appearance, as they may be competitors, mates, offspring and suchlike. Herrnstein, Loveland and Cable (1976) demonstrated that they can indeed easily learn to identify such kinds of variable objects, a particular person for example, as different from other persons on a collection of slides and that they are then capable of extending this recognition to new, previously unseen slides. A further step is the recognition of different objects as belonging to a particular class. For pigeons this might be predators, conspecifics, trees, nesting sites, all categories whose recognition is likely to be important for Darwinian fitness. Again Herrnstein, Loveland and Cable (1976) have demonstrated that pigeons can learn to recognise items belonging to such categories. For example, they showed that pigeons would learn to pick slides showing water in its various forms (puddles, lakes, rivers, seas, etc.) from slides not showing water and that again they were capable of extending this distinction to novel slides.

We have been interested in finding out whether pigeons would be able to learn about a more abstract category, bilaterally symmetrical shapes as different from non-symmetrical shapes. We used a free operant successive discrimination technique to train the discrimination using 52 different shapes. The acquisition of the discrimination was so efficient that we are inclined to think that we did not teach the pigeons the perceptual concept symmetry/asymmetry but rather only to apply one that they already had, perhaps even innately. Later we inserted transfer trials under extinction conditions with over 200 novel stimuli. Even when the test stimuli were quite different in geometrical style from the training stimuli the pigeons' performance was excellent. This was also so when the orientation of the symmetry axis of the test stimuli differed from that of the consistently vertical orientation of the training stimuli. Pigeons also mastered the concept-like discrimination of symmetric versus non-symmetric stimuli when they could use only one eye. This indicates that the recognition of bilaterally symmetrical patterns has little to do with the gross symmetrical organisation of the visual system (Delius & Nowak, 1982). We have rather hypothesised that the recognition of symmetry is based on the fine, multiple-symmetric structure at the histological level seen in tangential sections of the optic tectum. We contend that systems that analyse in parallel surface information like pictorial images in a largely homogeneous manner must have such a structure. If this reasoning is correct, the salience that bilateral symmetry has for humans and apparently for pigeons moves into the neighbourhood of many visual illusions, useless side-products of otherwise useful information processing networks. If so it is perhaps better

to talk of bilateral symmetry as a feature rather than a concept (Delius & Habers, 1978).

CONCLUSION

I have described phenomena and processes that have caught our interest in the recent past. All were related to just one kind of behaviour, the pecking of pigeons. Nonetheless the tale meandered through various scientific fields. Probably most of the few explanations offered are wrong, but can it be conceived that the problems raised can all be answered by just one discipline, just a single tradition? It is my contention that besides experimental analysis and ethology there are a multitude of other branches of knowledge, from genetics to robotics, from economics to ecology, from histochemistry to sociobiology, that contribute or can contribute to the description, explanation, understanding of behaviour. I have yet to hear convincing reasons why they should not. After all, even the microcephalic pigeon has a brain that contains some 10^8 neurones times some 10^3 synapses, a remarkable high performance biological nano-computer dedicated to the very special purpose of maximising its owners fitness. That allows for no mean complexity and makes the task of accounting for behaviour so difficult that any useful suggestions must always be welcome. Everybody should join the meleé!

ACKNOWLEDGEMENTS

Thanks are due to Mrs D. Hagenkötter, Mrs P. Ohmann-Jamal, Miss A. Lohmann and Miss J. A. Delius for excellent assistance. Dr P. Deviche, Dr V. D. Hollard, R. Jäger, H. J. Jahnke and O. Güntürkün kindly allowed me to refer to as yet unpublished work of theirs. Dr J. Emmerton criticised an earlier version and made useful suggestions. The research reviewed was supported by the Deutsche Forschungsgemeinschaft through its Sonderforschungsbereich 114, the Heinrich Hertz Stiftung and the Research Fund of the Ruhr-University.

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