

Biology Can Use Trained Animals¹

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ANIMALS (especially the higher ones) tend to do whatever earns them reward and avoid whatever leads to punishment. This commonplace observation has, for about 75 yr (ref. 1), tantalized psychologists with the promise of a useful and enlightening science. To fulfill the promise, psychology studies the nature of rewards and punishments, their interrelationships, the underlying physiological machinery, the differences and similarities among species in these respects, the relations between current behavior and past rewards and punishments, and so on. None of these subjects, however, will concern me here, for the theme of this paper is not to summarize how our science is progressing, but to show that there already exists a technology of reward and punishment that is simply waiting for application in other fields of biology, particularly when questions of sensory or motor capacity are involved. My case will rest on several examples, already in the psychological literature, in which the use of trained animals has solved problems not easily solved by more common biological procedures.

The experimental paradigm was per-

fectured by B.F. Skinner in the early 1930's (ref. 2), working not in a psychological laboratory, but in W.J. Crozier's laboratory for general physiology. The original "Skinner box" was a chamber measuring about 0.3m³ cubed into which a hungry rat was placed and simply allowed to move freely about (ref. 3). Protruding through a wall of the chamber was a horizontal lever that could be depressed and thereby operate a device that dropped a food pellet down a chute and within the rat's reach. Acting in accordance with principles that need not be explicated here, a rat in the box quickly learns to depress the lever with fair regularity, until its hunger is spent. Now imagine a slightly more complex procedure. Suppose pressing the lever is rewarded only when a lamp is turned on and off from time to time, at irregular intervals and independent of the rat's behavior. The pattern of reward and non-reward follows along: After a little practice, the rat is guided by the lamp, pressing much more in the light than in the dark. Note, however, that the relation is arbitrary. The absence of light could just as well have been made the signal for work, if reward had been correlated with darkness and non-reward with light. How reliably the rat obeys the lamp

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depends on many factors—the degree of hunger, the amount of work involved in pressing the lever, the rate and pattern of lamp on and off, the size and composition of the food pellet, the schedule of reward, and, no doubt, factors not yet identified. However, the lamp's power to control responding also depends upon the rat's visual sensitivity and the size of the stimulus change. If the light is very dim, then turning it on and off will control behavior less decisively than if the light is quite bright, all other factors held constant. In the limiting case, if the light is dimmer than the minimum visible intensity, then lever pressing will simply occur independently of the state of the lamp, for the rat can hardly attend to a light it cannot see.

This hypothetical experiment is supposed to suggest how a training procedure may be applied to a question of sensory process, in this instance a visual threshold. The remainder of the paper deals with actual experiments, in which the procedures are usually (but not always) a good deal more complicated. Among other things, I hope to show that the complexity is appropriate to the task, which is to say that the experiments use the simplest procedure for getting at the desired question.

SENSORY CAPACITY

The first experiment I would like to describe was done by a Harvard undergraduate (ref. 4) who wanted to know whether pigeons can smell, a question that had not yet been unequivocally answered. Since some of the mystery surrounding animal navigation and orientation is similarly a question of sensory capacity, Michelsen's work has special relevance here. Olfaction in birds, in spite of the interest and scientific efforts of such eminent figures as Audubon in the 19th century and Grey Walter in the 20th, was still an

open question when Michelsen undertook his research. The apparent ability of birds to find or flee from odorous objects, like carrion or predators, could be based on smell or on other sensory modalities—sight or hearing in particular—and the relevant evidence was ambiguous. Michelsen's approach was to devise a training procedure such that if a pigeon can smell, then it would learn a correlation between the odorant and reward, but that if it is without a sense of smell, its responding would be random.

Figure 1 shows the pigeon's eye view of the front of the experimental chamber, of which the internal geography was crucial for the success of the procedure. On one wall were three switches (1,2,3) that the pigeons were trained to peck at in a manner to be described later. The square (B) was a feeding device that could be activated for brief periods, at which times the pigeon would eat. Two of the three switches (1,2) were in a partially enclosed cylinder. The pigeon could get at these two switches only by inserting its head through an opening (A) in the cylinder. Also inside the cylinder was the access to the feeding device, but food was found there only when the procedure called for reward. The third switch (3) was beside the cylinder, available for responding while the pigeon did not have its head in the cylinder. There were also two sources of illumination: one inside the cylinder (E) and the other outside (not shown). The cylinder was constructed so that a stream of gas piped into it from the top (C) was exhausted from its bottom. In addition, several exhaust fans could evacuate any lingering gasses from the general interior of the chamber.

The testing procedure involved a sequence of responses and stimulus changes, as follows. At the beginning of a trial, the general chamber light is on, but the interior of the cylinder is dark. A peck at the switch (3)

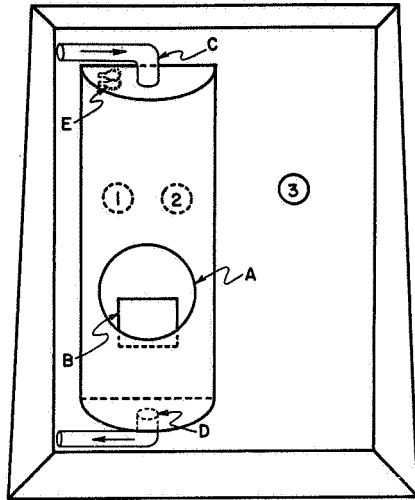


FIGURE 1. Interior view of front wall of apparatus for studying olfaction in pigeons. Redrawn from Michelsen (ref. 4).

outside the cylinder starts the flow of gas within the cylinder, and also starts a nine-second timer. At the end of the nine-second period, a peck on switch (3) turns the lights off outside the cylinder, illuminates the inside of the cylinder and thereby signals to the pigeon that the switches inside the cylinder are operative. The pigeon will then insert its head into the cylinder to peck at either of the two inside switches.² If the stream of gas contains an odorant, then the seventh peck at the left switch is rewarded; if it does not contain an odorant, then the seventh peck at the right switch is rewarded. However, in any case, a fourth incorrect peck before the seventh correct peck terminates the trial without

² The intermediate stages of training will not be described here, neither for this experiment nor the others to follow. Usually, the final procedures must be approached in small increments allowing the subject to become thoroughly acclimated at each level. Unfortunately, there appears to be no general rule for this process of successive approximation. Some points can, however, be found in Skinner (ref. 5).

any reward at all. The reason for this seemingly arbitrary asymmetry of correct and incorrect responses is that it penalizes the pigeon for alternating randomly between the two switches. If the criterion for right and wrong were equal, then the pigeon would be rewarded half the time for just random responding. With asymmetry, the likelihood of reward for random responding is quite low, apparently low enough so random responding is precluded, as Michelsen's results showed.

At the end of a trial the gas stream is shut off and there is a one-minute rest period, during which the exhaust fans cleanse the chamber of any lingering odors. On any given trial, the gas stream either contained an odorant or else air passed through distilled water. Whenever a trial ended in failure, the stimulus conditions were repeated for the next trial. After a successful trial, the next trial randomly presented the odorant or the non-odorant. The reason for this procedural complication, called a "correction procedure," is to keep the pigeon from always choosing just one switch. Without the correction procedure, a pigeon which responded to just switch (1) or just switch (2) all the time would, given the random alternation of stimulus conditions, be rewarded on half the trials. And being right half the time is good enough for most pigeons, so they would not bother to learn that by attending to the presence or absence of the odorant, they could be right up to 100 percent of the time. With the correction procedure, however, such perseverative responding would soon lead to no reward at all, for as soon as responding was on the wrong switch, then perseveration would prevent the stimulus condition from changing.

Michelsen tried several different odorants and found that performance levelled off at about 85 to 90 percent of the trials correct, with chance dictating 50 percent (discount-

ing trials repeated because of the correction procedure). The more irritating odors—like sec-butyl acetate—got a somewhat better score than the milder odors—like isooctane. No doubt, trigeminal nerve irritation simply added to olfactory nerve stimulation, probably more so for irritants like sec-butyl acetate. However, the discrimination in all cases was unmistakable. Various control procedures confirmed that the stimulus was the odorant itself in the air stream, and not some procedural or apparatus artifact. Of course, such artifacts cannot be absolutely excluded, but a reasonably thorough search failed to uncover any.

The conclusion of the study is that pigeons, and therefore probably other birds, possess a sense of smell, which is reassuring, given the well-developed olfactory bulbs that many birds have. However, until this study had been done, the apparent neurological basis for olfaction was not evidence of olfaction, but only a hint of it. A sense modality is, in the last analysis, a psychological phenomenon, not a physiological organ. This is not to deny the physiological basis of sensation or any psychological process, but to note that the *sine qua non* of a sense is some sort of behavioral manifestation.

Michelsen's experiment illustrates a number of key ingredients in the use of behavioral techniques for answering questions of sensory capacity, and is therefore worthy of some further consideration. The only points of contact between the experimenter and the subject are the contingencies of stimulation and reward. The pigeon responds so as to be rewarded, but it cannot be assumed that it will attend to stimuli unless doing so has some significant effect on the outcome. In fact, all other things being equal, the animal is disposed not to attend to redundant stimulation.

How to arrange the dependency between stimulus and reward and how much differ-

ence attention is to make are important practical questions, unfortunately without general answers, only specific ones for specific questions. The skillful experimenter is guided by his subject's behavior toward the optimal level of complexity, where the subject is maximally disposed to attend to the relevant stimuli. Michelsen's procedure is the outcome of such an interaction between subject and experimenter. Thus, the asymmetry of the criteria for right and wrong trials discouraged random responding. Because it took seven pecks to be right and only four pecks to be wrong, there was a significant premium for paying attention to the olfactory stimuli as compared to just random responding. The correction procedure similarly kept the pigeon focussed on the right aspect of the situation, from the experimenter's viewpoint. Without it, responding could have become stereotyped and still be rewarded half the time. Other features of the procedure, although mainly concerning matters of house-keeping, were also important. The third switch and its associated nine-second interval held the pigeon and the presentation of the stimulus in the cylinder in phase with each other. By letting the pigeon pace the experiment, the stimuli to be attended to were only presented when the subject was ready to work.

LIMITS OF SENSORY CAPACITY

Michelsen's experiment is a good model for finding out whether an animal has a sensory capacity at all. Obviously, any adaptation of it must take into account the nature of the stimulation at question. Delivering an odor is not much like delivering a magnetic field or indicating a compass direction; but careful analysis and trial and error should extend the method to other instances. The basic notion of using the animal's interest in

being rewarded to find out about its sensory processes is, however, far from limited to such simple questions as whether a given sense exists. Because it exemplifies a more exacting field of study, I should like to describe an experiment by Blough (ref. 6) that traced the course of visual dark adaptation in pigeons. The question is not whether vision is present in general, but what is the absolute visual threshold from moment to moment.

The experimental chamber permitted the showing of visual stimuli under precise control. As in Michelsen's apparatus, there was an enclosure (see figure 2) into which the pigeon had to insert its head to get at the response switches (A,B) and the feeder, and within which the stimuli were presented. Once inside the enclosure, the pigeon could look at a stimulus patch which provided the sole source of illumination for the chamber. The function of the shutter, wedge, and record are described below.

Blough's procedure is an adaptation of Békésy's method for tracing the absolute auditory threshold, which is the standard measurement of clinical audiometry. The human subject for an audiogram wears a pair of

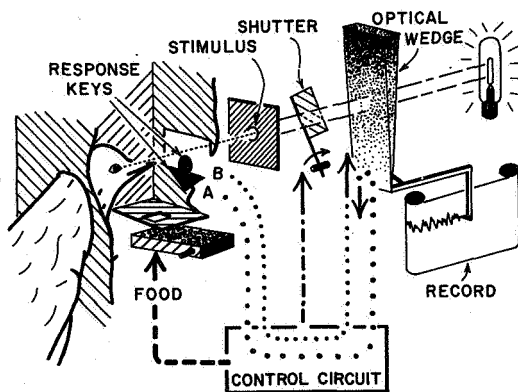


FIGURE 2. Schematic rendering of apparatus for tracing visual dark adaptation in pigeons. Redrawn from Blough (ref. 6).

earphones and listens for a pure tone whose intensity grows with the passage of time. He is instructed to press a button if he hears the tone, but pressing the button drives the intensity of the tone down. When the tone drops below his absolute auditory threshold, he no longer hears it and should therefore release the button, which allows the tone to resume its upward course. The interaction of subject and apparatus thus produces a tone whose intensity fluctuates around the absolute threshold. In standard audiometry, the frequency of the tone sweeps up and down the audible range, so as to give the clinical audiogram, but other parameters, of the stimulus or the subject himself, may be varied instead.

Blough's problem was to find a way to instruct the pigeon to keep the light similarly at the threshold, but his only points of contact were the contingencies of stimulation and reward. The pecking of one switch (key A) reduced the intensity of the light by driving the optical wedge (usually by a small amount like 0.03 log units), while the pecking of the other (key B) increased it (by an equal amount.) This differs from Békésy's method, in which the stimulus intensity rose simply with the passage of time, by having both decrements and increments produced by discrete response. If the pigeon ceased pecking, the light would hold at its current intensity. Since Blough's procedure takes into account the possibility of moments of inattention, it might improve the results even with human subjects.

Superimposed on this control of light intensity, pecking had several other effects. Pecks at key B (the stimulus-increasing switch) were occasionally rewarded with a bit of food, and the pigeons were always studied when they were hungry. The rewards were intermittent and irregular, but never given unless the light was actually out. Pecks

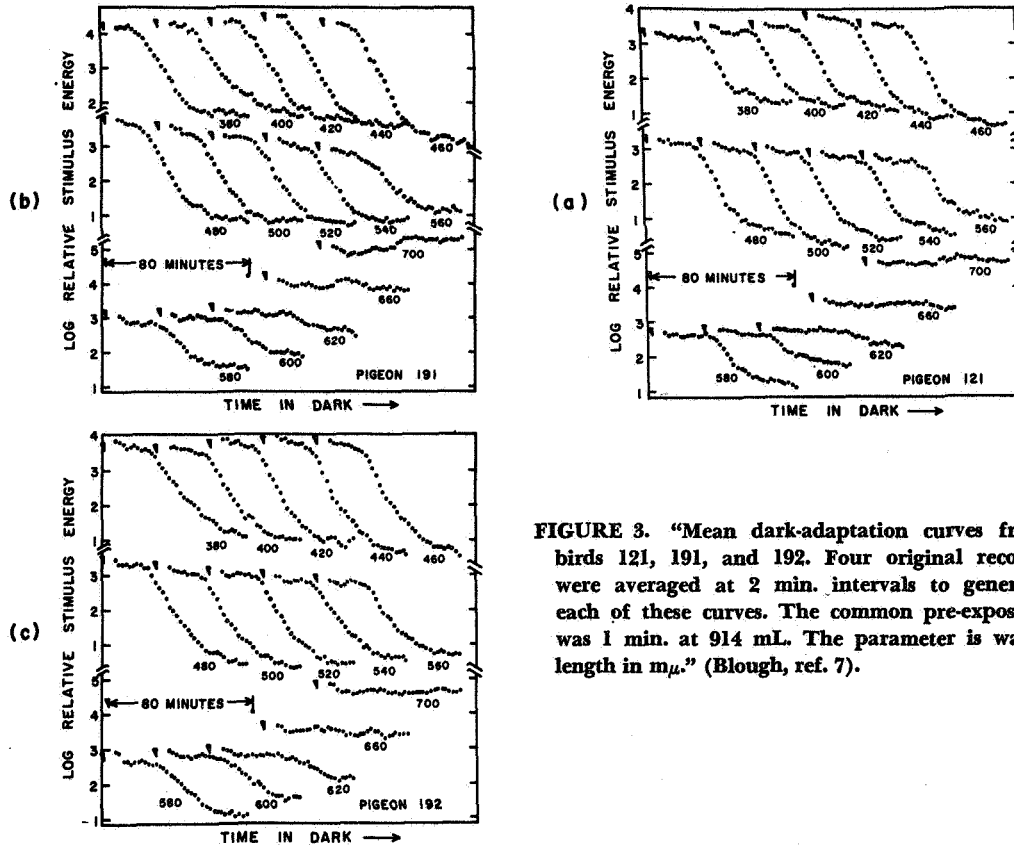


FIGURE 3. "Mean dark-adaptation curves from birds 121, 191, and 192. Four original records were averaged at 2 min. intervals to generate each of these curves. The common pre-exposure was 1 min. at 914 m μ . The parameter is wavelength in m μ ." (Blough, ref. 7).

at key A occasionally turned out the light by operating the shutter. The shutter closures were intermittent and irregular, but remember that pecks on key A also had a continuous effect on stimulus intensity via the wedge and independent of the shutter action.

Combining the various effects, the procedure made a psychophysical observer out of the subject. Each peck at key A automatically decreased the intensity of the stimulus by 0.03 log unit, and, in addition, occasionally blanked out the light entirely. When the light was actually out, pecks at key B were occasionally rewarded with food. Because both shutter closures and food were given on aperiodic, intermittent schedules, the pigeon was

deterred from simply alternating between the two keys without regard to the stimulus. The various schedules were designed so that random alternation would only rarely lead to reward. Pecking at key A drove the stimulus down in small increments, until the pigeon could no longer see the light, which looked to the pigeon like the right time to move to key B. But switching over to key B raised the light intensity above the absolute threshold, and so the pigeon would go back to key A to drive the stimulus down again, and so on. Occasionally, when a key A peck actually closed the shutter, pecks to key B would unpredictably produce the food, but this was relatively uncommon. Most of the time, the

pigeon just switched back and forth between the two keys, as the light dipped down and rose above the threshold. As in audiometry, the subject traces out its threshold as the experimenter varies whatever he is interested in. Blough's actual procedure was even more complicated than I have indicated, for there were slight penalties for incorrect responses and delay contingencies for switching too rapidly from one key to the other, but these are not described here. The foregoing shows amply that the conditions of reward are correlated with the stimulus so that the more fully the subject reveals its sensory capacity the more successful it is in gaining reward.

A sampling of Blough's findings is the best argument for the general method. In one experiment (ref. 7) on three pigeons, he examined the course of dark adaptation for lights of various wavelengths, following pre-exposure to one minute of white light of an arbitrary intensity. Figure 3 shows the results for the three pigeons, one beneath the other. Each tracing is an average of four runs through the dark adaptation curve, with the wavelength indicated as the parameter. The ordinate is log stimulus intensity on a relative scale, and the abscissa is time. These curves show, first, that pigeons are not unlike people as regards dark adaptation and, second, that Blough's method is a valid way of finding this out. When the stimulus was at the short end of the spectrum, there were clear rod-cone breaks in the threshold, but toward the red end, the rod section disappears, as expected. The first few minutes of each curve are deleted because the pigeons tended to be unstable at the beginning of each session.

From the data in figure 3, Blough constructed the analogues of human photopic and scotopic luminosity functions. The photopic function was taken from the average of the first five data points on each tracing, while the scotopic curve was taken from the

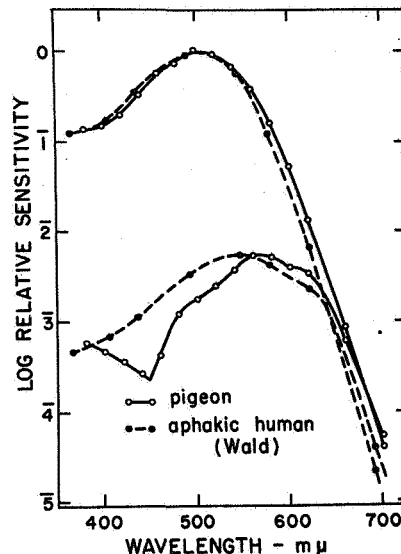


FIGURE 4. "Mean data from Figure 3 plotted together with Wald's spectral sensitivity curves for aphakic human subjects. The human photopic and scotopic curves are independently matched to the pigeon data. Wald's published data have been corrected for calibration errors in accordance with a personal communication." (Blough, ref. 7).

average of the last five points. These are shown as reciprocals (i.e. sensitivity instead of stimulus intensity) in figure 4, which also plots Wald's (ref. 8) data for human subjects who lack lenses (aphakics) to take account of the pigmentation of the human lens. The two sets of data agree to a fair extent, but it should be noted that the scotopic and photopic curves were matched independently, so that the figure contains no information about the scotopic-photopic separation (the "achromatic" interval). Finally figure 5 shows the agreement between Blough's data on the one hand, and, on the other, Granit's (ref. 9) and Donner's (ref. 10) electrophysiological data for the pigeon eye. The physiological data plot the firing of retinal elements in the pigeon eye, using a given level of nervous activ-

ity as the criterion of response. The response was obtained as the wavelength of the incident light was swept back and forth through the visible range. At each wavelength, the minimum intensity for the criterion response is plotted. Donner used a dark-adapted eye, while Granit used a light-adapted eye, so that their data are, respectively, applicable to scotopic and photopic processes. Once again, the size of the achromatic interval cannot be taken as equal since the curves were matched independently. The agreement nevertheless further indicates that Blough's psychophysical method reveals something about the visual process itself and not just the accidents of the training procedure.

SENSORY MAGNITUDE

The study of sensation has long sought a quantitative measure of psychological magnitude. We start by knowing, for example, that some lights appear to be brighter than others, and also that, in general, the appearance depends on the physical energy. But we also know that physical measures rarely predict psychological magnitudes in quantitative detail. For most of man's modalities, the sensory intensity is non-linearly related to the physical measure of the stimulus, but psychologists try to describe the non-linearity more exactly. After about a century of thinking that sensory magnitudes are logarithmic functions of physical intensity (ref. 11), we now have reason for believing that the general relation is a power function, with various exponents for the various modalities (ref. 12). For example, psychological brightness in vision is proportional approximately to the cube root of luminance for man. In contrast, loudness is proportional to the 0.6 power of sound pressure. Taking all modalities, the exponent ranges broadly, the known maximum being for the sensation caused by an electric shock

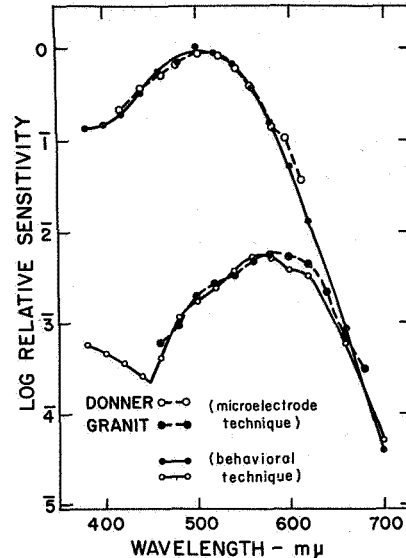


FIGURE 5. "Mean data from Figure 3 plotted together with electrophysiological threshold data on the pigeon eye obtained by Granit and by Donner. The electrophysiological curves are independently matched to the behavioral curves." (Blough, ref. 7).

to the skin, for which sensory magnitude grows as the 3.5 power of the current passing through the finger. These exponents are established in experiments that require human observers to make judgments relating to the intensity of their sensations. Sometimes the observer is asked simply to say numbers proportional to his sensations as the stimulus is varied by the experimenter; sometimes he is asked to adjust the stimulus intensity himself, until it seems to be in a given ratio to an arbitrary stimulus; sometimes he is asked to match the ratio of the apparent intensities of one pair of stimuli to that of a given pair, and so on. In general, the observer's task is to respond overtly in some way proportionate to the sensory magnitude. Can this sort of experiment be done with animals? Must we teach animals about ratios and proportionalities to find out how intense stimuli seem to them?

The experiment described below yields some information about the apparent magnitudes of sensation in pigeons, without having imparted any mathematical sophistication to them.

Van Sommers and I (ref. 13) were trying to learn something about the pigeon's experience of visual brightness, in particular whether it obeyed the power law, the logarithmic law, or, more fundamentally, whether such a question can be asked sensibly of a pigeon. As usual, the pigeons were hungry and were trained to peck at a key for food reward. In this experiment, however, pecking was rewarded if and only if it occurred at a certain rate, defined by the duration of the inter-peck interval. For example, the pigeon got fed when two consecutive pecks were no more than 11 and no less than 10 seconds apart. A premature or tardy peck got no food and restarted the interval. Pigeons on this procedure are known to be able to conform roughly to the required rate, tending on the average to respond a bit too quickly. However, because their responding remains somewhat variable in rate, they continue to receive occasional rewards notwithstanding the tendency to speed.

In our experiment, the pigeon's task was further complicated by an imposed correlation between the visual stimulus and the required rate of responding. When the light (which was projected directly on the response key) was bright, a high rate of responding was called for; when it was dim, a low rate was required. In between, medium intensities were correlated with intermediate requirements. All in all, there were five "training" intensities correlated with five required rates of responding, picked so that brighter lights called for faster pecking. The stimulus intensities covered a range of 2.4 log units with a stimulus every 0.6 log unit, while the corresponding required rates of respond-

ing were from about 0.7 to 0.005 responses per second. Expressing these as inter-peck durations (which are the reciprocals of the rate), the pigeons were required to peck at intervals of about 1.4 seconds for the brightest light and of about 200 seconds for the dimmest, with three intermediate values for the three stimuli in between. To be rewarded, the response had to fall within ± 5 percent of the required interval. As noted above, the responses tended to be premature. The size of acceptable range around the required interval is the main way to control the frequency of reward—the broader it is, the higher the proportion of rewarded responses. The ideal frequency of reward is the minimum which sustains performance, for then the animal is satiated with food most slowly and is not likely to rely on reward itself as the distinguishing feature among the five training stimuli and the four "test" stimuli, the latter to be described below.

During each experimental session, the stimuli came on at irregular intervals and in an irregular order. After sufficient practice, the pigeon's responding adjusted rapidly to whatever stimulus was presented, shifting its rate up or down as required. At this point, the test stimuli were added to the procedure. The four test stimuli were intensities falling at the geometric centers of the intervals between the five training stimuli. Since the training stimuli were separated by 0.6 log unit (6 dB in fig. 6), the tests were always 3 dB from the adjacent training stimuli. The presentation of test stimuli was randomly interspersed among the training stimuli. A test stimulus stayed for variable periods of time, during which no responses were rewarded. However, as noted, the generally low rate of reward kept the absence of reward during tests from becoming distinctive.

The main result of the experiment (see fig. 6) was the responding to the test stimuli,

enclosed by squares in the figure. The required rates of responding are shown by the hatched functions in the figure ("training curve"). The rates of responding actually obtained to the training stimuli are at 0, 6, 12, 18, and 24 dB for each pigeon. The rates to the test stimuli are at 3, 9, 15, and 21 dB. In each of the eight cases (four for each pigeon), the rate of responding to the test stimulus fell between the rates to the two adjacent training stimuli, even though the pigeons were never rewarded at all during the tests, let alone for these rates. Responding to the test stimuli must, therefore, have had something to do with how bright the lights looked to the pigeons. It can be shown mathematically that the logarithmic law predicts that the responding to the test stimuli, which are each at the geometric center of a training interval, should be at the arithmetic mean of the responding to the adjacent training stimuli. However, the power law predicts responding at the geometric mean. As figure 6 shows, the responding to the test stimuli fell at the geometric means (note logarithmic ordinate), thereby supporting the power function.

No doubt, this experiment could have been done more easily with human observers, who could simply have been instructed verbally to respond to the lights. However, there may be occasions when animal observers would be preferable, as, for example, when the physiological basis of sensation is to be studied.

HEDONIC VALUE

Thresholds and magnitudes are by no means the only interesting sensory parameters. Sometimes, we may want to know whether a stimulus is itself rewarding or punishing, not just whether it is detectable or more or less intense. This more purely psy-

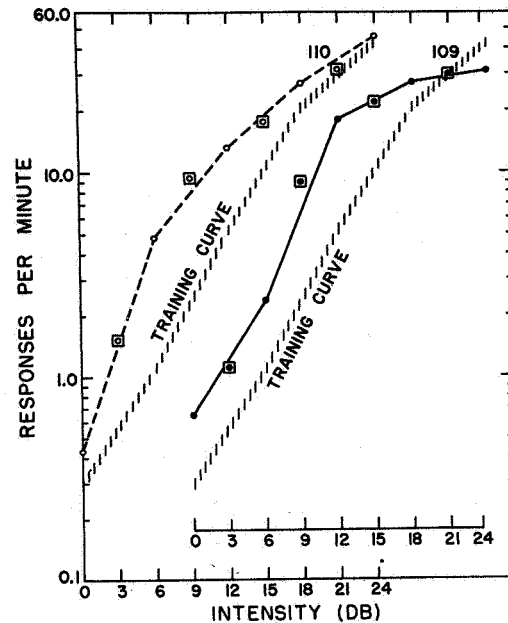


FIGURE 6. "Rate of pecking as a function of the luminance of the stimulus, for two pigeons (Nos. 109 and 110). The training curve shows the prescribed rate of responding at the training stimuli (0, 6, 12, 18, and 24 db). Points enclosed in square give rates obtained with test stimuli (3, 9, 15, and 21 db), in whose presence responding was never reinforced." (Herrnstein and van Sommers, ref. 13).

chological question, which may be called the question of hedonic value, pervades the contact of animals with their environment. For example, the well-known ability of animals to select a proper diet arises from the hedonic effects of stimuli rather than from the straightforward sensory parameters. The mechanisms of dietary selection are largely concerned with how physiological states are translated into reward and perhaps into punishment. See, for example, Rodgers and Rozin (ref. 14) on thiamine and Kriekhaus and Wolf (ref. 15) on sodium chloride. The translation can take many forms. In some cases, the food is rewarding because of its

nutritive value, but in other cases, the reward is owing to a collateral property of the food, such as its taste. Over the course of evolution, one might expect that such collateral properties would have, at least in some instances, acquired the power to reward. The behavioral effects of sugar nicely exemplify this range of possibilities. It has been shown (ref. 16) that sweetness, independent of caloric content, rewards responding, since saccharine and other non-caloric sweet substances will sustain behavior, at least in rats, and, undoubtedly, human beings. However, it has also been shown (ref. 17 and 18) that at least monkeys and rabbits are somewhat rewarded by the direct injection of glucose into the bloodstream, bypassing the entire ingestive machinery. Other studies (ref. 19) have shown that nutriment at various other points in the physiological chain have some rewarding power over behavior. All in all, it seems that nature is highly redundant in its allocations of the rewarding power of carbohydrates, which is perhaps to be expected given their importance to survival. Other foods and dietary ingredients have also been studied from this point of view, and the tale, though interesting, is far too long for retelling here. My main point is that the study of nutrition is in part a psychological study, centering on the capacity of certain events to control behavior.

No doubt it is obvious that eating involves behavior, for the finding of provender usually requires action. But other contacts between organisms and their environment may also be regulated through the mechanisms of reward and punishment, albeit more subtly. Consider, for example, the diurnal cycle of activity in canaries, which is apparently endogenous as in many creatures. Wahlström (ref. 20) has shown, however, that a canary will, if given a chance, turn the lights in its birdcage on and off to produce a light-dark cycle

if the cycle is not externally provided. Then, having produced its own cycle, its general activity waxes and wanes in tempo. The diurnal cycle is not just a passive fluctuation of activity—like the passive fluctuation of air temperature during the 24-hour period—but an active hedonic swing that undoubtedly affects profoundly the animal's natural patterns of life. The distinction is psychological, best studied by behavioral techniques of the type described here.

It may be that such hedonic mechanisms are the rule rather than the exception and that in many physiological systems, the contact between organism and environment is shaped by the dynamic effects of reward and punishment. Van Sommers, for example, has shown (ref. 21) for rats, turtle, and goldfish—representing the three main classes of vertebrate—that respiration involves such a reward system. To pick the intermediate example, figure 7 shows the apparatus devised by van Sommers (ref. 22) to keep a turtle

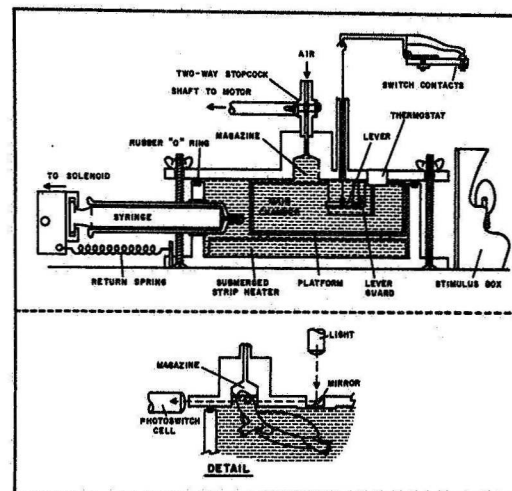


FIGURE 7. "Cross section of turtle apparatus. (Detail: Photoswitch arrangement for recording the entry of the turtle's head into the magazine.)" (van Sommers, ref. 22).

(*Pseudemys scripta elegans*) submerged in water ("main chamber") until a lever was pressed and opened up a small airfilled chamber ("magazine") by operating the syringe and lowering the water level. The first and main point of this study for our purposes is that the turtles did depress the lever and keep themselves adequately ventilated, which is by no means a foregone conclusion. One could imagine an animal whose need for air does not tie into the rest of its effectors so as to permit such adaptability, but the turtle's does. Furthermore, van Sommers found the rate of lever pressing a most flexible instrument of adjustment, for it:

- (1) Increased with decreases in the duration of access to air
- (2) Decreased with increases in the CO₂ concentration in the air given as reward
- (3) Increased with increases in the nutritional richness of the diet (presumably associated with an effect on metabolism level)
- (4) Increased with increases in the water temperature (again perhaps associated with metabolism)

And finally, the Q-10 for turtles in the range of temperatures used is a factor of about 2, which approximates the factor by which responding increased for a 10° increase in water temperature.

Contrary to common intuitions (particularly among biologists), it may be that learned responses will prove to be sensitive indicators of physiological states, for local events in the nervous system (such as blood temperature) may affect behavior before the rest of the organism's reactions have taken place. It may, in other words, be misleading to say that in van Sommer's experiments, behavior reflects metabolism, if, in fact, behavior has already begun to restore normal physiological conditions before metabolism has changed materially. Substantial evolutionary advantage would seem to accrue to a crea-

ture whose behavior adjusted quickly to the immediate circumstances, both within and around it. But however the physiological details are arranged, van Sommers has shown that respiration in turtles involves more than just breathing: it involves the behavior of the entire turtle, under the control of rewards and punishments. The findings for rats and goldfish were comparable, except that CO₂ regulated the behavior of the mammal and O₂, that of the fish. Here, as in countless other instances, homeostasis extends to the commerce with the external environment, where reward and punishment guide the outcome to produce behavior that is appropriate to the given circumstances. The pattern defines a vast and fertile field of study, as yet largely neglected, no doubt because it falls on the boundary between biology and psychology, but without which both subjects are incomplete.

CONCEPTUAL CAPACITY

The last section moved toward physiology; this one moves in the opposite direction. One may, for example, wonder whether an animal possesses color vision—which is a straightforward question of capacity—or whether its color perception has three, four, five, or more principal colors or whether there is just a simple continuum. None of the procedures so far described are well suited to the latter kind of question, which is more conceptual than perceptual, although this is not to argue for a hard and fast distinction between the two. The problem is to get at how animals sort stimuli that vary in some way and the solution is again to set up contingencies among stimulation, reward, and responding.

A straightforward example of such an experiment was done by Loveland and me (ref. 23), again using pigeons as subjects. We

wanted to know whether pigeons could be trained to detect the presence of people in photographs, for reasons that now have little relevance to our findings. Over the years, many experiments had shown that animals can be trained to respond to the presence or absence of a particular stimulus—a light, a color (given color vision), a geometrical form, a sound, an odor, and so on. All of the procedures described thus far in this paper have relied on such training in one way or another. However, the problem of responding to pictures of people is different from all of these, because the attributes of the appearance of a person are undefined. When we look at pictures, we can see people in a limitlessly large number of different geometrical configurations. People are not fixed geometrical or visual entities, like triangles or red lights, but instances of a class to which we respond without being able to state its properties. A picture may be seen as containing a person whether seen from front, profile, or back, at right angles or obliquely, close up or in the distance, in bright light or dim, with a red tint or green, or with more or less of the body obstructed. A finite list of visual characteristics can give neither the necessary nor all the sufficient attributes. Our experiment with pigeons was thus an attempt to see if such a "natural" class—as distinguished from the contrived stimuli of psychological experiments—can be used as the occasion for responding, and in this respect it seems to have been unique.

The pigeon chamber contained a screen onto which the pictures (35 mm slides) were presented, plus the usual response key to peck at and the standard feeder for giving food reward. Pictures were shown for about a minute at a time and pecking was rewarded with food if the picture contained a person or part thereof. Such correct responding was rewarded only intermittently, so that the re-

ward itself did not become the primary signal that a person was present in the picture. If the picture did not contain a person, then responding was not only unrewarded, but penalized. When the pigeon pecked in the presence of pictures without people, the picture was not withdrawn unless the pigeon had not pecked for at least a certain number of seconds. By responding inappropriately, the pigeon would thus be postponing the removal of pictures in whose presence no reward was given. Without incorrect responding, these negative pictures were automatically withdrawn after about one minute. Each experimental session contained approximately 40 pictures with people and 40 without, presented, of course, in random order.

The pictures themselves were as heterogeneous as we could make them. Some were taken especially for this experiment, in natural settings both indoor and out. Most, however, were just slides that we borrowed or bought from individuals and agencies of one sort or another, taken in all parts of the world, under every conceivable photographic condition, and with an unknown, but likely large, number of different cameras and films. We looked at the pictures ourselves first to determine whether or not they contained people. Then we tested the pigeons.

Within a few weeks of daily practice sessions with a large variety of pictures, the pigeons became highly competent, responding rapidly in the presence of pictures of people, and more slowly or not at all in the presence of pictures without people. The pigeons dealt with the pictures about as accurately as we could ourselves, even pictures they were seeing for the first time. Moreover, their infrequent errors usually made sense if one assumes that they were doing about the same thing a human subject might do with the task. False dismissals—pictures with people, but responded to as if they were without peo-

ple—typically were of hard pictures, which is to say the people in such pictures were obscure, either because of distance, lack of contrast, or some obstruction. However, many such marginal pictures were responded to correctly. False alarms—pictures without people, but responded to as if they contained people—also made sense. Pictures with stimuli that might be taken as people—such as goats or telephone poles in the distance—or objects that are associated with people—such as automobiles or bicycles—were sometimes reported as containing people. Here, too, the general rule was correct performance, but the exceptions were nevertheless revealing and interesting. Then there were, of course, errors that made little sense to a human viewer, except as simple inattention.

This experiment proves that the category of person, which as noted above is not well defined visually, is within the grasp of pigeons—or at least a category sufficiently like person so that a highly mixed set of pictures, both positive and negative by our standards, were correctly sorted. Note, however, that had the pigeons failed, it would not have been because of a sensory deficit in the usual sense. Pigeons are adequately endowed with visual acuity and brightness and color sensitivity to find the people in most of the pictures. As regards visual capacity, pigeons are probably at least the equal of man. Success or failure here depends on some higher level of processing of the stimuli, hence the designation as conceptual. And not only is the level higher, it is also more closely related to the pigeon's natural use of vision than called for in the usual psychological experiment. In nature, as distinguished from the laboratory, stimulus objects representing classes are bound to vary, as they did in this experiment.

We are continuing with experiments of this general type with other classes of stimuli

in an effort to find the underlying rule that enables a representative creature, a pigeon, to respond invariantly to highly variable classes of objects. At the same time, we are finding out something about the pigeon's visual world, a possibility that might easily have seemed out of the reach of science a few years ago.

DISCUSSION

QUESTION: What is the degree of complication that you can manage? We have no scale describing complexities.

HERRNSTEIN: We can train pigeons to do some extraordinarily complicated things. Some time ago I thought it would be interesting to see if I could train one pigeon to train another pigeon to stand in the corner. I found that it was well within the animals' range given the appropriate setting. From a practical point of view, for the purposes of studying sensory capacity, the pigeon seems to be quite plastic enough.

QUESTION: What about color perception?

HERRNSTEIN: It can be shown that pigeons have color vision and also that they seem to have the principal colors about in the same regions that we do.

QUESTION: What has been done on shape discrimination?

HERRNSTEIN: The last experiment that I described on discriminating human figures in pictures is probably the limiting experiment in the literature since the shape of a person is so complicated that it exceeds our ability to characterize it.

GRIFFIN: Can you give us any specific practical suggestions on how to apply operant techniques to the search for possible "new" or unknown sensory capabilities, such as sensitivity to the Earth's magnetic field?

HERRNSTEIN: The only way to become competent in these techniques short of recapitulating the countless errors that one can make along the way is to work in a laboratory where these techniques are being used.

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