The neural and chemical basis of reward: new discoveries and theories in brain control of feeding, mating, aggression, self-stimulation and self-injection

BARTLEY G. HOEBEL
Department of Psychology. Princeton University. Princeton, NJ 08540, *USA*

Discovery of endogenous opiates raises the possibility that they serve as a reward for behavior, including law-abiding behavior. This paper begins with a discussion of homeostatic behavior, drinking, feeding, and then social behavior, mating and aggression. It is possible that peptide fragments of longer protein chains serve as "drive peptides" in the sense that each is evolutionarily adapted to serve a battery of body and brain function. Dual function, gut-brain peptides have recently been discovered for digestion and satiety, blood volume and thirst, and ovulation and sexuality. Aggression-control peptides are a logical possibility.

Studies are described in which feeding, mating and killing responses are induced or blocked by electrical or chemical stimulation of the hypothalamus in the rat. Animals will also work to stimulate their own *brain electrically or with the catecholaminergic drug, amphetamine, or with the opiates morphine and enkephalin. These reward systems could conceivably reward not only homeostatic behavior and self-centered social behavior, but also altruistic behavior. A hypothetical model of brain function is proposed in which endogenous catecholamine and/ or opiate rewards are released by behavior that matches a memory or "rule" of prior behavior. Thus complying with internalized laws or expectations is in itself rewarding. Altruism as such is not necessarily innately rewarding, but matching performance to expectation probably is. Behavioristic, physiological psychology can explore the role of opiates in legal expectations; behavioristic cultural anthropology can explore the legal expectations that people depend on for their reward. In summary, a theory is presented in which innately coded peptides prime physiological and behavioral patterns for feeding, mating and aggression; catechola mines modulate arousal and activation; and opiates reward successful compliance with rules, most of which are learned, some of which are laws.*

INTRODUCTION

Gruter (1979) and Danielli (1980) have suggested that endorphins in the brain could serve as opiate rewards for altruism and law-abiding behavior. This is an interesting idea. Endogenous opiates could provide all kinds of satisfaction including the satisfaction of eating, drinking, mating, child rearing, aggression, defense and other forms of individual and social responsibility. Neuroscientists and physiological psychologists have an unusually clean and elegant way to test these theories. If the opiate antagonist, naloxone, blocks the opiate- supported behavior, then the behavior is mediated by endogenous opiates. For example, naloxone blocks morphine analgesia, acupuncture analgesia, morphine euphoria and morphine-induced feeding. Therefore parts of the systems for pain, pleasure and hunger motivation involve opiate receptors. Similarly, endogenous opiates have been shown to playa role in pain suppression by placebos and pain anticipation after a warning (Fanselow, 1979); thus opiate release can be conditioned. Reacting to a warning could be taken as a model of law-abiding behavior. Even more to the point of this conference, certain social behavior patterns are innately reinforced by opiates. Chicks display cries of distress if they wander off from their mother and siblings. The same reaction occurs if they are removed to a "jail" or given naloxone. The reaction of distress and anxiety is unmistakable at the appropriate age. Obeying innate law to stay by mommy is rewarded by opiates; breaking nature's law is punished by opiate withdrawal symptoms. If someone develops a clear, simple model of altruism in a laboratory animal such as the rat, then I could explore ~ the role of endogenous opiates in altruism as well. At present I can tell r you more about opiates in feeding behavior .

Opiates were discovered in the brain when Hughes *et aL* (1975) recognized a morphine-like compound within the structure of a long '\ protein isolated from the pituitary gland. It was named endorphin (short for "endogenous morphine"). We now know the parent compound is split by enzymes to produce a variety of important peptides, including endorphin, that control both physiological processes and pain. Clearly an animal's genetic codes for producing the long parent compound and the enzymes that split it up will influence the animal's physiology, its reaction to pain and perhaps certain behavior patterns.

There are strains of mice and rats that have agenetic tendency to be obese. According to Mendelian laws a predictable fraction of the offspring will be fat. It was discovered that the fat ones had more beta-endorphin in their pituitaries than the lean litter mates (Margules, 1979). If it could be shown that endorphin affects feeding behavior, then we would have a clear link between genetics, brain peptides, and a life-long motivated behavior pattern. Such a jump from genetics to motivation is a primary concern of this conference.

MOTIVATION

Investigators in several laboratories tried injecting morphine and beta-endorphin into a region of the hypothalamus, just above the pituitary where norepinephrine (i.e. noradrenalin) is known to induce feeding. Morphine or beta-endorphin induced feeding after some delay. More- over the effect was reversed by naloxone which proved that there are opiate receptors for feeding in that brain region (Sanger, 1981).

Meanwhile, relatively short opiate peptides had been discovered inside neurons of the brain and spinal cord. Made up of a string of amino acids, these potent little peptides are cracked off of larger proteins made by the genetic apparatus in the nerve cell bodies. These short, opiate peptides, called enkephalins, are released directly into the nerve synapses instead of into the blood circulation. Thus they are more like neurotransmitters than hormones. In the spinal cord enkephalin neurons can close the gate on incoming pain signals. Apparently specific local stimuli such as pricks to acupuncture haku points in the skin can release enkephalin in various segments of the spinal cord. There the en kephalin may suppress the painful stimulus and even pain from other sources. Generalized stimuli, such as stress and exertion, on the other hand, can release endorphin in the general *r* circulation. Given that opiate receptors for feeding had been found in the hypothalamus the next step was to try injecting en kephalin to see if feeding was a generalized endorphin effect or perhaps a more specific enkephalin-mediated effect.

We found that enkephalin caused rats to eat just as norepinephrine and beta-endorphin had done. The effect was partially reversed by naloxone. One thing is strange. The enkephalin-like compound we used acted very slowly. Norepinephrine injected in the hypothalamus can induce eating in a minute; the enkephalin analogue took half an hour. Norepinephrine seems suited to controlling meal size; enkephalin is slower and may have more to do with the urge to eat, rhythms of eating or other slow cycles.

We eat because food tastes good, and because we feel good after a meal. There may be two separable systems for these two pleasurable aspects of eating. Belluzzi & Stein (1977) proposed that brain opiates give the satisfaction that comes after successful consummatory behavior. According to this view, opiates may be the chemical basis of pleasure, the goal of drive reduction. Our task now is to figure out which neurochemicals and which brain systems cause "drive induction" such as appetite for food, and which give "drive reduction" such as satiation.

Another question is why we stop eating at all. Something must stop us from eating all day so we can do something else such as make love, play with the children, compete, create or what have you. Again, glandular pep tides have been discovered first in the circulation and then in brain neurons. Peptides secreted by glands in the gut are thought to act as satiety signals. They have been discovered not only in the general circulation, but also within neurons of the brain. Neuroscientists surmise that these pep tides might be released at synapses to act as neurotransmitters, or they may be released to modulate the effects of other faster-acting neurotransmitters. It looks as if the nervous system, which derives from ectoderm, may have incorporated these chemicals into neurons to control feeding, and the endodermal organs may have adapted the same chemicals as signals about fuel availability and digestion. Peptides from the gut could conceivably diffuse out of the bloodstream into the brain synapses and have modulatory effects concordant with the brain's neural transmitter. The end result would be a neural circuit for feeding that could be biased by the same peptide from either source, either the brain or the body. There may be a .general principle here. It is as if a given peptide is used by the brain and the body to control the same overall need in all its aspects from modulating organs to modulating behavior. This hypothesis remains to be proven for feeding systems. Studies of drinking are further along.

Drinking is more essential than eating. People on self-imposed hunger fasts have been known to live for 40 days and 40 nights, but the punishment for not drinking is swifter. Without the right amount of water, chemical reactions are disrupted because the fluid concentrations are wrong; circulation fails for lack of blood volume; the body overheats for lack of coolant, and food sticks in the craw. Regulation of water balance depends on two stimuli, osmotic *concentration* of the body fluid as signaled mainly by osmoreceptors in the hypothalamus, and by blood *volume* as measured by receptors in the kidney. In the first case of low osmotic concentration many things happen at once. Hypothalamic receptors send a hormone (ADH) telling the kidneys to reabsorb water that would otherwise become urine; the same hormone contracts blood vessels (Guillemin, 1980). A neural signal peps up the heart; and a message goes out to the rest of the brain to prime reflexes for drinking. The triple result is a yellow, concentrated urine, elevated blood pressure and "thirst." This is all a reaction to too much salt relative to water in the body fluids. The concentration must be close to that of the sea water in which we evolved. The points to notice are the physiological redundancy, the chemical feedback loops, the neural orchestration and the role of behavior in homeostasis.

Let us look at it again, this time focusing on blood volume instead of concentration. Suppose an animal has been in a fight and is bleeding. The kidney sends a hormonal message (angiotensin) that does the same three things as ADH. Water is reabsorbed, blood vessels constrict and the sensory-motor system is "primed" to drink. In most cases of "priming" the threshold for detection is not lowered, but instead the sensitivity to particular stimuli is raised; more sensory neurons fire and the motor output is more vigorous. In addition, there may be a strong sensation. In the present example there is an awful thirst.

The motivation called "thirst" translates into something measurable in three ways. People can say it in words; this is the verbal variable. Animals prove it by overcoming obstacles between themselves and water. For example, rats run faster, pull more weight, or press a water pump more frequently. This is the "drive," "motivation," or performance variable. Third, animals repeat the performance that paid off. This is the operational definition of "positive reinforcement," the reward variable."

These same principles seen in feeding and drinking also seem to hold true for the complex social behavior known as mating. Again, a newly discovered peptide seems to choreograph the beautiful interplay of brain and behavior. Actually I should say brains and behaviors, because mating is an emergent property of the back and forth interaction of stimuli from two animals acting as one system.

A peptide, leutinizing-hormone-releasing-hormone (LHRH) is produced in cells of the hypothalamus and released to trigger leutinizing hormone (LH) from the pituitary (Adler, 1981). LH is the hormone that causes development of the egg, ovulation and copulation. It is released after estrogen causes courting and before progesterone causes embryonic development and nesting. In each case a pituitary sex hormone adjusts the physiology of the sex organs for a particular phase of reproduction. Everyone knows that the primary sex organs develop during this process; vocal chords and hair or feathers take on signal functions. It is less well known that brain areas for receiving sex signals also grow, and the erogenous zones change their sensitivity. For example, estrogen actually increases the size of the pubic area that will generate sensory nerve impulses when caressed. Estrogen also potentiates the spinal output for copulatory postures. Of course the sex equipment, sex signals, sexual sensitivity and mating reflexes are not enough. Complex behavioral output is also primed. LHRH has just been discovered in long neurons reaching out from the hypothalamus to all the brain nuclei involved in sexual behavior patterns. LHRH is probably an overall organizer of orgasmic sex. It commands the master gland to secrete the LH surge, and it stimulates a million synaptic contacts in sensory and motor relays for sexuality. I would not be surprised if it someday proved to modulate the rewarding incentives we feel during intercourse and the satisfaction of orgasm. LHRH, in both men and women, has all the earmarks of a "drive peptide" (Olds, 1977) for mating and reproduction.

Aggression plays a major role in survival. It starts when a pup must struggle for a nipple, and the behavior grows into the struggle for food and living territory. The link between aggression and feeding is unmistakable in carnivores, but there has always been some controversy as to whether feeding and aggression have clearly separable brain mechanisms, or whether they are just two manifestations of the same basic system. We have done studies in which brain stimulation with electricity or chemicals produced mouse killing in totally naïve rats that had never killed a mouse before {Smith, King & Hoebel, 1970). They had never even seen a mouse killed until we stimulated their hypothalamus, and then they proceeded to commit muricide. This suggests to me that some types of aggression have separate neural components which are innate. Prior learning also plays a major role {Cools, 1982). The murderous behavior may never be performed unless triggered by appropriate environmental stimuli or brain stimulation. In one study rats worked for mice to kill even though they were never allowed to eat the mice. Such killing satisfies the laboratory definition of a reward.

There are many stimuli for aggression. They are so varied that they define many types of aggression; for example, prey aggression, male-male aggression, aggression for infant protection, and aggression that is triggered by pain {Valzelli & Morgese, 1981). The link between sex hormones and aggression is very clear in many species; thus one cannot study aggression without being aware of the underlying hormonal state. A "drive peptide" for aggression has not been found yet, although we can predict it on the basis of the foregoing discussions of feeding, thirst and mating.

If a specific aggression peptide were discovered it would finally prove that aggression is a distinct behavioral category, extricable from feeding and mating. Such a peptide should have the same general properties as angiotensin for inducing thirst, cholecystokinin for satiety and LHRH for mating. It should have an organizing effect on several physiological and behavioral systems to favor an aggressive response at the expense of feeding, drinking or mating responses.

In the last five years scientists have learned to intervene in these motivational processes. For example, the new drug Captopril blocks the angiotensin signal and thereby lowers blood pressure. Now people can lower their blood pressure by chemical intervention to prevent heart attacks. Our laboratory is looking for a drug that could block the physiological and behavioral manifestations of hunger. Then people who eat and have a body weight suitable for a cold climate or a famine, could have a normal body weight instead. Even though feeding seems to be organized in much the same way as drinking, it is more complicated because there are more stimuli. Taste, stomach fullness, intestinal contents, liver store of glycogen, blood sugar, circulating fat, insulin, and even the outdoor temperature can all control food intake. For thirst there were two important stimuli, blood concentration and volume, for hunger there may be a dozen. Mating is more fascinating, for here there are crucial stimuli that must be properly sequenced between two individuals. Nevertheless, the newly discovered peptides provide the missing link between the classic hormones and behavior. Manipulating the enzymes that make or break these peptides is one of the new hopes of the drug industry. Another is manipulating the genes that make the enzymes.

In summary, any given motivated behavior seems to consist of sub- systems which can be brought into action over the course of a few hours by hormones, driven in minutes by peptides, and triggered in a split second by the appropriately coded sensory signal or direct electrical stimulation. The next step in our analysis is to go beyond motivation, beyond "reflexes," "priming," "drives" and "sign stimuli," all of which create behavior tendencies. These propensities to behave in certain ways are the essence of sociobiology, but to understand law we have to go further and study brain systems that are necessary for reward and punishment.

AROUSAL

Various motivation systems have to compete with each other for access to the animal's attention and response mechanisms. Superimposed on all this is a flip-flop mechanism in which the hierarchy of priorities can be switched by the parasympathetic and sympathetic nervous system. Under the calm dominance of the parasympathetic system, breathing comes before temperature regulation, which in turn takes precedence over drinking which comes before eating, which comes before mating. Under the emergency conditions that bring the sympathetic system into action, fight or flight comes first, sex may dominate eating, feeding may erupt with regard to energy level and a drink of water is the last thing on the animal's mind. The animal may even disregard its temperature, or for a minute forget to breathe.

Adrenaline and noradrenaline are the physiological signals from the adrenal gland that prime our bodies for emergency action. In the brain, the same chemicals are released from neurons that modulate all the motivation systems discussed above. The well-known reticular activating system in the hindbrain contains a system of widely ramifying neurons that modulate most of the brain. These neuro-hormones arouse us to pay attention. They also inhibit processes that can wait. For example, some of the neural pathways for inhibition of feeding have been discovered (Hoebel & Leibowitz, 1981). Interestingly, they inhibit both the hypothalamic systems for eating and for not eating. It is as if they were evolved to control meal quantity and quality in the parasympathetic relaxed state, and to inhibit the whole works during emergencies. Apparently specific neurons inhibit food intake after a meal when the input coming from the gut signals a full stomach or full intestines. Other adrenergic neurons may inhibit mating after copulation. Note that the same adrenergic synapses would inhibit both feeding and mating in an emergency when adrenaline from the adrenal gland pours into the bloodstream and diffuses into these synapses. This theory that adrenaline leaking into the hypothalamus blocks feeding and mating is unproven, but it makes sense.

It is curious that a relaxed state is usually necessary for eating or courting; whereas ejaculation involves a switch to the sympathetic aroused state. Thus feeding and courting occur in a common physiological state, and ejaculation shares a state with some kinds of aggression. Animals, even humans, may display some confusion in their response to the excited state. If a person is made excited with a shot of adrenaline in the absence of any natural internal code to guide their behavior, then they base their response largely on environmental cues. They may be either morose or joyful, murderous or ecstatic depending on the social context. This is one way in which excited animals can be entrained to exhibit a socially cohesive response. An emergency, such as an earthquake, will set up the sympathetic state in everyone. The individuals who see the problem, or think they do, will tip the first domino that pushes everyone into the same emotion. Thus, in emergencies, feeding and courting will stop. Whether the person then has an orgasm, commits a murder, laughs or cries depends on the internal factors such as the pep tides that set the stage for appropriate behavior. In the absence of such preparation, environmental stimuli, real or imagined, play a bigger role. Environmental stimuli include the law. Internal factors have a "law" of their own. The brain somehow synthesizes the two and makes active choices.

ACTIVATION

After motivation and arousal the next step is activation. The story goes that bed-ridden Parkinson patients could only activate themselves if there was afire in the hospital. Such a life and death emergency could activate them to run out to the sidewalk where they would collapse again. The greatest breakthrough in modern psychopharmacology

.

was the discovery that Parkinson Disease patients needed I-DOP A to make the neurotransmitter, dopamine. The dopaminergic system has its neural cell bodies in the midbrain. The nerve axons project up through the hypothalamus to the forebrain. Part of this dopamine system is absolutely necessary for initiating movement. Dopamine gives us the willingness to work {Hoebel & Novin, 1982). Without it, we only sit and dream. "

IMAGINATION

There is a very primitive set of serotonin-containing neurons in the hindbrain that projects up, down and all around the brain like the adrenergic arousal type discussed earlier. It has been possible in the last few years to record from these big, old cells in awake cats. The faster they fire, the more alert, active and tense the cat becomes. During sleep they gradually slow down. When they stop firing, postural muscles relax, the head drops and dreams start. Imagination runs wild. Perhaps that is why some discoveries are made during sleep. Part of this serotonin system clearly inhibits imagery when it is active. It seems to ready the animal for concentrating on a single problem and a quick motor response. When this readiness is missing the animal can either lose muscle tone and dream, or maintain muscle tone and hallucinate. Normal, everyday creativity and imagination probably require an in-between state of medium tone and free flowing imagery. The hallucinating schizophrenic overdoes it. The LSD freak loves it. The peyote cult worships with it. In this unfocussed state the stream of imagery can be influenced by either internal or external stimuli. Alarm bells remind us of phone bells, rain reminds of urine, crickets can sound like railroad trains and eagles become gods. Freud seemed to think that dreams got him closer to the laws of sociobiology unfettered by the lessons of later life. I know of no hard evidence that dreams are a representation of the innate or childlike any more than a representation of socialization and culture. However, it is fairly clear that when serotonin cells shut up, suppressed ideas can speak up.

In sum, the animal, be it cat or person, seems to have its thoughts "loosely coupled" or disinhibited when serotonin turns off. We do not know the functional significance of this. Is it time for regeneration of chemicals for arousal, activation or reward? Is this a state for new learning? A time for novel associations? Or just an epiphenomenon of the age-old need to lie low when our defenses are weakest?

ARTIFICIAL STIMULATION OF INNATE BEHAVIOR

The sociobiologists would have us believe that there are genetically preprogrammed properties lurking in the brain. If so, it is conceivable that one could use electrical stimulation to induce behavior patterns that the animal never learned. I would not make such a bold statement if we had not already done it. Brugger and Hess long ago showed that hypothalamic stimulation in cats could induce voracious feeding (Hess, 1957). Flynn (Adams, Bandler, Sheard & Siegel, 1981) showed that cats would kill rats during hypothalamic stimulation and that the stimulation sensitized the cat's snout and enlarged the area that would trigger a snapping response. As mentioned earlier, we found that hypothalamic stimulation could induce mouse killing, "muricide," in rats that had never even seen a mouse killed. Chemicals injected into the hypothalamus could do the same thing, and other drugs to block the endogenous neurochemicals could block mouse-killing (Smith, King & Hoebel, 1970). Apparently non-killers had the latent propensity to become killers, and muricidal rats could be inhibited with drugs. Incidently, the tendency to kill varies from strain to strain, and it can be modified by crowding, food competition and other environ- mental variables (Karli, 1982).

Even though brain stimulation can induce any of several behavior patterns, its main effect seems to be general arousal and activation. The precise behavior which emerges depends a great deal on the physiological state of the animal (Hoebel, 1976, 1979) and on the environmental stimuli (Valenstein, 1973). Stimulation-bound feeding can be blocked by a full stomach or a lack of edible objects in the cage. In such cases the stimulated animal will search around and then probably drink water or copulate or shred wood, or hoard food pellets, or jog in a running wheel, depending on what is available.

We have already discussed motivation in terms of innate and learned shifts in an animal's hormonal, peptide and catecholamine chemistry. These shifts, we saw, biased neural development and neural activation. This approach is relatively new because it depends on modern neuroscientific procedures to measure the relevant chemicals in the relevant parts of the brain. The older approach was to define motivation entirely in terms of stimulus deprivation or behavior output. Behavioral biologists such as Dethier (1970) thought that directed activity, such as a fly flying up wind, was sufficient to apply the label "motivated." Physiological psychologists such as Teitelbaum

(1967) insisted that learning of an arbitrarily chosen behavior (i.e., operant behavior) was the key to a successful definition. The two sides rested their cases and the jury has been out ever since. Is drive directional activity where the direction can be innate? Or is it goal- directed activity where the response is dictated by the environment? Olds (1977) was one of the first to attribute drives to peptides, essentially a chemical definition of drive. The latest breakthrough in neuroscience has been the discovery of peptides inside of catecholamine neurons. Can it be a coincidence that a gut peptide has been discovered inside of nerves of the dopamine activation system? We are now working on the possibility that parts of the dopamme system are coded for various behaviors such as feeding. They may be coded not only in their anatomical arrangement, but also in their dual-transmitter system. One transmitter could be for activation and one for a particular drive or motive. In this way a circuit for feeding, for example, could be inhibited by either the neural input that releases CCK, or by chemicals in the circulation that influence CCK receptors. This is hypothetical, but it goes a long way toward explaining how an activated animal can be biased towards eating, or mating or aggressing. It also suggests that the genetic code for manufacturing various drive- controlling chemicals is in some sense the animal's code of behavior. Time and research will tell whether the chemical code is detailed enough to be in any way analogous to a legal or ethical code. From what we are discovering about feeding, I would predict that pep tides lay down the detailed rules of motivation. We have seen that there are two peptides for different types of thirst, and peptides for satiety. We have hints that there may be different peptides for different types of hunger, specifically, salt hunger, sugar hunger, fat hunger and protein hunger. We also know there are different hormones promoting courting, copulation, nesting and nursing with peptides for at least some of them. Therefore logic suggests, although the evidence is missing that there will be different chemicals promoting each of the dozen different forms of aggression. However, there is no evidence whatever to suggest that peptides could innately code any law as detailed as incest taboo, nor all the rules of fair fighting.

Let us suppose that an animal is primed for action by the motivation system, aroused, willing to work and awake enough to deal with reality, the next step for the animal is to learn from experience.

LEARNING

In classical conditioning one stimulus is substituted for another; in instrumental conditioning one response leads to another. In classical conditioning the experimenter more or less arbitrarily picks any neutral stimulus which, with training, takes on the power to elicit a relatively fixed response. It is amusing from a sociopolitical point of view that Russia seems to place particular stock in this approach. America has championed instrumental conditioning which is response training instead of stimulus training. The response to be learned can be picked by the trainer within limits set by the animal's response capabilities and its level of motivation, arousal, activation and rationality.

Research suggests the short-term "reward" for learning is partly catecholaminergic, dopamine for the incentive to work (Mogenson & Yim, 1980) and norepinephrine for stamping in a memory of what pays off (Belluzzi & Stein, 1977). Long term satisfaction is probably an opiate-like state involving the brain's own opiates. These chemicals have been shown to be *necessary* for each of the functions named. They are not *sufficient* by themselves because many neural systems interact to produce learned behavior. As necessary chemicals, we can use them to talk about the functions they serve. Something subtle, but important has been going on in this paper. I have been trying to tell you about brain chemistry as we know it and then to attach concepts that seem to fit the chemical function. The object is not to get trapped into looking for chemicals to fit psychological or ethological concepts. Once we find important chemicals and circuits we can define the concepts to fit. Some of our classic concepts may not be discoverable at the chemical or simple circuit level; they may be emergent properties of large systems. In a sense we are trying to find the minimum neurochemical standards for to-be-named components of operant behavior. These neurochemical and neuroanatomical functions will be the internal rules of willful behavior; the rules which legislate how we learn. This information is not necessary to lawyers, because to control behavior one needs to know laws of stimulus and response, not laws of brain function. This information is, however, very interesting to those who want to know how laws emerge from brain.

How does "reward," i.e. positive reinforcement, emerge from the chaining together of many sensory-motor reflexes in the motivated, aroused, activated animals? Teitelbaum (1981) has recently been struck by the fact that seemingly complicated acts like walking over to a lever, orienting, pressing it and eating the food reward are all made up of many tiny actions each triggered by an environmental stimulus. The floor triggers an action in the foot; that foot triggers the other; the smell turns the head; the turning head turns the eyes, the eyes the whiskers, the whiskers the mouth, the mouth the tongue, the jaw the swallow, and all this proceeds in a beautifully choreographed sequence of reflexes leading to food in the stomach. If any step is interrupted the chain may be broken. The willful act when seen under a behavioral microscope is "mere reflexes"; each spontaneous voluntary behavior had its source. Just as a ballet which exhibits the pinnacle of athletic control and deep emotions can be reduced to an orchestra score and a motion score, so also any skillful act is seen as a program of linked reflexes. What we need to understand is the energy source that welds the links in the chain. The simplest view is that each link, once forged, leads to another, and no part of the brain needs to know the whole pattern. The common sense view, on the other hand, is that some part of the brain has a goal in mind. Fortunately we have neurochemicals and neural circuits necessary for both. Both link-by- link, action-by-action, catecholaminergic reward that could weld operant behavior, and the grand finale of opiate intoxication that could signal success in hedonistic terms.

Let us assume that the homeostasic mechanisms we spoke of at the beginning utilize hormones and pep tides for specific drives as described, and that these chemically-defined drives do two things. They increase the available opiate for feeding, for mating, for aggression, or whatever, and they also open the gates for appropriate classes of reflexes which are triggered in proper order by the natural sequence of stimuli in the environment. When the environment changes, then the behavior will change almost randomly until the reward system links one new successful act to the next. The program of reinforced synapses which led nerve impulses from one reflex to the next will then lead the animal through the same routine again and again. Each time, I suppose, opiate is released. It must last for minutes, hours, or even days. Each biteful of food, each genital stimulus, each prey killed, hypothetically releases more opiate until tolerance builds up or an anti-opiate (opiate receptor blocker) takes effect. The behavior will stop when any of the necessary chemical substrates shut down or are inhibited. A drive peptide like angiotensin may diminish and thus fail to cause thirst. A satiety peptide like CCK may inhibit feeding, adrenergic arousal may fail and the animal gets lazy. When opiate tolerance sets in it is time to try a new behavior with which reward is still accessible. Heaven help the animal that can find no reward sufficient to satisfy one of these basic systems. Then a state like opiate withdrawal sets in. These may be the animals that become sick with hunger, sick with grief, dying of thirst, and as for aggression the urge to beat someone at something is all too well known. If these are really withdrawal states, then heroin or morphine should cure them. The proper experiments have not been done, but opiate sales lend some credence to the idea.

By putting electrodes or hollow cannulas into the brain we can short-cut some of these processes. We can artificially drive the animal to eat, copulate or kill. We can also reward almost any sequence of behavior electrically or chemically.

All mammals, and some of our more distant relatives too, can learn to stimulate their own brains electrically. Rats, cats, dogs, dolphins, monkeys and humans all appear to delight in pressing a switch to turn on a stimulator that is connected to an electrode in an appropriate part of the brain. We use rats to study self-stimulation in our laboratory. They respond at a rate of 3000 times per hour. This well-known phenomenon was discovered by Olds & Milner in 1954. In the next 20 years it was shown that the rewards of self-stimulation are similar to the natural rewards of feeding and mating (Hoebel, 1976, 1979).

Recently, rats have been trained to stimulate their own brains chemically instead of, electrically. This will allow us to break the chemical code for brain reward. As you could predict, the chemicals that animals will self-inject into their brain are the drugs that people abuse. Rats will press a lever to self-inject morphine or amphetamine (Hoebel & Novin, 1982) through hollow needles implanted in carefully chosen brain regions. Soon we will be able to describe the neural pathways and the neurochemicals that are primarily responsible for generating rewards.

Skinner (1938) defined a reinforcing stimulus as one that changes the frequency of a foregoing response. Examples are palatable food, sexy stimuli and painful stimuli. A given response followed by a reinforcing stimulus usually causes the stimulus. Reaching into afire *causes* pain. Taking morphine *causes* the pain to go away. Thus animals learn to be careful of fire and learn to use morphine. Similarly, some responses are socially painful and some are socially rewarding; thus animals adapt to social usages. E. A. Hoebel (1954) has concluded that one of the four main functions of law is "to redefine relations between individuals and groups as the conditions of life change. It is to maintain adaptability." Thus law fosters learning.

There is one sure-fire way to tell whether or not a stimulus is a reinforcer. If you, the experimenter, can *arbitrarily* pick a response and have it learned merely by following it with the stimulus, then the stimulus satisfies the definition of a reinforcer. In other words, if the animal adapts its behavior, if it learns, then we have reinforcement. Similarly if a pair of animals, or a group, alters its behavior then we may find some cause and effect relation between the group behavior and a stimulus that reinforces the behavior. According to E.A. Hoebel's analysis we are looking for law. I will squeeze Hoebel's description of the function of law into my own Skinnerian jargon by proposing that law functions as a reinforcer. That is how it "maintains adaptability." Law as a reinforcer is in the same conceptual realm as food or sex. Therefore, if I can find the neural basis of feeding and sex reward, it may be like the neural basis for law reward.

Skinner, the experimenter, can write a law defining a response- stimulus relationship and then try to teach it to a pigeon. E.A. Hoebel, the anthropologist, works the other way around. He can observe the behavior of primitive tribes and then deduce the functions of their laws. Both stress two facts. First individuals or groups often mistake fortuitous response-stimulus relations for cause and effect relations. this is superstitious behavior in Skinner's terms, and legalized magico-religious belief in superhuman spirit beings in Hoebel's terms. Second, both stress that individuals or groups have regularities in their behavior. If there is a cause and effect relation for Skinner's pigeons to find, then the pigeons not only learn it, but almost all pigeons react alike. For example, "variable interval schedules of reward" produce a perfectly standard pattern of behavior. The behavior is basically just a rational approach to maximizing the reward. Skinner sees no need to postulate any innate laws except to say that the animal is equipped to learn that effects follow causes. Similarly, Hoebel assumes that a group's law ways are rational, acquired solutions to law-jobs. "When the law-jobs get done, these "norms inevitably become the common denominator of legal culture {Hoebel, 1954-: 287). It is not how the job gets done, but the outcome that counts. There are no reflexes, no innate givens, no motoric programs to be played out. What is interesting is the function that the behavior fulfills. The function is to get the rewarding stimulus, i.e. to get law. The strict behaviorist always picks a response for the animal to learn, and thus the behaviorist himself learns relatively little about goals of behavior. The culturist tries to find out what the people are getting done, and thereby learns what is rewarding to them. The excitement that the behaviorist Skinner generated came from the demonstration that a rule (a schedule of reinforcement), led rats '" and pigeons to respond rationally.

The excitement the culturist Hoebel offers is that different cultures have similar goals. The response topography may be drastically different from one culture to the next, even weird or superstitious, but if the responses are doing the law-job, then there is purposefulness. Hoebel discerns common purposes. Just as food, sex and killing are rewards for most rats, issues of food sharing, wife stealing and murder seem to be paramount in achieving law. Perhaps the accomplishment of such law goals is rewarded in part by endogenous opiates. The pathway to the law goal is probably not innate, but the capacity for rules, *per se*, to be reinforcers could well be innate. It is a small step from eating food to feeding babies, and from there to feeding refugees; small steps from sex to sexuality to love, or from opiate supported affiliation to social altruism; small steps also from muricide to homocide to genocide, and an even smaller step from neurochemical rewards to drug addiction. The path of behavior as it seeks reward is as varied as the path of water trickling down a hillside. The "gravitational force" that gives anthropological outcome an appearance of purposefulness could be a genetically programmed brain circuitry that releases rewarding chemicals when law rules are followed.

According to this theory, when we pick a rule, any rule, and obey it, perhaps the brain will compare the rule model with the actual behavior. If there is a match, then the brain releases some opiate. That much could be innately programmed.

Where do the rule models come from? Some of the neural circuits for basic reflex rules could be built in, for example the "rules" for swallowing. Some rules could be learned, such as rules for washing food, or washing someone else's food, or altruism. Other rules could be created fresh, funny and different every time, like the sanctions of colorful, spirit beings. After anyone of these rules for model behavior is in the brain, then a match, mismatch decision would determine opiate release. A match-up would feel good. A mismatch might cause "cognitive dissonance" that leads to another attempt at either achieving the cognitive model or at altering the model to fit one's behavior. My social psychologist friends call that attitude change.

As a physiological psychologist, I am simply suggesting that if Gruter (1979) and Danielli (1980) are right about opiates playing a role in law abiding behavior, then perhaps the mechanism includes the elements discussed above: (1) hormones to program cellular development and change sensory sensitivity and motor capability; (2) "drive peptides" to create behavior tendencies in concert with physiological needs for water, energy and hormone regulation; (3) catecholamines such as norepinephrine and dopamine for arousal and activation; (4) monoamines such as serotonin for imagining and dreaming; (5) a match, mismatch mechanism for comparing rules and reality; (6) chemical rewards for reinforcing a match-up achieved through either superstition or correct logic; and (7) a chemical punishment for failure to match up.

The above mechanism is largely genetic. Genes program the proteins, fats, carbohydrates, neurotransmitters, hormones, enzymes to split off peptides, monoamines, opiates and maybe opiate antagonists. The brain theoretically develops a wiring diagram in which hedonism comes about by matching behavior patterns to internal models of behavior patterns. This could be the key to releasing opiates. Thus the genes program relatively few specific laws, as long as one general law is there: "Thou shalt match behavior to behavior model, and if you fail, adapt either the behavior or the model." Model matching is the law of laws. Model matching based on homeostatic hedonism, the pleasure principle, is a relatively simple matter for the genetic code. The sociobiological fun starts when we do the law-job. That is discovering the evolutionary, neural and social principles by which people redefine their relationships as the conditions of life change. The mischief starts when we use artificial sweeteners, aphrodisiacs, ritualized aggression, amphetamine, exogenous opiates, and explanatory fictions to bypass the process or impose conformity. I hope and trust our research into homeostatic hedonism, self-stimulation and self-injection will create more happiness than mischief.