Table 2. Equations representing independently obtained AEP's manipulated to yield three pairs of identical residuals of exogenous processes and three identical residuals of endogenous processes.

Eq. No.	Trial outcomes	Processes represented in AEP's	Residuals
		Exogenous processes	
1	$V_1CR_1 - V_2CR_1$	$= [\bar{V}_1 + (V_1 \rightarrow CR_1)] - [\bar{V}_2 + (V_1 \rightarrow CR_1)]$	$= \bar{V}_1 - \bar{V}_2$
2	$V_1CR_2 - V_2CR_2$	$= [\bar{V}_1 + (V_2 \rightarrow CR_2)] - [\bar{V}_2 + (V_2 \rightarrow CR_2)]$	$= \bar{V}_1 - \bar{V}_2$
3	$V_1CR_1 - V_3CR_1$	$= [\bar{V}_1 + (V_1 \rightarrow CR_1)] - [\bar{V}_3 + (V_1 \rightarrow CR_1)]$	$= \bar{V}_1 - \bar{V}_3$
4	$V_1CR_2 - V_3CR_2$	$= [\bar{V}_1 + (V_2 \rightarrow CR_2)] - [\bar{V}_3 + (V_2 \rightarrow CR_2)]$	$= \bar{V}_1 - \bar{V}_3$
5	$V_2CR_1 - V_3CR_1$	$= [\bar{V}_2 + (V_1 \rightarrow CR_1)] - [\bar{V}_3 + (V_1 \rightarrow CR_1)]$	$= \bar{V}_2 - \bar{V}_3$
6	$V_2CR_2 - V_3CR_2$	$= [\bar{V}_2 + (V_2 \rightarrow CR_2)] - [\bar{V}_3 + (V_2 \rightarrow CR_2)]$	$= \bar{V}_2 - \bar{V}_3$
		Endogenous processes	
7	$V_1CR_1 - V_1CR_2$	$= [\bar{V}_1 + (V_1 \rightarrow CR_1)] - [\bar{V}_1 + (V_2 \rightarrow CR_2)]$	$= (\bar{V}_1 \rightarrow CR_1) - (\bar{V}_2 \rightarrow CR_2)$
8	$V_2CR_1 - V_2CR_2$	$= [\bar{V}_2 + (V_1 \rightarrow CR_1)] - [\bar{V}_2 + (V_2 \rightarrow CR_2)]$	$= (\bar{V}_1 \rightarrow CR_1) - (\bar{V}_2 \rightarrow CR_2)$
9	$V_3CR_1 - V_3CR_2$	$= [\bar{V}_3 + (V_1 \rightarrow CR_1)] - [\bar{V}_3 + (V_2 \rightarrow CR_2)]$	$= (\bar{V}_1 \rightarrow CR_1) - (\bar{V}_2 \rightarrow CR_2)$

a high correspondence between residuals representing hypothetically similar processes.

Figure 2 shows that the histograms of correlation coefficients representing hypothetically similar processes are markedly skewed to the right, while the distribution of correlation coefficients between randomly selected AEP's is symmetrical around zero. These results indicate that the hypothetically similar residuals predicted by the equations did in fact exist, supporting the contention that the postulated separable exogenous and endogenous processes were present in the AEP's recorded under these circumstances.

Figure 3 shows, for numerous anatomical regions, the results obtained by plotting the mean correlations between the residuals due to exogenous influences against the mean correlations between residuals due to endogenous influences. These data reveal a hierarchical organization in the representation of exogenous and endogenous processes in different structures and suggest that a logarithmic relationship exists between these two different processes in any given brain region.

Evidence that endogenous influences represent the readout of specific memories and are not to be attributed to nonspecific factors has been presented elsewhere (*7*). This evidence was obtained from several experiments in each of which a group of animals provided a control for a particular nonspecific factor. Results from all these experiments were subsequently combined to provide the largest possible amount of data on which to base the statistical computations described herein. Although examination of the data from each control group revealed no clearly apparent contradiction to the relationship illustrated in Fig. 3, the possibility of heterogeneous variance among these groups has not been excluded.

These findings suggest that the representation of an experience, the engram, is widely distributed throughout the neuraxis. This diffuse representation of the engram might explain the resistance of memories to lesions and might underlie the phenomena that led Lashley to the formulation of the laws of mass action and equipotentiality. On the other hand, the data show that the participation of an anatomical region in the representation of an experience is logarithmically proportional to the impact of those sensory events upon that region. The great quantitative range spanned by these data may explain why severe specific functional deficits are sometimes caused by localized lesions in some structures but not in others.

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Operant-Controlled Evoked Responses: Discrimination of Conditioned and Normally Occurring Components

Abstract. *Rats were rewarded for signaling large and small sensory evoked components with appropriate bar presses. Most rats operantly generated large components and correctly signaled only these. Two rats correctly signaled successful and unsuccessful attempts to generate large waves. One rat discriminated component amplitudes without operantly attempting to generate specific wave types.*

Operant conditioning of sensory evoked components has been frequently reported (*1*, *2*). The phenomenon in humans and subhumans is not trivially mediated by changes in receptor orientation or by execution of discrete skeletal responses (*1*, *2*). It has been assumed that organisms control their neural activity by learning to discriminate and generate familiar psychological states whose neural correlates are the reinforcement-specified changes (*1*). Such a view suggests that organisms should be able to discriminate differences in a conditionable neural parameter, since operant conditioning of the neural event hypothetically proceeds by the organism's first learning to discriminate the reinforced event from other events. We explored this possibility by reinforcing rats for correctly signaling the size of a flash-evoked cortical component with an appropriate bar press. It was found that such discrimination behavior can be acquired, although rarely in the absence of attempts by the animals to generate particular kinds of evoked potentials.

Discrimination of neural events has been previously reported (*3*). In this

work, humans were trained to discriminate the presence and absence of certain electroencephalographic (EEG) frequencies. Although evoked components are more phasic than are EEG epochs, our results may be related to the EEG data in that phasic evoked components may be mediated by tonic states (*2*).

Ten male albino rats were implanted surgically with standard long-term recording plugs; nine rats survived all procedures. Evoked potentials were bipolarly recorded from a screw over the visual cortex and from a Nichrome wire 1.5 mm beneath the cortical surface underlying the screw. Potentials were amplified by a modified Tektronix 122 preamplifier with filters set to pass signals between 0.8 and 250 hertz. Signals were then led to an analog-to-digital converter of a PDP8L computer. Rewards consisted of 400-msec 60-hertz stimulations of the medial forebrain bundle. [Before any other training, the stimulation was confirmed as rewarding in a two-way approach-avoid box. (*4*)]. The animals were initially trained to press either of two bars protruding from one wall of an operant chamber for continuous reinforcement. Electrical circuitry prevented the development of bar preferences because reinforcement was delivered in initial training by a capacitative one-shot circuit that failed to operate after five or six rapid presses of one bar in succession. This training was then replaced by a computer-controlled, signaled, fixed-interval operant procedure in which the simultaneous onset of houselights and a constant-intensity 10-μsec stroboscopic flash (evoking stimulus) cued the animal that the bars were activated. The flash unit was mounted in the wall of the operant chamber perpendicular to the wall containing the operant bars. The houselight was overhead. A press of either bar in the next 3 seconds resulted in a single 400-msec brain stimulation reward. The bars were so spaced that they could not both be pressed at once. Houselights were turned off by the first bar press or by computer 3 seconds after their onset. Intervals between flashes (trials) were 4.5 seconds. The flash-evoked potentials obtained during a week of this training were collected to yield a median criterion segment for each rat, based on 3500 samples. A 30-msec segment of the surface-negative component, centered at 130 msec after the strobe flash stimulus, was averaged by computer on each trial to yield the criterion segment for the trial. Computer resolution was 1 msec per word. Henceforth, evoked component criterion segments exceeding the median are called positive waves (WP), and those below are called negative waves (WN). The final paradigm required rats to press one bar (B1) if a WP occurred on a given trial, or the other bar (B2) if WN occurred. Either correct press is called a hit; hitP means WP was correctly signaled; hitN means WN was correctly signaled. Miss trials, WPB2 or WNB1, were punished with nonreinforcement and a 5-second delay before onset of the next trial. For half the rats, a bar on the rat's left as he faced the bar-containing chamber wall was called B1 and the other bar (on his right) was called B2. The definitions were reversed for the remaining animals. Failures to press either bar occurred in less than 5 percent of all trials and are neglected. Before the final paradigm was instituted, waves were monitored during a further 5-day baseline period to verify that a priori probabilities for the following were each near their chance expected values of .5: hits, WP, WN, B1, B2, correctly signaled WP, and correctly signaled WN. All of these values were between 44 and 58 percent in the baseline period. In all phases of training, rats were given 500 trials per day. The final training phase of discrimination lasted 21 days.

A two-tailed, within-subject t-test was done to test the significance of the difference between the mean percentage of hits during the 5 days of the baseline period (48 percent) and during the last 5 days of training (61 percent). The training effect was significant ($t = 4.2$, $P < .01$). Close anal-

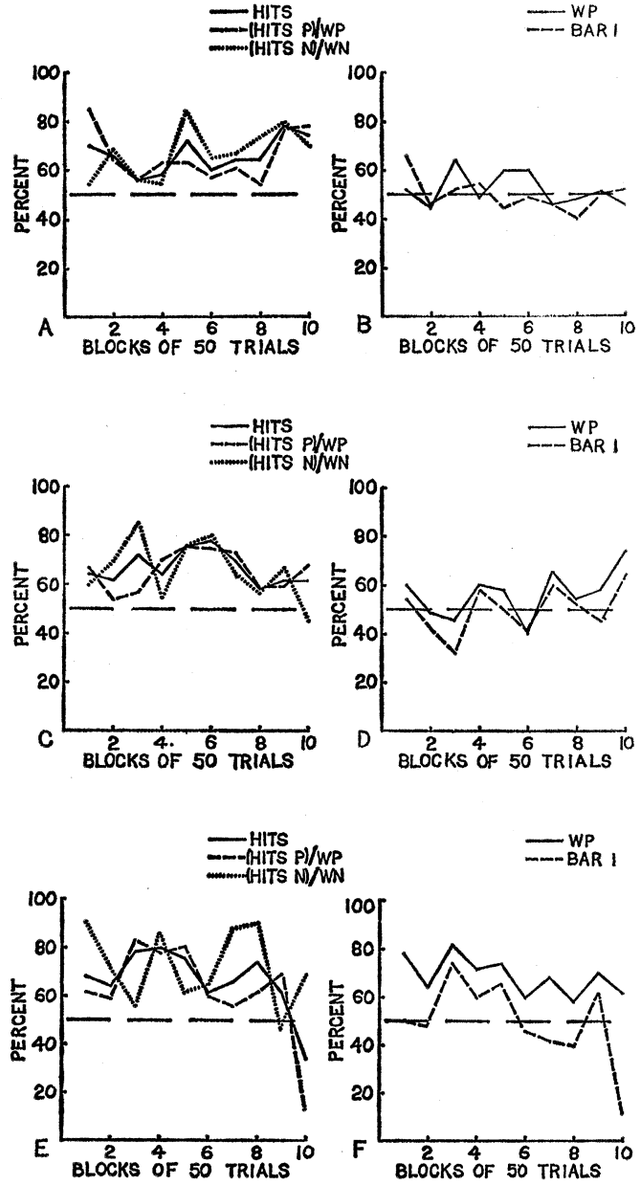

Fig. 1. Within-day data illustrating differing response styles in the last phase of training period. Each pair of panels represents data for 1 day. Percentage data are given for the following: hits, correctly signaled waves of both kinds, positive and negative; (hits P)/WP, positive waves correctly signaled; (hits N)/WN, correctly signaled negative waves; WP, positive waves; and bar 1, presses of bar to correctly signal a WP. (A to D) Pure amplitude discrimination without conditioning is illustrated. Both kinds of waves are correctly signaled more often than the 50 percent chance level, but WP responses remain around the chance level. (E and F) Discrimination of successful and unsuccessful attempts to produce WP is illustrated. Signaled events of both kinds are above the chance level but WP is likewise elevated.

ysis of individual data between and within days, however, showed that only one of the animals learned the discrimination without attempting to selectively generate WP or WN. One animal learned to generate WN and obtained rewards by remaining on the appropriate bar (B2). Two animals did not appear to show appreciable increases in hits. The remaining five animals learned to generate WP and obtained rewards by remaining on the appropriate B1 bar. However, two animals, following simple conditioning, also learned to signal failures to produce WP on given trials. Thus, they learned to discriminate their successes and failures. These conclusions are based on the kind of data shown in Fig. 1. Figure 1, A to D, is based on representative days of pure discrimination performance. The percentage of WP oscillates about the 50 percent chance level through the day, which indicates that the animal was not tending to generate either WP or WN. At the same time, the percentages of hits, of correctly signaled WP [100 × (hits P)/WP], and of correctly signaled WN [100 × (hits N)/WN] remain elevated well above chance levels. Careful visual monitoring of the rat's behavior during such discrimination showed that during sequences of consecutive hits, which at times were 12 in number, the rat never pressed one or the other of the bars in more than four consecutive trials. It usually alternated busily between bars from trial to trial. This suggests that there was no systematic tendency for clusters of WP or of WN to occur, and, further, that consistent receptor orientations could not develop. For animals that first learned to produce WP and then learned to signal successes and failures in attempts to generate WP, representative data are shown in Fig. 1, E and F. These rats consistently tended to produce WP but consistently correctly signaled the less frequently occurring WN as well as WP, so that correctly signaled WP and correctly signaled WN remained between 60 and 80 percent during the last asymptotic days of their training. The less frequently occurring WN trials were usually interspersed between WP sequences; WN clusters were atypical. Animals classified as exclusive WP operant conditioners gave 75 to 95 percent B1 responses and showed 60 to 80 percent WP throughout. Although 80 to 90 percent of WP were often correctly signaled, only 10 to 30 percent of WN were correctly signaled. These two curves were usually mirror images over trials, what one would expect of animals that predominantly generate WP and press B1. As expected, records for the sole WN generator were opposite to those of WP generators.

Figure 2 shows averaged evoked WP responses and criterion segment distributions in baseline and training periods associated with the different response styles. Dramatic changes in distribution parameters were associated with (i) exclusive operant WP production, (ii) WP production with correct signaling of successes and failures, and (iii) exclusive operant WN production.

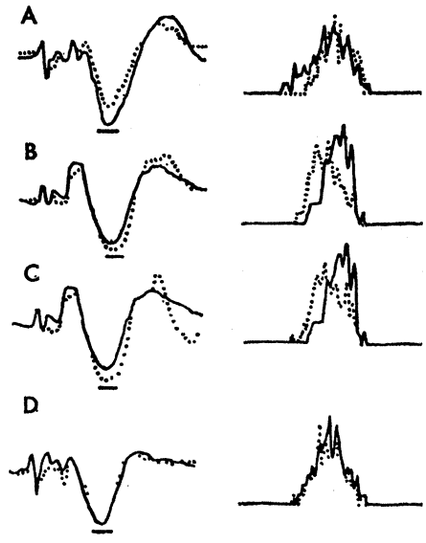

Fig. 2. Average evoked potentials within WP category (left column) and criterion segment amplitude distributions (right column) superimposed on baseline data (solid curves) and training data (dotted curves) associated with different response styles. Data are X-Y plotter outputs for (A) simple WN production conditioning; (B) simple WP production conditioning; (C) WP conditioning with correct signaling of failures and successes; and (D) pure discrimination. The WP tends to become more positive in simple and signaled WP conditioning and less positive in WN conditioning. In discrimination, relatively fewer changes are evident in superimposed waves and in superimposed distributions. Each training curve shown is data for a single day when performance best satisfied the training criteria for the particular response mode. Baseline curves are data for a day randomly selected from each animal's set of five baseline days. Average evoked potentials were usually in the range of 100 to 150 μv measured from the baseline before evoked activity to the down-going peak of the criterion segment. The bars below waves denote the 30-msec criterion segments. For amplitude distributions, the WP direction is to the left and each sequence of four raw data points is represented by one average point.

In contrast, for the pure discriminator, baseline and training distributions can be superimposed. We found a significant difference between the means of the most extreme values on the WP side of the criterion segment distribution in the baseline period as compared to the same measure on the best WP production day for all WP producers ($t = 2.9$, $P < .05$; two-tailed t-test). The same t-test done on extreme values at the WN end of the distributions was also significant ($t = 3.31$, $P < .05$). We also noted some tendency for a skew reversal of the criterion segment distributions between baseline and conditioning (Fig. 2, B and C), but this was not apparent in all rats.

We interpret these data as suggesting that operantly conditioned neural activity may not represent processes that typically occur during the baseline situation in normal animals. That is, a conditioned increase in evoked component amplitude may not represent the same information that spontaneous occurrences of enhanced amplitude represent in naive subjects. This view is suggested by the alterations of neural distribution parameters seen in the conditioned WP producers in this study. A previous study from this laboratory noted the emergence of correlations between activities in trained and untrained cortical loci in conditioning (*2*). Such results also suggest the development of processes in conditioning which do not exist in the naive subject in baseline periods.

The one animal that successfully discriminated amplitude in the absence of evidence for conditioning was, we feel, learning to discriminate states normally occurring during the baseline period, since its baseline distribution parameters did not change during training. The rats that learned to discriminate successes and failures at generating conditioned amplitudes seemed to be special cases of simple conditioners in that the neural distribution parameters of both response styles showed similar changes between baseline and training.

The fact that the neural concomitants of pure neural discrimination behavior appeared so different from the characteristics of simple or signaled conditioning suggests that operant conditioning of neural events does not proceed simply by the animal's learning to discriminate and then selectively generating states that commonly occur in the baseline situation. We are not necessarily suggesting that the state (or states) mediating neural conditioning

are unphysiological or that they have never or rarely occurred previously in the rat's life. Many different conditions may result in altered evoked potentials. Such conditions include arousal, sleep, attention, distraction, pharmacological intervention, brain stimulation, and so forth. The data do suggest, however, that the mediating states do not commonly occur during operationally defined baseline periods and that, therefore, the conditioning process does not involve selection of a baseline state for production. It follows that the neural processes activated during conditioning represent a distinctive set of states. Thus, the conditioning technique may not be an appropriate way of isolating for study a process that is occasionally observed in a baseline period. These implications, on the one hand, restrict the applicability of operant neural conditioning for the purpose of direct study of normal psychology and physiology. On the other hand, the intriguing possibility remains that neural conditioning methods may allow experimental isolation of unusual or even otherwise unobservable patterns of novel behavior or cognition of potentially adaptive value.

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Sexual Behavior: Normal Male Patterning in Androgenized Female Rats

Abstract. *Female rats treated with testosterone as neonates and as adults exhibited a temporal patterning of male copulatory behavior identical to that of normal males, although such females displayed few intromission reflexes and almost no ejaculatory patterns. With prenatal, postnatal, and adult testosterone treatment, female rats displayed all the characteristic masculine responses and intervals, including the ultrasonic postejaculatory vocalization.*

Females of many mammalian species exhibit several of the motor elements of male copulatory activity, especially mounting of receptive females (*1*). Among rats, normal estrous females often engage in male-like mounting activity, but they rarely display those motor elements that characterize the male's penile insertions and ejaculations (*2*). When adult female rats are treated with androgen, the proportion of animals mounting is comparable to that of males, but phallic development is not enhanced and there are few behavioral insertion responses by such females (*3*). Combining perinatal (pre- and postnatal) and adult treatment of females with androgen augments phallic development and yields a concomitant increase in the occurrence of the motor components of insertion (intromission) as well as ejaculation. Such females are similar to males in the number of intromissions displayed preceding each ejaculatory pattern and in the duration of the postejaculatory intervals (*4*).

The problem here was whether female rats treated with androgen at different times during development would differ from normal males in the temporal patterning of copulatory acts. This question could not be adequately answered with traditional measures of copulatory activity. With such measures direct comparisons between males and females are meaningful only if the females have been treated so that they can display the reflex patterns of intromission and ejaculation. However, with some treatments females mount, but due to, for example, inadequate phallic development, they have a lower probability than males of displaying intromission and ejaculatory responses. In such cases conventional measures are inapplicable, and comparisons based only upon proportions of animals displaying intromissions and ejaculations are inadequate and even misleading measures of copulatory performance. Measures are required that avoid confounding sexual dimorphism in copulatory activity with sexual dimorphism in genital apparatus.

It is possible to measure the rate of attempted copulations independently of the occurrence of intromission and ejaculation. This can be accomplished by measuring the temporal periodicity of clusters of mounts, or "mount bouts." When rats copulate the male's mounts tend to recur in bouts of one or more mounts which may or may not eventuate in intromissions. Under common laboratory conditions, mounts within a bout tend to be separated by 1 to 10 seconds, and the intervals between bouts tend to be about 30 to 60 seconds. Normal males prevented from gaining intromission (by penile anesthesia or by occlusion of the female's vagina) nonetheless show the same temporal patterning of mount bouts as when intromission is possible. The mount bout is apparently a fundamental unit in the timing of male copulatory activity (*5*).

We now report that neonatally androgenized females, which rarely display intromission, as well as perinatally androgenized females, which normally display intromission, have a temporal patterning of mount bouts that is indistinguishable from that of males. In addition, females capable of displaying the ejaculatory response do not differ significantly from males in their preejaculatory patterning or postejaculatory behavior, including the ultrasonic postejaculatory vocalization.

Female rats ($N = 25$) were injected within 24 hours of birth with 0.5 mg of testosterone propionate (TP) in peanut oil subcutaneously (*6*). Males ($N = 12$) from different litters were untreated at birth, but otherwise reared similarly. After weaning, the rats were housed in unisexual groups. The animals were gonadectomized at 70 to 80 days, and implanted with a pellet of TP (10 mg subcutaneously) at about 120 days of age. Testing began about 2 weeks later. Experimental animals were placed in an aquarium (50 by 30 by 30 cm) with wood shavings on the floor 5 minutes prior to the introduction of a receptive female. Testing continued for 24 minutes. Up to four tests were given at weekly intervals. For each animal, testing was terminated after criterion was met in two successive tests or after four weekly tests (*7*). Data analyses were based on the final two tests and included either the first 12 minutes of mating behavior or the copulatory series prior to ejaculation when that occurred in less than 12 minutes.

The criterion for maters was met by 58 percent of the males and 76 per-