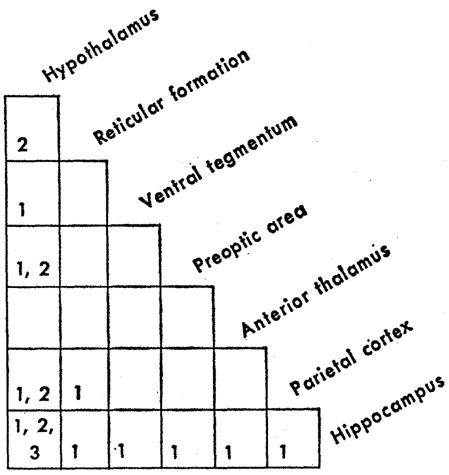

Fig. 3. Difference between groups of neurons in different brain areas significant at P equal to or less than .05 by the Mann-Whitney test. Entries are as follows: (1) changes from quiet to paradoxical sleep were different between the two areas, (2) changes from quiet sleep to quiet awake were different between the two areas, (3) changes from quiet sleep to the motivated awake state were different between the two areas.

recordings were regularly taken from the layer of hippocampal pyramidal cells in the dorsal anterior part. Neurons here were identified by their large ratio of signal to background (Fig. 2, right-hand column).

The increments over quiet sleep rates observed in the quiet awake state were not only smaller than those observed in paradoxical sleep, but were also less differentiated by anatomical structure. Units in the lateral hypothalamus again had the largest increments in rates, with an average increase of more than 200 percent, itself significant by statistical tests. Also, the hypothalamic group of neurons differed with respect to the size of the increase from those in reticular formation, parietal cortex, preoptic area, and hippocampus. The other brain areas had average rate increments of 50 percent or less. There were no average decrements and no other significant differences between areas.

There was an almost total absence of differentiation according to anatomical structure when differences between quiet sleep and motivated awake behavior were considered. From the 21 paired comparisons of the seven groups, taken two at a time, only one yielded a statistical significance; this was between the lateral hypothalamus which had the largest increments and the dorsal hippocampus which was unchanged.

Clearly, paradoxical sleep emphasized regional groupings of neuronal activity based on anatomical structure, whereas motivated behavior emphasized individual differences between units. If one might assume that a differentiated pattern of excitation and inhibition would occur within a structure under the influence of an information process, this would suggest a reduced information content in paradoxical sleep. It might nevertheless be involved in the clearing of temporary information registers on the one hand or in discharging unspent motive force on the other. The clear lead of hypothalamic process might favor a motivational interpretation because of the known "drive and reward" centers housed there. On the other hand, the reduction in hippocampal discharges might contribute to the clearing of any reverberatory processes involved in temporary information stores often suspected to occupy that region. One appealing supposition combines the two views. It is that the organism generates drive processes on the basis of physiological needs, but that there is an excess of drive which provides a cushion or safety factor. Paradoxical sleep would occur after it was established that the needs were filled, and it would function to dissipate the excess drive.

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9. Research supported by PHS research grants to the Brain Research Laboratory of the University of Michigan. We thank Giulio Baldrighi for technical assistance in the surgical preparation of animals, and Fred Coury and William Wetzel for assistance in the design and construction of apparatus. W.D.M. was a NSF science faculty fellow, and P.J.B. was a NSF postdoctoral fellow during part of the time of the research.

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Successiveness Discrimination as a Two-State, Quantal Process

Abstract. *The duration of the "psychophysical time quantum" measured through the application of a two-state model of successiveness discrimination is equal in magnitude to the modal zero-crossing interval of the alpha rhythm. The two quantities have similar distributions and they are correlated over individuals.*

The most recent review of the concept of a psychological unit of duration is the monograph by White (*1*). He considers many lines of evidence which indicate the existence of such a unit somewhere within the range from 50 to 100 msec and he raises again the speculation that the unit may be related to some rhythmic brain process. The alpha rhythm of the electroencephalogram has a period of approximately 100 msec and it is often suggested as a correlate. Later experiments by others (*2*) support this connection by showing associations between certain temporal characteristics of alpha rhythm and of behavior.

I have also presented some reasons for thinking of psychophysical time in quantal terms (*3*). In that paper, the time quantum is identified with three different behavioral parameters, and measurements show that the magnitude of the quantum is very close to 50 msec in all three cases. This is approximately the same as the interval between zero-crossings of the alpha rhythm, and additional measurements are given which indicate a positive correlation over individuals between this alpha interval and the behavioral quantum. However, the number of experimental subjects was small, and the average values of the behavioral parameters exceeded the average alpha interval by 6 or 7 msec in all three cases.

The present report is concerned with a further analysis of one of the three behavioral parameters and with its relationship to the alpha interval. Additional empirical relationships which support the time quantum hypothesis are also set forth. The parameter under consideration is called M and it is defined in terms of the successiveness discrimination function: the relationship between (i) the probability of discriminating a successive pair of sensory events from a simultaneous pair of sensory events and (ii) the time interval between the members of the successive pair (*4*).

A two-choice, forced-choice method is used in which a single trial consists of the presentation of two light-sound pairs. For the standard pair, a circular spot of light and a 2000-hertz pure tone begin simultaneously and terminate simultaneously. For the variable pair, the signals begin simultaneously but the light is terminated t msec before the sound. The rationale for using simultaneous terminations for the standard is discussed elsewhere (5). On half the trials, chosen at random, the standard is presented first; on the remaining trials the variable occurs first. The subject responds by indicating whether the offset of the light occurred before the offset of the tone in the first pair or in the second pair. When he indicates the variable he is scored correct and the proportion of correct responses is determined for each of a number of values of t. This proportion, $P(c)$, as a function of t, is the successiveness discrimination function.

The shorter member of each pair of signals has a duration of 2.0 seconds and the empty interval between pairs is also 2.0 seconds. An auditory signal immediately following the subject's response tells him whether the response was correct. Trials are run at the rate of one every 12 seconds. Usually only one 20-minute session is conducted each day for each subject. Equal numbers of the different values of t are randomly assigned to trials.

Under some conditions the successiveness discrimination function can be described adequately by a single straight-line segment (6). A line fitted to data intersects the level of chance performance; that is, $P(c) = 0.5$, at a value of t which is called x. The line reaches $P(c) = 1.0$ at a value of t of $(x + M)$ msec. The parameter M is the minimum amount of time which must be added to the interval between the light and sound offsets to bring $P(c)$ from 0.5 to 1.0.

I have reported (3) an average value of 54 msec for M from data obtained by using highly practiced subjects under conditions which were designed to maximize performance. This value was suggested as one estimate of the duration of a quantum.

However, with several subjects I have observed a strikingly different result under certain conditions. Instead of a "one-quantum" function they yield data which, while still linear in form, span about 100 msec. These "two-quantum" functions have always been observed early in practice, before the subject has ever attained the higher level of performance associated with the one-quantum state. And in every case a one-quantum function has been obtained in later sessions. A subject who enters a two-quantum state typically remains in that state for many sessions. Switching to the one-quantum state ordinarily requires some change in the experimental procedure.

These observations suggested the possibility that there are two distinct states such that when a subject is in state 1 his value of M is one quantum and when he is in state 2 his M is two quanta. Further, under some experimental conditions the probability of being in state 2, P_2, may be close to unity, while under other conditions the probability of being in state 1 may be close to unity.

If this conception is correct, then it becomes apparent that the earlier measurements of M were based on the assumption that a state 1 probability of unity was actually achieved. To the extent that this condition was not met, values of M would exceed the duration of one quantum.

These considerations lead to a two-state model of successiveness discrimination in which the successiveness discrimination function is the weighted mean of two linear functions having the same x but spanning one quantum in one case and two in the other. The weighting factor is P_2, the probability of being in state 2. The function consists of the following four regions:

when:	$P(c)$ equals:
$(x - M') < t < x$	0.50
$x \leq t < (x + M')$	$\frac{(t-x)}{2M'}(1 - 0.5\,P_2) + 0.5$
$(x + M') \leq t < (x + 2M')$	$\frac{(t-x)P_2}{4M'} + (1 - 0.5\,P_2)$
$t \geq (x + 2M')$	1.00

in which M' is the quantum size in milliseconds.

This two-state function rises from $P(c) = 0.5$ to $P(c) = 1.0$ as two linear segments, one connecting the points $(x, 0.5)$ and $(x + M', P)$ and the other connecting $(x + M', P)$ and $(x + 2M', 1.0)$. The intersection of these segments occurs at $P(c) = P = 1 - 0.25\,P_2$.

To apply this model requires obtaining data points over the range of t between x and $(x + 2M')$. In the earlier experiments this range was limited to the first quantum above x and most subjects did not quite attain a $P(c) = 1.0$ even for the greatest value of t. Therefore, a new experiment was done to test the adequacy of the two-state model. The ten values of t from 30 to 120 msec in 10-msec steps were used and the interval between offsets for the standard was fixed at 20 msec. All of these intervals have a positive sign which indicates that the light preceded the sound.

Twenty-three young, adult subjects participated, 14 male and 9 female. We eliminated four of them at the beginning because we were unable to obtain alpha in their electroencephalograms. The remaining 19 were run through one session per day and an electroencephalogram was taken before and after each session. Analysis of the electroencephalogram consisted of selecting monorhythmic single cycles of alpha and measuring the period of each to the nearest millisecond under a comparator. Twenty such samples were measured in each record, giving forty measurements per session. All of this analysis was performed by assistants who had no knowledge of the psychophysical analysis (7).

Obtained values of $P(c)$ are presented in Table 1 for 13 subjects. The other six subjects are not analyzed further, one because the two-state model failed to fit and five because they did not reach $P(c) > 0.90$ even at $t = 120$. An even wider range of values of t should be used.

The combination of the three parameters of the two-state model which yields the minimum squared-error fit was determined for each of the subjects. For this solution, values of x and M' were found to the nearest millisecond and P was determined to the nearest one hundredth. The results of these computations are listed in Table 2 along with the modal (peak) alpha interval.

The two-state function fits the data satisfactorily, as Fig. 1 demonstrates. This figure is a composite of all the subjects with each one entered in relation to his own parameters as explained in the caption of Fig. 1. The two segments of the function are both described adequately by the model, consistent with the deductions that there are two segments and that they span equal distances on the abscissa.

The quantities M' and alpha are very similar. They have the same mean, although the standard deviations suggest that M' is somewhat more variable.

Table 1. Two-state experiment. Proportion of correct responses for each value of the interval (t) between offsets of the variable. N is the number of trials upon which each proportion in the row is based.

Subject	Variable interval t (msec)										
	N	30	40	50	60	70	80	90	100	110	120
JE	200	0.55	0.55	0.60	0.67	0.72	0.83	0.89	0.97	0.96	0.98
MK	240	.56	.64	.75	.80	.93	.96	.96	.98	.99	.99
RW	220	.58	.62	.69	.81	.87	.92	.96	.96	1.00	.99
PR	90	.58	.68	.71	.76	.87	.88	.91	.98	0.98	.97
KH	140	.55	.56	.69	.74	.83	.91	.91	.97	.97	.96
VK	240	.56	.66	.60	.73	.81	.88	.94	.96	.99	.99
SK	160	.56	.61	.72	.84	.88	.93	.98	.98	1.00	.99
JA	180	.62	.67	.74	.90	.91	.94	.98	.99	0.97	.99
JS	150	.55	.66	.76	.82	.89	.94	.96	.98	1.00	.99
JK	230	.53	.58	.59	.68	.75	.84	.84	.95	0.93	.97
DU	128	.52	.54	.66	.66	.76	.84	.87	.93	.93	.98
TN	320	.53	.57	.61	.70	.74	.76	.84	.89	.92	.96
JM	224	.52	.56	.55	.70	.74	.83	.90	.93	.96	.99

Table 2. Parameters of the two-state model computed from the data of Table 1. M and x are to the nearest millisecond, P to the nearest 0.01; $P = 1 - 0.25\ P_2$. Peak alpha is the most frequently occurring interval between zero-crossings based upon the indicated sample size.

Subject	x (msec)	P	M' (msec)	Peak alpha	Alpha sample size
JE	23	.67	40	44	800
MK	24	.95	49	57	960
RW	24	.91	49	44	880
PR	20	.88	53	50	360
KH	27	.93	56	50	560
VK	20	.74	41	43	960
SK	25	.94	49	49	640
JA	20	.89	42	50	720
JS	23	.88	41	42	600
JK	33	.83	47	48	920
DU	34	.85	47	46	320
TN	26	.77	51	50	800
JM	36	.94	60	51	560
		Mean =	48.1	48.0	
		Standard deviation =	5.9	4.0	

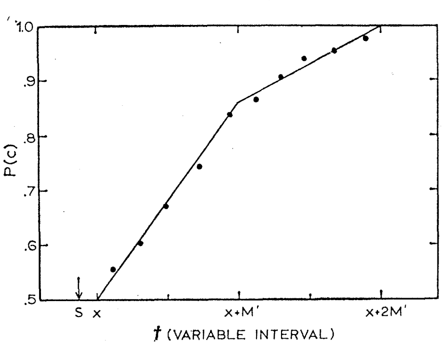

Fig. 1. Composite two-state successiveness discrimination function for 13 subjects. The line is the theoretical function with $P = 0.86$, the obtained average value. For each data point for each subject, t was converted into $(t - x)/M'$, and $\bar{P}(c)$, the value of $P(c)$ predicted by theory, was calculated all from the individual's own parameters. Then the error of prediction $[P(c) - \bar{P}(c)]$ was calculated. These errors were grouped together in intervals of 0.2 on the $(t - x)/M'$ scale and averages were taken of them and of their corresponding values of $(t - x)/M'$ within each group. These averages determine the coordinates of the points in this figure.

Their ranges are similar, 40 to 60 for M' and 42 to 57 for alpha.

As in the earlier study (*3*), the correlation between the quantum size and alpha is significant, the rank-order coefficient being 0.74. If one uses position with respect to the median of alpha to predict position with respect to the median of the quantum size and combines the results of the two studies, 19 of the 21 subjects are classified correctly.

In interpreting the degree of association between these two quantities one should consider the errors of measurement. I cannot estimate the reliability of M' at the present time; however, the reliability of alpha is something short of perfect. If one compares peak alpha obtained in the before-session records with that obtained at the ends of the sessions, the means are 47.7 in both cases and the rank-order correlation is 0.86 for the same 13 subjects (*8*).

The values of P which were obtained imply a range of P_2 extending from 0.20 to 1.0. No subject exhibited pure state 1 performance under the conditions of this experiment. The variables which influence the percentage of trials on which a subject is in state 1 rather than state 2 have yet to be identified. One possibility, for which I have some evidence, is that the range of values of t is itself such a variable. When the range is narrow, making the task a more difficult one, as in the earlier experiments, the probability of being in state 1 is higher than it is when the task is relatively easy. Another effective factor may be whether or not the subject is informed of the correctness of his decisions.

My interpretation of successiveness discrimination has recently been presented elsewhere (*3*). Briefly, the suggestion is that discriminating two independent signals as successive requires that attention switch from the channel containing the first signal to the other channel after the first signal occurs but before the second. If attention can switch only at the end of a time quantum, and since the first signal is equally likely to occur at any time during a quantum, then the successiveness discrimination function should be linear and it should span one quantum. This accounts for the state 1 function. The two-state model requires some elaboration of this view. One could speculate that state 2 occurs when an additional quantum of time is inserted in the visual information pathway prior to the display area or when the switching of attention can occur only in every second quantum (for example, only at positive-going zero crossings) (*9*). Either of these assumptions brings the two-state hypothesis into the theory but there seems to be no basis for a choice between them at this time.

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7. Since these data were analyzed we have begun computing electroencephalographic power spectra with autocorrelation functions. Comparisons between this computer analysis and the visual analysis used in this report indicates that they agree very well in determining peak frequencies and individual differences in peak frequency.
8. Nine of the original subjects are female. Three of these were excluded by the electroencephalogram screening and three failed to give adequate psychophysical data in the time that was available. The remaining three (MK, JA, and JM in Table 2) are the ones for whom the discrepancies between M' and alpha are the largest.
9. Statements of this kind do not imply a causal role for the electrical changes which constitute the electroencephalogram. In fact, there is evidence that contradicts such a view. For example, G. K. Smith and H. Langsam of this department have experiments under way which show that the spontaneous spike activity in single cortical neurons is unaffected by voltage clamping of the cells' environment.

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