

importance. To test the possibility that spontaneous afferent inflow was affecting the postsynaptic membrane of this particular motoneuron, the nerve of the gastrocnemius-soleus muscle was furthermore blocked by the application of procaine. However, the threshold for direct stimulation as well as the inhibition from posterior biceps stretch remained unchanged, again demonstrating the postsynaptic character of this inhibition. Such postsynaptic inhibitions by muscle stretch without effect on the average membrane potential have earlier been described (10). In Fig. 1E is again shown the inhibitory effect of a 1000-g stretch of posterior biceps on the firing induced by injected current. Between E and F of Fig. 1, picrotoxin was administered intravenously in a dose of 1.0 mg/kg. A few minutes later most of this strychnine-resistant postsynaptic inhibition had been removed by picrotoxin (Fig. 1F, to be compared with E of the same figure). This result is in agreement with what has been found in a previous study (7).

In the cases where KCl microelectrodes were used, it was possible to demonstrate the postsynaptic nature of these stretch-induced inhibitions in an additional way: by injecting chloride ions from the impaling microelectrode into the motoneurons the inhibitory effects could be reduced or even reversed into excitatory responses, showing that the reduction in excitability was not caused by a removal of background excitation (see also 7, 11).

Figure 2 summarizes the results of the 22 gastrocnemius-soleus motoneurons investigated in this study. For each motoneuron several recordings were made in order to obtain an average estimate of the amount of inhibition from posterior biceps stretch on repetitive firing induced by injected depolarizing current (plotted on the y-axis) and on repetitive firing induced by autogenetic muscle stretch (plotted on the x-axis). Therefore, in a situation where, for example, only presynaptic inhibition is involved, the points would fall along the x-axis. On the other hand, if only postsynaptic inhibition is activated, the points would fall along a line with unit slope. A line of unit slope is drawn in Fig. 2 and the points are seen to be more or less randomly distributed around this line. The ratio $\Sigma y / \Sigma x$ was calculated and found to be 1.037, indicating only an insignificant deviation from unity.

It may therefore be concluded that, even when the experimental conditions are chosen so as to favor presynaptic inhibition (3, 4), postsynaptic inhibition is by far the more powerful mechanism of the two in determining motoneuron activity during maintained stretch reflexes. Therefore, it may not be possible to use primary afferent depolarization and changes in the size of the excitatory postsynaptic potential produced by synchronous nerve stimulation (1, 3) to assess the importance of presynaptic inhibition in normal reflex activity.

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21 February 1966

Perception of Temporal Order and Relative Visual Latency

Abstract. *Judgments of temporal order to monocular pairs of flashes of equal luminance delivered at various onset asynchronies to the light-adapted fovea and periphery show that uncertainty of temporal order results when the onset of the foveal flash is delayed. Relative latencies vary as a function of peripheral (nasal vs. temporal) locus stimulated.*

When a person is stimulated by two spatially discriminable flashes of light and is asked to report which flash appeared first, his choice of one or the other alternative is generally deter-

Table 1. Onset asynchronies required for maximal uncertainty of temporal order judgments (50 percent response) and corresponding probable errors (PE). Negative asynchrony indicates that the peripheral flash occurred first.

Subject	Foveal—30° nasal pair		Foveal—30° temporal pair	
	50% (msec)	PE	50% (msec)	PE
LR	-12	16	-34	20
JR	-25	14.5	-34.5	16
ER	-60	27	-75	16
DH	-46	15.5	-57.5	17
DD	-52.5	18.5	-31	21

mined by the temporal relationships between the onsets of the two stimuli. Physical changes in the direction and magnitude of the onset asynchrony between two flashes are likely to produce concomitant changes in perceived onset asynchrony, thus influencing judgments of temporal order. Maximal uncertainty about temporal order is reflected by an equal probability of a subject's choosing between the two alternatives under a given condition of stimulation. A report by Hirsh and Sherrick (1) presents data to the effect that maximal uncertainty regarding the temporal order of two flashes at different eccentricities obtains when they are physically simultaneous, regardless of the retinal positions of, and spatial separation between, the two stimuli. These authors concluded that a relatively fixed onset asynchrony of 20 msec is required for 75-percent-correct detection of the temporal order of two events, independent of sense modality employed and stimulus conditions.

This study was conducted on the initial assumption that the temporal interval between the onsets of two visual stimuli which yields maximal uncertainty about their temporal order represents an estimate of the average amount of latency difference to the two flashes. The experiment was designed to investigate the dependency of judgments of temporal order on the location of the flashes on the retina. Within the framework presented here, Hirsh and Sherrick's generalization is questioned in the light of both existing reaction time (2) and psychophysical (3) measures of latency differences across the retina, and evidence that judgments of temporal order are a function of attributes of the stimulus (4).

The stimuli were pairs of light flashes generated by Sylvania R1131C glow modulator tubes. Each target sub-

tended $1^{\circ}12'$. The flashes were delivered to the subject's right eye against a spherical background of uniform luminance (0.5 millilambert). Flash luminance was 125 mlam; flash duration was 500 msec. On each trial, one flash stimulated the fovea and the other a point on the horizontal meridian either 30° to the right of center (nasal retina) or 30° to the left (temporal retina). The sequence of fovea-right and fovea-left pairs was randomized. The onset asynchrony between the flashes was varied in 10-msec interval

steps according to the method of constant stimuli. Taking the onset of the foveal flash as $t = 0$, asynchronies were positive (foveal flash delivered first), negative (foveal flash delivered second), or zero (physical simultaneity). The subject fixated the center target and, after the presentation of each flash pair, gave a forced-choice judgment as to which appeared first, "foveal" or "peripheral." No knowledge of results was given. The five subjects tested were given approximately 800 trials with each of the two flash pairs.

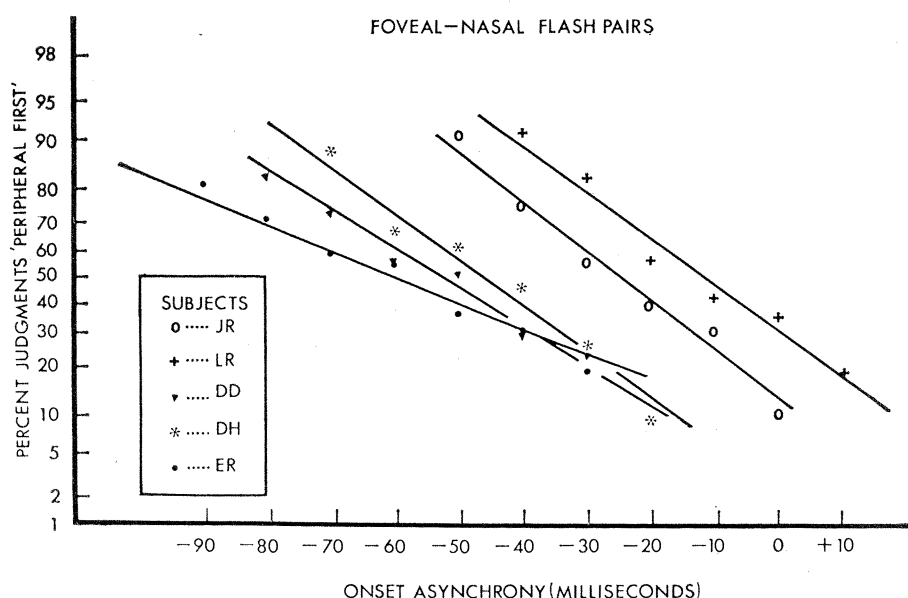


Fig. 1. Proportion of responses "right first" to foveal-nasal flash pairs as a function of the time interval between onsets (negative asynchrony indicates that the peripheral flash was physically first).

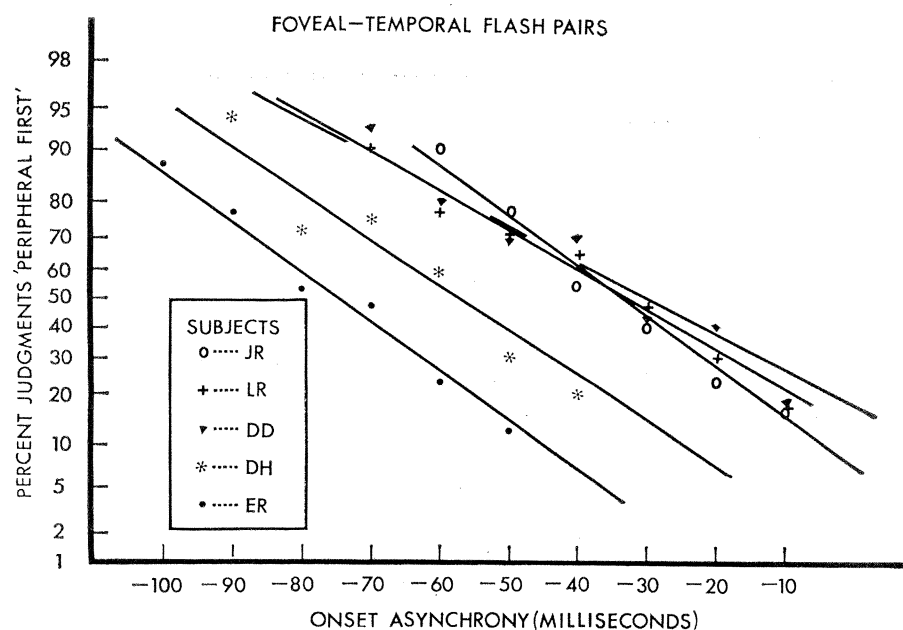


Fig. 2. Proportion of responses "left first" to foveal-temporal flash pairs as a function of the time interval between onsets (negative asynchrony indicates that the peripheral flash was physically first).

The data of all sessions for each subject were pooled and plotted on a probability grid relating proportion of responses "peripheral first" to the onset asynchrony between the flashes. Foveal-nasal (Fig. 1) and foveal-temporal (Fig. 2) proportions were plotted separately, and straight lines were fitted to the data points by the method of least squares. The onset asynchronies associated with 50 percent response and the corresponding probable errors (denoting the slope of the functions) are presented in Table 1. All subjects require negative onset asynchronies (peripheral flash physically first) for maximal uncertainty about temporal order, and the data show that four of the subjects report "foveal first" 75 percent of the time when the foveal flash was in fact physically second. With a single exception, the negative asynchronies are greater with the foveal-temporal than with the foveal-nasal flash pair. The functions shown, however, do not exhibit a systematic difference in slope between flash pairs, indicating that the variability of judgments of perceived temporal order was comparable under the two conditions. It should be noted that, although there are individual differences in the absolute magnitude of the time intervals yielding indeterminacy of temporal order, the slopes of the five individual functions under both conditions of stimulation are similar. In all cases, the range of asynchronies required to bracket the psychometric functions was of the order of 60 to 80 msec.

These results are clearly at variance with those of Hirsh and Sherrick (1). Physical simultaneity does not produce uncertainty regarding the temporal order of two flashes stimulating the retina at two different places. Furthermore, given the large proportions of "foveal first" responses to flash pairs whose actual sequence was peripheral-foveal, the data cannot be discussed in terms of "correct" detection of temporal order. The findings indicate longer latencies to peripheral flashes than to foveal flashes of equal luminance; this result is on the whole consonant with the measures of latency variations as a function of locus of stimulation reported in the literature (2, 3). An interpretation of the effect in terms of the apparent brightness or sensory magnitude of the stimuli appears circular at this point, given the possibility that apparent brightness itself varies as a function of retinal location. None

of the subjects here, however, reported perceiving systematic brightness differences between the foveal and peripheral flashes. The difference obtained in the onset asynchronies producing maximal uncertainty between the foveal-nasal and foveal-temporal flash pairs indicates greater latency to a stimulus applied to the temporal side of the retina. This finding presents a trend similar to the average differences between foveal and peripheral reaction times reported by Poffenberger (2).

In Poffenberger's study, the excess of peripheral reaction times over foveal reaction times at 30° on the nasal retina was of the order of 9 msec; at 30° on the temporal retina, of the order of 13 msec. By comparison, the estimates of relative latency obtained here show greater latency differences both between the fovea and periphery and between the nasal and temporal positions. These latency differences are apparently a function of the specific retinal location of stimuli and there-

fore cannot be attributed to the amount of spatial separation (angular distance) between the stimuli. This conclusion is lent support by the finding (5) that the perceived temporal order of foveal-peripheral flash pairs is dependent on both the laterality (right or left eye) and eccentricity of the peripheral flash.

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6. Supported in part by PHS grant MH 03616, and conducted at the Department of Psychology of the New York State Psychiatric Institute, Columbia University Medical Center. I thank Jacques Rutschmann for his assistance and the subjects for volunteering their services.

28 March 1966

List Differentiation with Varied Trials on Both Lists

Abstract. *Differentiation, defined as the discrimination of list membership, was studied with a recognition procedure. In each of the two studies, the number of learning trials was varied for one list and the trials on the other list were held constant. Differentiation was a U-shaped function of trials, passing through a minimum when both lists were shown equally often.*

Interference theory attributes forgetting to the learning of other material which interferes with the retention of the forgotten material. In a typical interference experiment on retroactive inhibition, subjects learn two successive lists of verbal items and are then tested on recall of the first list. The loss in retention of the first-list items, as compared with the loss in a control group not learning a second list, is a measure of retroactive inhibition and is attributed to interference from second-list learning. Retroactive inhibition has been shown by several investigators to increase with the number of second-list trials, but a problem associated with this finding has been the lack of correlation between overt intrusions (the occurrence of second-list items during first-list recall) and the amount of retroactive inhibition (1, 2). To account for this discrepancy, the concept of differentiation was introduced (2, 3).

Differentiation is usually defined as the discrimination of the list membership of response items. It is assumed

that, because of differentiation, subjects may inhibit intrusions if they implicitly recognize some responses as coming from the second list. Thus, at high degrees of second-list learning, subjects are assumed to be unable to recall first-list items but able to discriminate the inappropriateness of second-list responses.

A general assumption of interference theorists has been that differentiation is a U-shaped function of second-list learning, with differentiation lowest when both lists have been equally learned. Such a function would help to explain both the retroactive inhibition findings just referred to and the puzzling finding from transfer studies that overlearning the first of two lists leads to a decrease in negative transfer on learning the second list (4).

The importance of differentiation has led recently to the development of procedures that have made possible the measurement of response availability while attempting at the same time to minimize the contribution of differen-

tiation (5). We report here data from a procedure designed to measure list differentiation directly while minimizing the contribution of availability. The effects on differentiation of manipulating the number of second-list trials in one study, and first-list trials in another study, are reported.

To study list differentiation directly, subjects, after having been exposed to two lists of verbal items successively, were required to indicate in a test to which list each item belonged. By showing subjects all of the items from both lists during the test with the assurance that all test items were items already seen, and by demanding that the subjects state on which list each item appeared, a test of differentiation was accomplished. In effect, memory for context was tested.

In the first experiment, the number of first-list trials was held constant and the number of second-list trials was varied for different groups. In each session, groups of from two to ten subjects sat facing a screen. A list of 25 common English nouns was projected serially at a 3-second rate for three trials, with an intertrial interval of 15 seconds. Subjects were instructed to learn the words but were not told that there would be a second list. During the learning trials, the items were shown in different orders on successive trials. After the third trial on list 1, subjects were told that they would now be shown a second list and that they were to learn these words also. The interval between the showing of the lists was 45 seconds. List 2 was shown for one, three, or six trials, making combinations of trials on both lists of three and one, three and three, and three and six. In the second experiment, trials on list 1 were varied, with presentations of list 2 held constant at three trials. Combinations of list 1-list 2 trials of 1-3 and 6-3 were obtained. The data of the 3-3 group of the first study were used as a middle group in the second study as well.

Five groups of 20 subjects each were used. The subjects were male Columbia College students who were paid for their services. Two lists of 25 common English nouns equated for frequency (6) were made up. Each list served as list 1 for half the subjects in each group and as list 2 for the other half.

After the last trial of list 2, test instructions were read and the differentiation test was presented. During the test, which started approximately 4