matographic plates when viewed under ultraviolet light. The gibberellins, GA_1, GA_3, GA_4, GA_7, and GA_9, were identified by their chromatographic similarity to authentic samples (*9*). Other gibberellins were not identified because standards were not available.

A cross was made between two strains of *G. fujikuroi* (2794a × 2900A) that differed in their gibberellin phenotypes (Table 1). The high-producing strain, 2794a, produced GA_1, GA_3, GA_4, GA_7, and GA_9, plus other unidentified gibberellin-like materials. The low-producing strain, 2900A, produced only trace amounts of GA_4 and GA_7; GA_1, GA_3, GA_9, and other gibberellin-like materials were not detected. Four asci from this cross were dissected. In each case, there was a 2 : 2 segregation for gibberellin production (Table 1); cultures derived from two of the tetrad of spores produced gibberellin, whereas cultures derived from the remaining two spores produced little or no gibberellin. The response differences between the high-producing and the low-producing strains were of the order of 100-fold. The low-producing progeny had either no detectable gibberellin or only trace amounts of GA_4 and GA_7. The high-producing progeny, with one exception, had relatively large amounts of GA_1, GA_3, GA_4, GA_7, and GA_9, plus other unidentified gibberellin-like materials.

A second cross was made with the progeny obtained from the first mating. One of these progeny strains repeatedly failed to produce any detectable gibberellins or gibberellin-like substances, whereas the other was indistinguishable from the high-producing parent (strain 2794a). From this cross 91 asci were dissected. In each case there was again a 2 : 2 segregation for gibberellin production. These results suggest that total gibberellin production is under the control of a single pair of alleles.

Among the four tetrads studied in the first cross, one was of special interest. Although there was a 2 : 2 segregation for gibberellin production, qualitative differences were observed among the producing members of the tetrad. One strain produced relatively large amounts of GA_1, GA_3, GA_4, GA_7, and GA_9, plus other unidentified gibberellin-like materials; the other strain also produced relatively large amounts of GA_4, GA_7, and GA_9, plus unidentified gibberellin-like materials, but no GA_1 or GA_3. One explanation for the latter phenotype may be the presence of a second mutant gene which affects the production only of GA_1 and GA_3.

Our results indicate that *Gibberella fujikuroi* can be used for genetic investigations of gibberellin production. The analysis of 95 asci provides evidence that a single pair of alleles controls total gibberellin production. This gene may exert its effect early in the gibberellin biosynthetic pathway, since it controls the production of all the gibberellins and gibberellin-like materials assayed for in this study.

CALVIN SPECTOR*
BERNARD O. PHINNEY
Department of Botany and Plant Biochemistry, University of California, Los Angeles 90024

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2. Strains of *Gibberella fujikuroi* were obtained from the late W. L. Gordon, Plant Pathology Laboratory, Canadian Department of Agriculture Research Station, Winnipeg.
3. The crossing medium was prepared by autoclaving young stems of *Citrus medica* L. in 125-ml erlenmeyer flasks which contained 10 ml of water. The medium was autoclaved for 15 minutes. Inoculations were made the same day as the medium was autoclaved.
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* Present address: Department of Biology, University of Pittsburgh, Pittsburgh, Pennsylvania 15213

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Metacontrast: Its Relation to Evoked Potentials

Abstract. *Electrophysiological correlates of metacontrast were studied by means of averaged evoked potentials recorded from the scalp in man. Under conditions in which the brightness of the first of two successive stimuli appears diminished there is no accompanying attenuation of the evoked potentials to that stimulus. The results suggest that the amplitude and latency of evoked potentials correlate with stimulus intensity but not with brightness.*

When two equally intense visual stimuli with adjacent contours are presented in rapid succession, the brightness of the first stimulus appears greatly reduced. This type of brightness suppression, generally referred to as metacontrast (*1*), is one of several visual phenomena showing that brightness can be modified by a temporal interaction between stimuli.

Metacontrast has been extensively studied by psychophysical methods (*2*). It is readily observed under these conditions: A disk is presented very briefly and is followed, after a variable interval, by a surrounding ring of equal area, intensity, and duration. When the interval between disk and ring is short (0 to 10 msec), both are clearly seen. As the interval is increased, the brightness of the disk diminishes. At interstimulus intervals between 40 and 100 msec, metacontrast suppression becomes maximal and the disk virtually disappears. With further increases in the interstimulus interval the disk becomes progressively brighter again. When the two stimuli are separated by 200 to 250 msec, the disk appears to have regained its original brightness. Throughout a sequence of such presentations, the appearance of the ring remains relatively unchanged.

Several different theories have been proposed to explain metacontrast suppression in terms of retinal (*3*), subcortical (*4*), and cortical (*5*) interactions between neural responses to the two stimuli. In order to evaluate such interpretations, one should be able to specify the neural correlates of brightness perception. This is not yet possible, but recent work with evoked potentials recorded from the scalp in man has shown that evoked potential amplitude increases and latency decreases as stimulus intensity (and therefore brightness) is increased (*6*). Are these covariations due to the altered stimulus intensity, or to the change in brightness, or both? In attempting to answer this question we wished to know whether the brightness reduction observed under metacontrast conditions (where brightness changes but intensity does not) is accompanied by evoked potential changes comparable to those that normally occur when stimulus intensity

is varied. The finding that metacontrast suppression (like intensity reduction) is accompanied by a decrease in amplitude and increase in latency of the evoked potential to the initial stimulus would suggest that these aspects of the cortical evoked response correlate with the psychological variable of brightness perception rather than with physical variations in stimulus intensity per se. However, the finding that evoked potentials change only when brightness and intensity covary, and not when brightness alone is reduced (as in metacontrast), would suggest that, while the amplitude and latency of the evoked response may correlate with physical aspects of the stimulus, they do not necessarily correlate with the perceptual response of the subject.

The same procedure was followed for each of five subjects. The subject was seated with his head on a chin rest facing the stimulus display unit 150 cm away. He was instructed to fixate binocularly on a faint red light 12 cm to the right of the center of the stimulus display. The experiment was carried out in a darkened room. Each subject was dark-adapted for at least 10 minutes before the beginning of a session.

The stimulus display consisted of a disk, 10 cm in diameter, surrounded by a ring with an inner diameter of 10 cm and an outer diameter of 14 cm. The face of the display assembly was machined from ¼-inch (⅔-cm) opal Plexiglas. The disk and ring could be separately transilluminated by mercury-argon cold cathode lamps mounted behind them (*7*). A tachistoscopic programmer (*8*) was used to trigger the lamps and to control the sequence and duration of stimulus presentations. On all trials, exposure durations for the disk and the ring were equal and constant at 5 msec. On all metacontrast trials the intensity of each stimulus was 135 ft-lam (1453 lu/m^2). The following conditions of presentation were employed: disk alone; disk followed by ring at interstimulus intervals of 3, 30, 60, 100, 150, and 200 msec; ring alone, with equivalent delays. In order to compare evoked potential changes produced by metacontrast suppression with those produced by stimulus intensity reduction, we also presented the disk alone at 13.5 and 1.35 ft-lam. For each subject 100 consecutive trials were run under each condition; the recycling time was 2.1 seconds.

For recording the evoked potentials we used a conventional electroencephalographic machine, a tape recorder, and an average-response computer (*9*). A midsaggital area of the subject's scalp, 4 cm above the inion, was cleaned with acetone and treated with a paste composed of bentonite and saturated $CaCl_2$ solution. A single, 0.5-cm-diameter disk electrode was taped to the scalp at this point. An ear lobe, similarly cleaned and treated, served to locate the indifferent electrode.

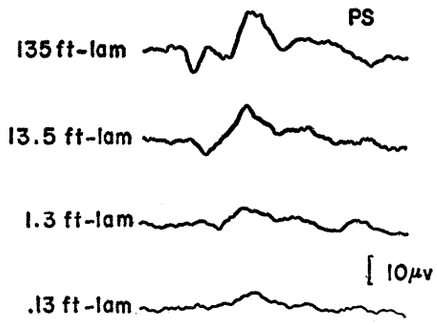

Fig. 1. Averaged evoked potentials to disk presented alone at four intensity levels. Sweep (500 msec) starts at onset of light flash. Negativity down.

Figure 1 shows changes in the averaged evoked potential recorded from one subject as stimulus intensity was decreased. The characteristic reduction in amplitude and increase in latency are consistent with previously reported findings (*6*). Initial observations showed that during optimal metacontrast suppression a disk at 135 ft-lam actually appears less bright than a disk presented alone at 1.35 ft-lam (*10*). Therefore, if the brightness reduction occurring during metacontrast suppression is accompanied by evoked potential changes like those that occur when stimulus intensity is reduced, the amplitude and latency of the averaged evoked response to the 135-ft-lam disk under metacontrast conditions should be similar to the amplitude and latency of the evoked response to the 1.35-ft-lam disk presented alone.

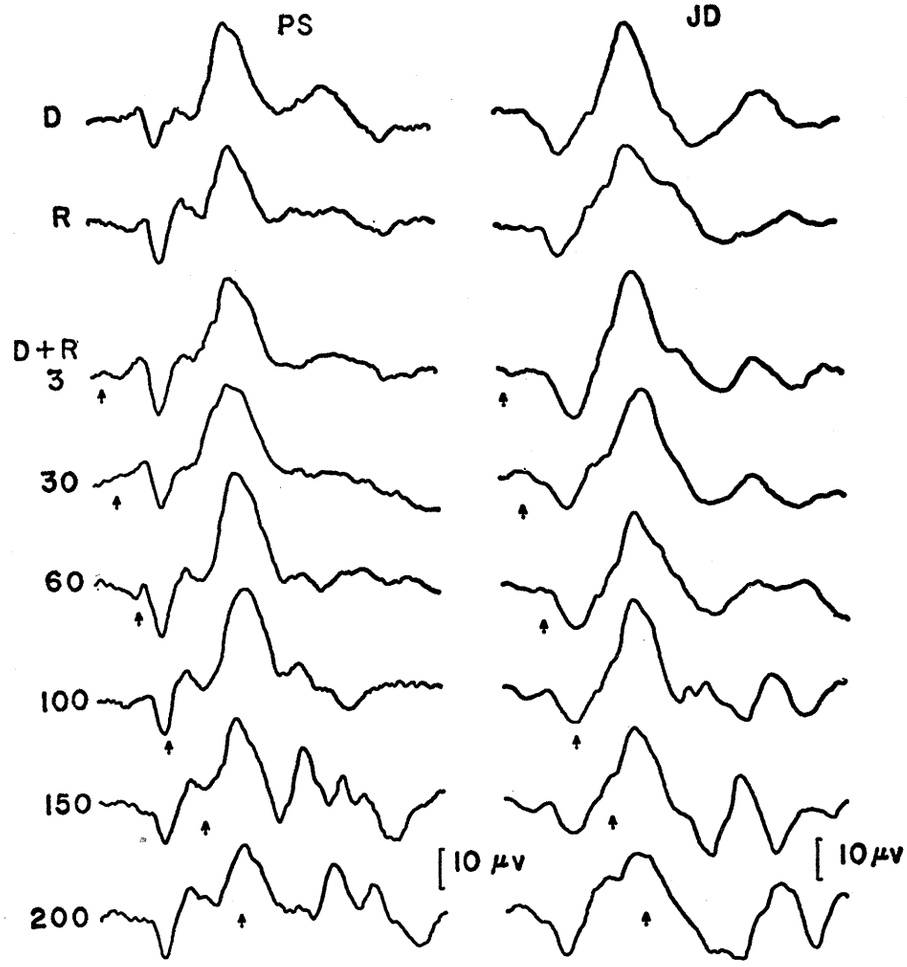

Fig. 2. Averaged evoked potentials recorded from subjects PS and JD: *D*, disk alone; *R*, ring alone; *D* + *R*, paired presentations. Numbers at left indicate the interval between *D* and *R* (paired) in msec. Sweep (500 msec) starts with onset of first stimulus. Arrows show onset of second stimulus.

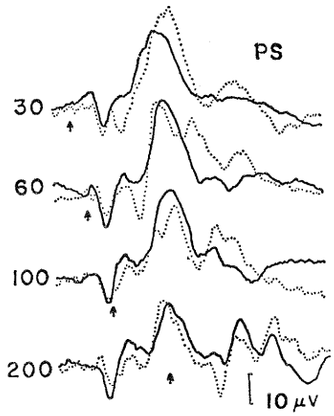

Fig. 3. Averaged evoked potentials to paired presentations (solid lines) compared with synthetic averaged evoked potentials obtained by summing responses to single stimuli (dotted lines). Sweeps are 500 msec.

Figure 2 shows data obtained from two subjects during paired presentations, together with the averaged evoked response to the disk and ring presented separately. At all interstimulus intervals (including those at which metacontrast suppression is maximal), the initial negative wave of the evoked response to the disk remains essentially unchanged (*11*). At interstimulus intervals of 60 and 100 msec the disk is virtually invisible, yet the amplitude and latency of the evoked response do not vary as they do when stimulus intensity is reduced (Fig. 1).

The finding that the evoked response to the first stimulus is relatively unchanged, at interstimulus intervals producing maximal metacontrast suppression, helps to explain two observations that have previously been made in metacontrast experiments: (i) Reaction time to the first stimulus is not affected by metacontrast suppression (although reaction time normally increases as stimulus intensity is decreased); and (ii) in a forced-choice paradigm, the first stimulus is equally detectable at all interstimulus intervals (*12*).

It has been suggested (*13*) that in some cases cortical evoked potentials to paired stimuli are additive (that is, are the resultant of evoked responses to the two stimuli presented singly). In order to test whether or not this is the case in the metacontrast situation, we selected appropriate delay intervals and artificially combined evoked responses that had been recorded during presentations of the disk and ring alone (*14*). Synthetic averages produced in this way are shown in Fig. 3 (dotted lines) superimposed upon the directly recorded averaged evoked responses (solid lines) obtained during paired presentation of the stimuli. Since the initial negative response to the ring is clearly present in all of the synthetic tracings and since there are many other notable differences between the directly recorded and synthetically produced records, there appears to be little support for the view that later components of the evoked response to paired stimuli under metacontrast conditions represent a summation of evoked responses to the individual stimuli.

The results obtained for the paired presentations (Fig. 2) also show that the wave form of the evoked potentials to the ring are considerably modified by the disk preceding it. Some effect is observable even with an interstimulus interval of 200 msec (*15*). These results seem to be analogous to those observed with paired overlapping stimuli (*16*).

Comparison of our results with those obtained by Donchin and Lindsley (*17*) for visual masking reveals an interesting contrast. In visual masking, which has frequently not been distinguished from metacontrast, two stimuli of unequal intensity fall successively on the same retinal locus. At certain interstimulus intervals, the second, brighter flash (BF) masks perception of the initial test flash (TF). Under these conditions, Donchin and Lindsley found no detectable evoked response to the initial stimulus. They concluded, in part, that ". . . the masking phenomenon is due to a displacement of the neural response to the TF by the response to the BF and that this interaction occurs prior to the stage at which the evoked potential is elicited" (*17*, p. 334). That no such displacement occurs under metacontrast conditions is clear from Figs. 2 and 3. The disparity in results suggests that the perceptual suppressions obtained in masking and metacontrast experiments are mediated by different neural mechanisms.

In summary, the initial negative wave of the average cortical evoked potential manifests an increased latency and decreased amplitude when brightness is reduced by lowering stimulus intensity (Fig. 1). However, comparable latency and amplitude changes do not occur under metacontrast conditions when brightness is reduced without lowering stimulus intensity (Fig. 2). These findings suggest that a direct correlation between psychophysical indices and evoked potentials cannot always be assumed (*18*). Although metacontrast provides rather special conditions of stimulation, dissociation between brightness and intensity occurs commonly in normal visual perception (*19*). Further work is needed to determine the extent to which our findings are applicable to such situations.

PETER H. SCHILLER
STEPHAN L. CHOROVER
Department of Psychology,
Massachusetts Institute of Technology,
Cambridge 02139

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11. For two of the five subjects, evoked potentials were also recorded from additional scalp placements. Although the overall response patterns were slightly different for the various placements, the general relationships described in the report were obtained for all electrode locations.
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