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Spatial memory during the tropism of maize (*Zea mays* L.) coleoptiles

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Abstract. Photo- or gravitropic stimulation of graminean coleoptiles involves the formation of putative tropistic transverse polarities. It had been postulated that these polarities can be extended by stabilization to developmentally active polarities. Such polarities are known from unicellular spores and zygotes of lower plants and regeneration experiments in dicotyledonous plants. In coleoptiles, photo- or gravitropic stimulation results in stability to counterstimulation of equal strength (with only transient bending in the direction of the second stimulus), as a result of a directional memory, if the time interval between both stimuli exceeds 90 min. This directional memory develops from a labile precursor, which is present from at least 20 min after induction. Once it is stable, spatial memory is conserved for many hours. The formation of spatial memory involves at least one step not present in the common tropistic transduction chain. The spatial expression of memory as curvature is restricted to three distinct responses: (i) curving in the direction of the first stimulus (for time intervals exceeding 90 min); (ii) curving in the direction of the second stimulus (for time intervals shorter than 65 min); and (iii) zero-curvature (for time intervals between 65 and 90 min). This can be interpreted in terms of a stable transverse polarity, which is not identical with the putative tropistic transverse polarity, but might be an extension of it.

Key words: Coleoptile – Gravitropism – Phototropism – Polarity, transverse – Spatial memory – *Zea* (tropisms).

Introduction

It is widely accepted that asymmetric stimulation of graminean coleoptiles by either gravity or blue light establishes an internal transverse polarity. There is, however, little information concerning the qualitative nature of this supposed polarity. Because of the nature of the inducing agent, gravitropic polarity might be expected to be a feature of cell polarity rather than be caused by integration over the whole coleoptile cross-section (Volkmann and Sievers 1979). In contrast, early investigations into phototropism led to the conclusion that, here, a systemic polarity was induced (Buder 1920).

Although polarity must be regarded as a fundamental problem in developmental biology, detailed investigations in plant systems have been confined to two experimental systems:
(i) *Thallus-rhizoid polarity* in phaeophycean eggs (mainly *Fucus*) and pteridophyte spores (mainly *Equisetum* and *Osmunda*), where orientation can be induced by a range of environmental factors including ion gradients, temperature and blue light (Weisenseel 1979). In the case of ion gradients, it has been suggested that thallus-rhizoid polarity might be caused by a lateral displacement of ion pumps towards the side with lower external ion concentration. These pumps are presumed to drive a calcium current into the cell, thus enlarging the initial ion gradient (Robinson and Jaffe 1975; Robinson and Cone 1980). This is consistent with theoretical considerations postulating self activation and lateral inhibition (or competition for limited substrates) as the main mechanisms of polarity formation (Gierer 1981).
(ii) *The apical-basal polarity* of dicotyledonous stems and roots with respect to regeneration (Vöchting 1878; Sachs 1880; Goebel 1908), where a self-activating flux of a putative growth factor was postulated (Goebel 1908). More recent studies on the polarity of vessel regeneration (Sachs 1984) showed self activation of auxin transport to be the driving force of polarization. This is consistent with the classical studies of Goebel (1908) and the theoretical considerations of Gierer (1981).

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It has long been disputed as to whether polarity is produced de-novo or only reoriented (Sachs 1880; Vöchting 1878). In *Osmunda* spores, experiments involving stimulation by linearily polarized red light with high intensity can sometimes give rise to embryos having two equal poles. This indicates that polarity is produced de novo (von Wettstein 1965). In higher plants, this point is still under dispute, although regeneration experiments on clinostats can be interpreted as favouring the concept of reorientation of an already-existing polarity (Vöchting 1880; Goebel 1908).

It has been postulated that the development of polarity could be related to tropism, and a model including similar mechanisms, i.e. self-activation and lateral competition, has been put forward for phototropism in *Phycomyces* (Hertel et al. 1980). This model omits only the last (stabilizing) step in the model for polarity-formation postulated by Gierer (1981).

In the course of investigations into the interaction between photo- und gravitropic stimulation in maize (*Zea mays* L.) coleoptiles, it was concluded that the transduction step, where the interaction takes place, is able to compare the directions of both stimuli (Nick and Schäfer 1988). Thus, there would appear to be an interaction between different types of transverse polarity: presumably cell-based gravitropic polarity and the systemic phototropic polarity.

If the mechanisms producing tropistic bending are by their nature identical with those involved in induction of polarity, and only one stabilizing step is required to extend tropism into polarity, the presence of irreversible, memory-like phenomena in connection with the tropism of graminean coleoptiles must be considered likely. The existence of such phenomena in tropism is investigated here.

Materials and methods

Plant material. Maize seeds (*Zea mays* L. cv. BRIO 42.HT, Asgrow GmbH, Buxtehude, FRG; stored at 3° C in the dark) were grown in a growth chamber and prepared for experimental use as described by Nick and Schäfer (1988).

Light sources. The red-light source used in the phytochamber was as described by Mohr et al. (1964). For phototropic induction, a Prado Universal projector (Leitz, Wetzlar, FRG) was used. Blue light was isolated by means of a DIL interference filter (451 nm, halfband-width 10 nm, maximal transmission 18%) and the fluence rate was regulated using neutral density filters (both filter types from Schott & Gen., Mainz, FRG). Irradiation time (30 s throughout) was controlled by means of an automatic shutter system. Between phototropic induction and excision, the seedlings were kept under symmetric, saturating red light (2.3 $W \cdot m^{-2}$, light source as described for the growth chamber). Light measurements were carried out using a digital photometer (J16/Option 2; Tectronix, Beaverton, Ore., USA).

Photo- and gravitropic stimulation. The whole shoot was irradiated unilaterally for 30 s with the longest transverse axis of the seedling parallel to the direction of the incident light. The blue-light fluence was kept at 0.88 $\mu mol \cdot m^{-2}$ throughout, using the photometer. This fluence is known to elicit maximal first-positive curvature (Nick and Schäfer 1988). After irradiation, plants were placed horizontally onto a clinostat at 0.5 rpm. After different time intervals, the seedlings were removed from the clinostat, given a second unilateral irradiation of equal fluence but from the opposite side and then returned to the clinostat. In a different set of experiments, the seedlings were kept in an upright position over the whole experimental period or only placed on the clinostat several hours after photostimulation. In some cases, one phototropic stimulation was replaced by a 30-min horizontal gravistimulation. This gravistimulus was given from the opposite direction to that of the remaining phototropic induction. Preliminary experiments showed that this gravity treatment induced curvatures comparable to those induced by the light fluences (Fig. 1). All treatments took place under continuous, symmetric red light so as to eliminate interference by blue-light-induced mesocotyl curvature mediated by phytochrome gradients (Iino et al. 1984).

Kinetic measurements. Time courses from curvature development were measured after the different treatments described above. The seedlings remained under symmetric continuous red light (2.3 $W \cdot m^{-2}$). Shadowgraphs were taken using unilateral red light (0.025 $W \cdot m^{-2}$, DEPIL interference filter, maximal transmission at 665 nm, maximal transmission 10%; Schott & Gen.). For shadowgraphing, the seedlings had to be removed from the clinostat and stood upright for roughly 30 s. This treatment has been shown not to affect curvature development on the clinostat (Pickard 1972).

Curvature measurements and statistics. Twenty-four hours after the beginning of treatments, the shoots were excised, attached to a strip of masking tape, and fixed to a Plexiglas plate in such a way that the longest transverse seedling axis was parallel to the plate surface. The plate was photocopied with an IBM copier III Model 20 and coleoptile curvature marked by drawing lines. The angles were measured with a Hewlett-Packard 986417 digitizer connected to an HP 982017 calculator. Mean and standard error were calculated for four seedlings per treatment. The shadowgraphs obtained from kinetic measurements were treated in the same way. Each point of the time courses shown in the figures represents the average from two independent experiments, whereby for each experiment eight seedlings were measured. Unless otherwise indicated, the bars in the figures represent standard errors. The plotted curves were obtained by means of a curve-fitting program using an spline-fitting method not necessarily corresponding to the mathematically simplest fit. For the frequency distribution plots (Figs. 7a–c) the curvatures of 180 to 220 seedlings were used for each plot, divided into curvature classes (width 20°) and counted. The frequency (in %) was then calculated for each class and plotted.

Results

Can gravistimulation from the opposite direction cancel the phototropic response? Owing to gravitropic counterstimulation normal phototropic

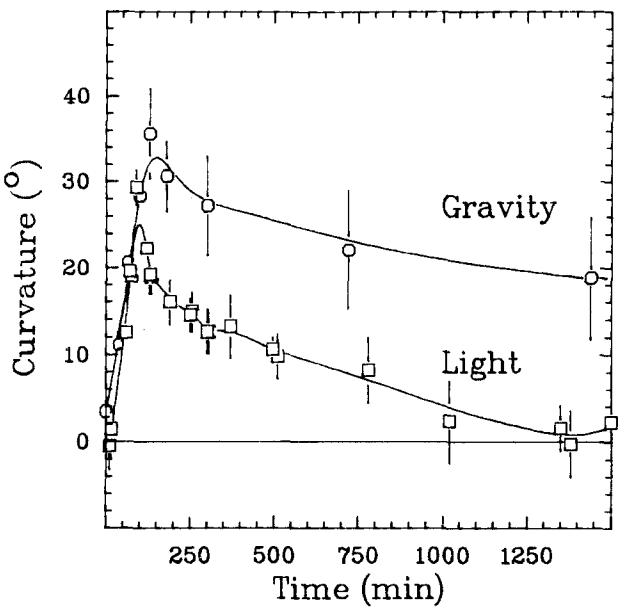

Fig. 1. Time course for curvature development in maize coleoptiles after unilateral stimulation with 0.88 $\mu mol \cdot m^{-2}$ blue light (seedlings remained in an upright position) and 30 min horizontal gravistimulation (seedlings curved on an horizontal clinostat), respectively. Both time course were followed under saturating and symmetrical red light (2.3 $W \cdot m^{-2}$) for the whole experimental period

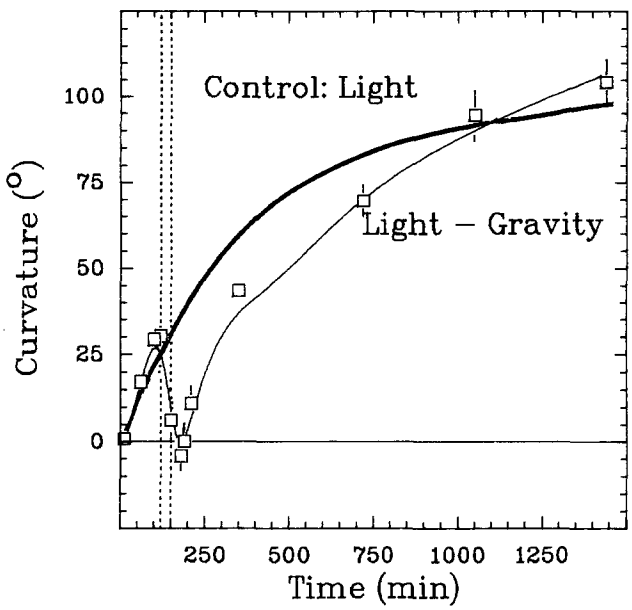

Fig. 2. Time course for curvature development on a horizontal clinostat after unilateral stimulation of maize coleoptiles with 0.88 $\mu mol \cdot m^{-2}$ blue light. After 2 h the clinostat treatment was interrupted, the seedlings were subjected to 30 min horizontal gravistimulation from the direction opposite to the phototropic stimulation and then returned to the clinostat. Seedlings were kept under saturating and symmetrical red light (2.3 $W \cdot m^{-2}$) for the whole experimental period. *Bold curve*: control; phototropic induction alone with curvature development on a clinostat. *Dotted verticals*: duration of the gravistimulus

curvature is transient, reaching maximal values 100 min after induction. On the clinostat, however, phototropic bending continues for many hours reaching values of more than 90° (Nick and Schäfer 1988). Thirty minutes of gravistimulation (stimulation angle 90°) result in approximately the same curvature as 0.88 $\mu mol \cdot m^{-2}$ blue light (known to elicit maximal first-positive phototropism), when one compares the time courses up to 120 min after the onset of stimulation (Fig. 1). At this time after induction it could be shown that photo- and gravitropic stimulation act additively when applied in opposing directions (Nick and Schäfer 1988). An attempt was therefore made to cancel the effect of the blue-light stimulus by 30 min gravistimulation from the opposite direction. This gravistimulation was applied 2 h after photostimulation and subsequent growth on the clinostat. At the time of application of the gravistimulus, there is a curvature of about 25°, i.e. approximately the same value obtained for photostimulated controls not subjected to clinostat treatment (Figs. 1, 2). The gravistimulation causes the curvature to decrease transiently to zero. It then increases again, eventually reaching the same value as in seedlings treated with blue light alone.

Can photostimulation from the opposite direction cancel the gravitropic response? The second stimulus might cause only transient effects because it is a gravistimulus. Assuming additivity (Nick and Schäfer 1988) and taking into account that, even on a clinostat, gravity-induced curvature is partially transient (Fig. 1), one could well imagine a time course such as that described above. Of course this is only a rough qualitative description considering the rapid fall of curvature after the onset of gravistimulation in Fig. 2 compared with the slow decay in Fig. 1. Nevertheless, the experiment was repeated with a reversed order of stimulation, i.e. 150 min after the onset of gravistimulation, a blue-light pulse from the opposite direction was applied. Again, curvature was allowed to develop on a clinostat. Two hours after the onset, gravistimulation results in a curvature of between −40° and −50° with respect to the stimulation vector (Fig. 3). After application of the light pulse, positive bending begins immediately. Then the coleoptile returns rapidly to the "vertical" position at which it briefly remains. This is followed by a strong, stable negative curvature reaching −100° (corresponding to the curvature induced by blue light alone, if it had been given in the direction of gravistimulation). It should be noted that the gravistimulus alone would cause a much smaller

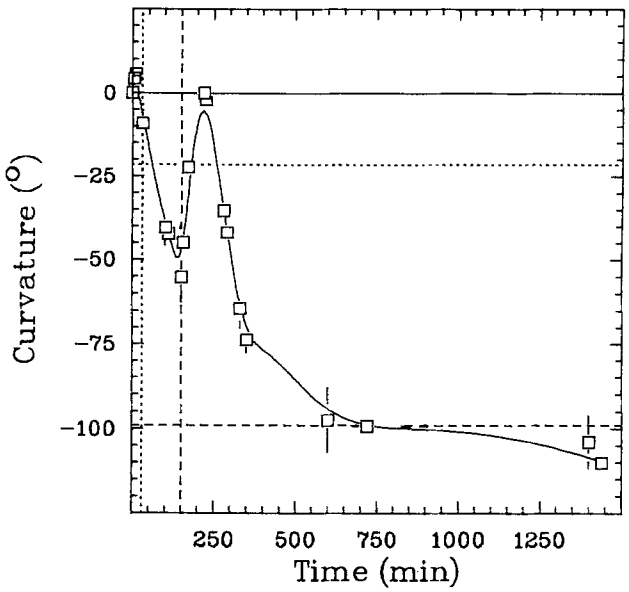

Fig. 3. Time course for curvature development in maize coleoptiles after 30 min unilateral horizontal gravistimulation followed by 2 h clinostat treatment and stimulation with 0.88 μmol·m^{-2} blue light from the direction opposite to the gravistimulation. The time course was again followed on the clinostat. Seedlings remained under saturating symmetrical red light (2.3 W·m^{-2}) for the whole experiment. *Dotted vertical*: end of gravistimulation. *Dashed vertical*: phototropic induction. *Dashed horizontal*: final curvature obtained after phototropic induction alone from the same direction as the gravistimulation and followed on a clinostat. *Dotted horizontal*: final curvature after gravistimulation alone when the seedlings were kept on the clinostat

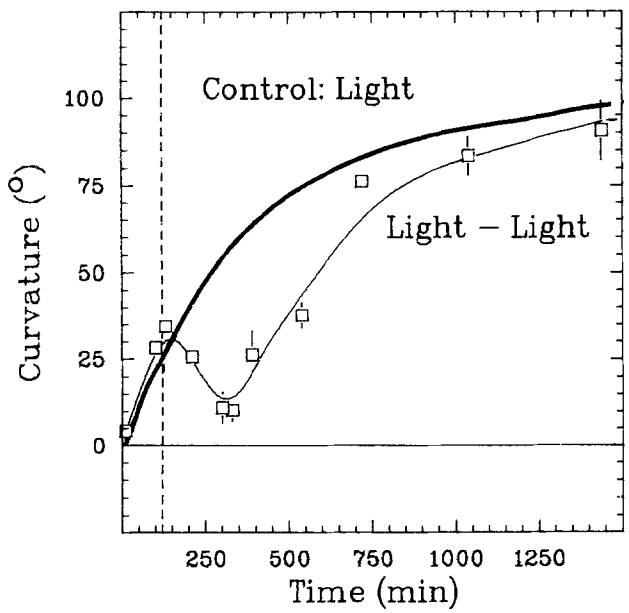

Fig. 4. Time course for curvature development in maize coleoptiles after unilateral stimulation with 0.88 μmol·m^{-2} blue light followed by 2 h clinostat treatment and a second phototropic counterinduction of the same strength with subsequent clinostat treatment. The whole experiment was performed under saturating, symmetrical red light (2.3 W·m^{-2}). *Dashed vertical*: second phototropic induction. *Solid curve*: control; first phototropic induction alone, curvature development on a clinostat

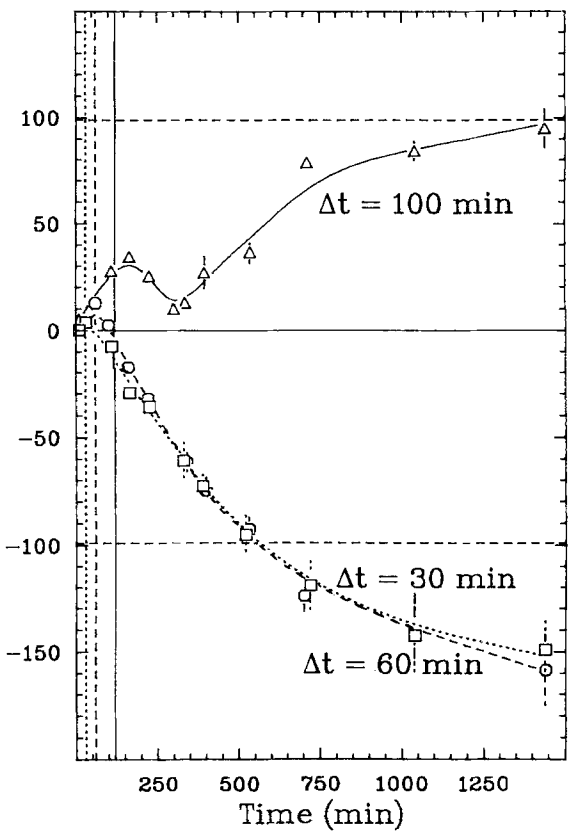

Fig. 5. As **Fig. 4,** but varying the time intervals between the blue pulses. Seedlings were kept under saturating and symmetrical red light (2.3 W·m^{-2}) for the whole experimental period. *Solid curve*: time interval 100 min. *Dashed curve*: time interval 60 min. *Dotted curve*: time interval 30 min. *Dashed horizontal*: final curvature after the first stimulation alone followed by clinostat treatment. *Vertical lines*: second stimulation for corresponding curves

(−20°) final curvature since gravitropic bending remains partially transient even on the clinostat (Nick and Schäfer 1988).

Can photostimulation from the opposite direction cancel the phototropic response? In the previous experiments the second stimulus was of a different nature from the inducing stimulus (gravi- and photostimulus). In order to test whether the transient effect of the second stimulus is due to this differing stimulus quality, stimuli of equal quality and strength (0.88 μmol·min^{-2} blue light) were applied in the next and all following experiments. The remaining conditions were unchanged. The time interval between stimulations was 2 h. As in the previous experiments, there is a transient decrease in curvature after the second stimulation. This is followed by a final stable increase in curvature in the direction of the first stimulus. Final curvature reaches values similar to those obtained when the first pulse was given alone (Fig. 4).

Variation of the time interval between two equal blue-light pulses from opposing directions. Curvature development on a clinostat. In experiments similar to that described immediately above, the time interval between the two light pulses was varied in a coarse frame so as to test whether the second stimulus showed any stable effects, when the interval between the two stimuli was shorter. For a time interval of 100 min, one finds the same response pattern as for 2 h, i.e. the effect of the second pulse is only transient (Fig. 5). For shorter intervals (60 min and 30 min, respectively), however, there is a fundamental change in behaviour. A stable, large curvature develops in the direction of the second pulse. No effects of the first stimulus can be detected after the second stimulation, apart from the fact that the final curvature is substantially larger than when the "second" pulse is given alone (Fig. 5).

Determination of the point at which the effect of the first stimulus becomes stable. As in the previous experiment, the time interval between both stimuli was varied, but this time more finely so as to analyse the transition between the response patterns found in Fig. 5. In order to avoid distortions resulting from sensory adaptation, only intervals exceeding 20 min were tested. Sensory adaptation effects can be expected with shorter time intervals (Iino 1987) and were indeed observed in preliminary experiments (data not shown). For convenience, only the mean final curvature 24 h after stimulation was considered (Fig. 6). Negative values indicate curvature in the direction of the second stimulus, positive values bending in the direction of the first pulse. The data can be described by a sigmoid curve with strongly negative curvatures for intervals shorter than 65 min, a steep increase from $-120°$ to $+100°$ between 65 and 110 min and a constant positive curvature for intervals exceeding 110 min. This value remains positive even when the time interval is extended to several hours (Fig. 6, dashed line). For a time interval of 85 min, zero average curvature is found. It should be noted that standard deviations in the transition range (between 65 min and 110 min) were exceedingly high. Frequency-distribution plots of curvature (Fig. 7a–c) show that there are three clearly distinct value clusters with peaks at $-130°$, $0°$ and $110°$, respectively. For time intervals shorter than 65 min (Fig. 7a), more than 90% of all curvatures are negative. At 85 min, where the average curve (Fig. 6) crosses the zero line, the negative values loose in favour of the intermediate, and to a lesser extent, in favour of the positive values (Fig. 7b). For time intervals exceeding

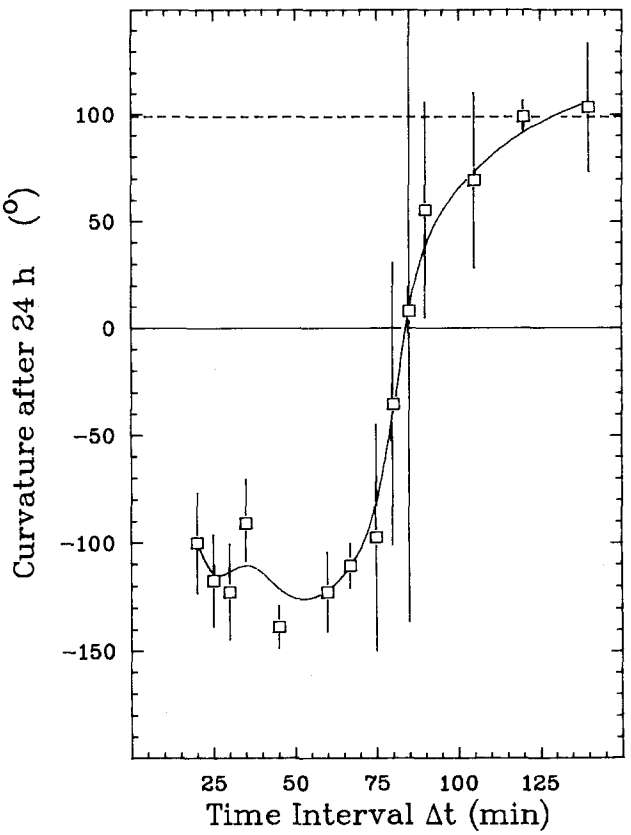

Fig. 6. Average final curvature of maize coleoptiles after sequential stimulation with two equal blue-light pulses (0.88 $\mu mol \cdot m^{-2}$) from opposite directions, measured 24 h after the first pulse. Curvature is given in relation to the first stimulus. *Bars* indicate $2 \times SE$. *Dashed line*: final curvature for a time interval of 4 h. Seedlings were kept under saturating and symmetrical red light (2.3 $W \cdot m^{-2}$) for the whole experiment

95 min the positive values prevail, negative and intermediate values being very much reduced in number (Fig. 7c). Thus, the large standard deviations in Fig. 6 can be explained by the presence of three distinct responses for the transition range between 65 min and 95 min: a strongly negative response ("the second wins"), a strongly positive response ("the first wins") and an intermediate response, where curvature is cancelled.

Variation of the time interval between two equal blue-light pulses from opposing directions. Curvature development without the use of a clinostat. The experiment of Figs. 4 and 5 was repeated without a clinostat so as to test whether the clinostat is essential for the achievement of first-stimulation stability. Again, for an interval of 120 min between stimulations, one observes transient bending towards the second stimulus followed by curvature towards the first stimulus. In contrast to the clinostat experiments, where this final bending is stable, curvature eventually falls to zero (Fig. 8). For time

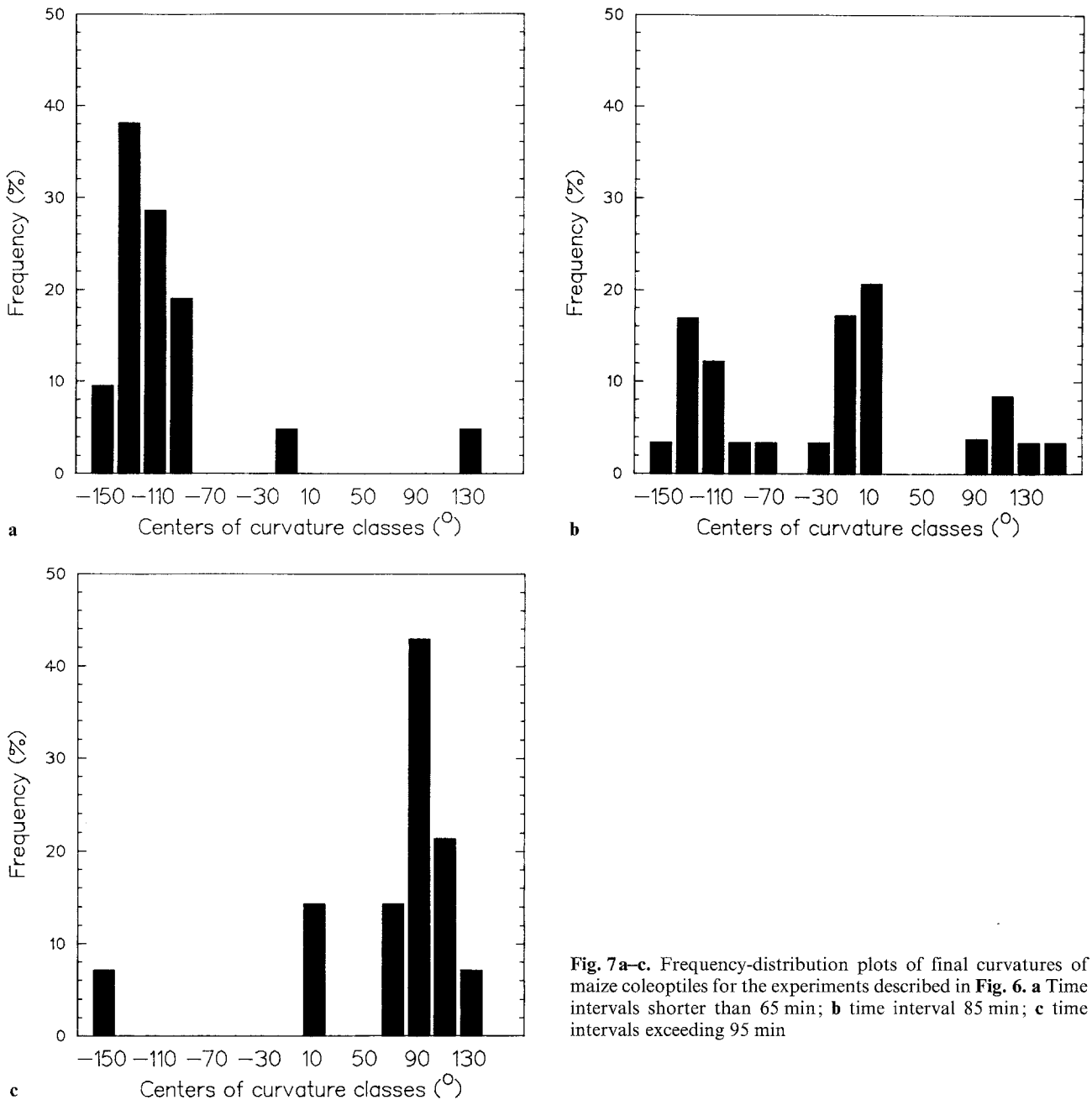

Fig. 7a–c. Frequency-distribution plots of final curvatures of maize coleoptiles for the experiments described in **Fig. 6. a** Time intervals shorter than 65 min; **b** time interval 85 min; **c** time intervals exceeding 95 min

intervals of 60 min and 30 min, however, the pattern is different. Instead of a finally positive, slowly decaying curvature as for an interval of 120 min, one finds, after a strong negative curvature in consequence of the second pulse, a transient fall of curvature to zero or even slightly positive value followed by renewed bending towards the second stimulus (Fig. 9). As for 120 min, this curvature is not stable, but slowly returns to zero. Nevertheless, the curvature after application of the second pulse, except the points at 320 min, when a slightly positive curvature is observed, remains negative with respect to the first pulse (Fig. 9).

Delayed clinostat treatment after stimulation with two equal blue-light pulses from opposing directions. To test the possibility that the final decrease of curvature in the previous experiments indicates the absence of stable effects of the first stimulation, the seedlings were initially treated as in the experiments described above (Figs. 8, 9). At the time, when curvature had fallen almost to zero (i.e. 10 h after the first pulse), the seedlings were placed on a clinostat. After the onset of clinostat treatment a strong, stable curvature develops, whose direction corresponds to that found if seedlings had been on the clinostat over the entire experimental

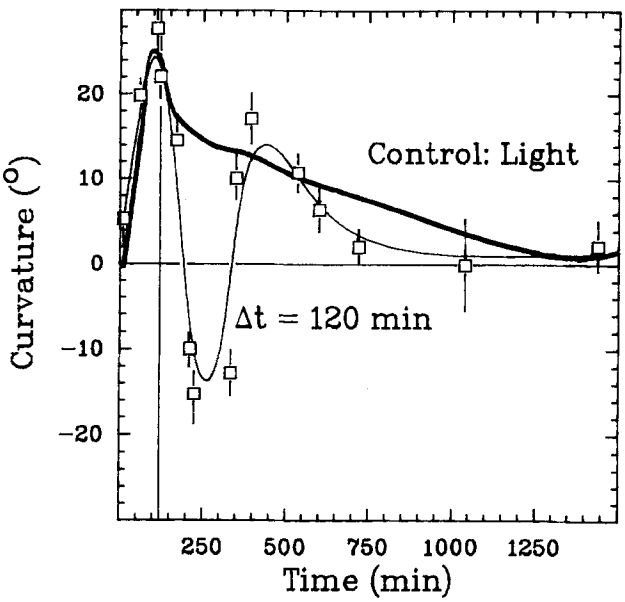

Fig. 8. Time course for curvature development in maize coleoptiles after stimulation with two blue-light pulses of the same fluence (0.88 $\mu mol \cdot m^{-2}$. The time interval between the stimulations was 2 h. Seedlings remained in an upright position under saturating and symmetrical red light (2.3 $W \cdot m^{-2}$) for the whole experimental period. *Solid vertical*: second stimulation. Curvature is indicated with respect to the first stimulus. *Solid curve*: control; curvature development after first pulse alone

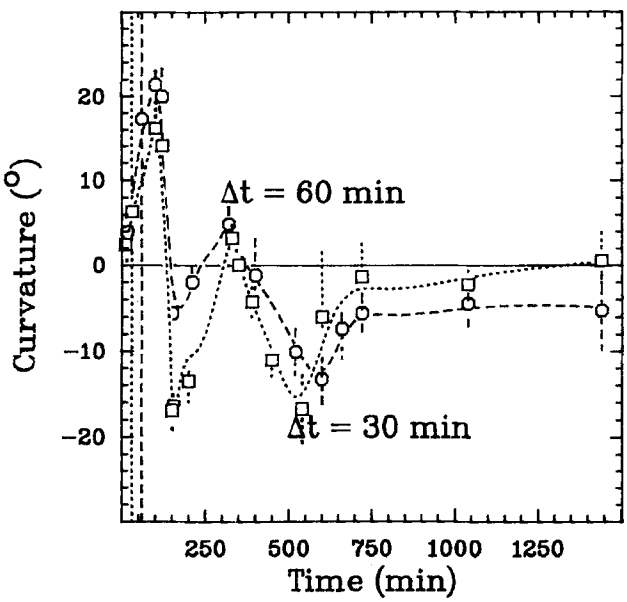

Fig. 9. As **Fig. 8,** but for time intervals of 60 min (*dashed curve*) and 30 min (*dotted curve*), respectively. *Dashed vertical*: second stimulation for the dashed curve. *Dotted vertical*: second stimulation for the dotted curve

period (Fig. 10). Thus, for an interval of 60 min the final curvature is negative, but for an interval of 120 min it is positive with respect to the direction of the first stimulus.

Discussion

Tropistically effective stimulation induces a stable spatial memory, irrespective of the stimulus quality. If unilateral stimulation by blue light or gravity is followed by an equivalent counteracting stimulation 2 h after the first stimulus, one observes only transient curving towards the second stimulus, followed by a stable, strong bending in the direction of the first stimulus (Figs. 2–4). This effect is independent of whether the same or differing stimulation qualities are used. Even during the transient phase, when seedlings bend towards the second stimulus, they appear to retain an internal tendency to curve according to the first stimulus. This tendency is reexpressed after a lag of about 1 h after application of the second stimulus. This can be interpreted as the effect of a spatial (directional) memory, induced by the first stimulus.

Spatial memory develops in two steps. Analysing the kinetics of formation of this spatial memory, one can distinguish a labile phase (up to 65 min), a transient phase (between 65 min and 95 min), and a final stable phase (after 95 min; Figs. 5, 6). In the labile phase "the second wins" type dominates, but effects caused by the first stimulus are still present, since the curvature induced by the second stimulus is substantially enhanced. However, this directional memory caused by the first stimulation is not yet stable. The second stimulus is able to produce a strong negative curvature, thus reversing the effects of the first stimulation. The observed enhancement of the bending in direction of the second pulse might be due either to a scalar amplification of the ability to curve or to reversion of the directional effects (induced by the first pulse) by the second stimulus.

At the transition towards the stable phase, the appearance of the intermediate response type indicates that both effects cancel each other, and that the process of stabilization is taking place, making it impossible for the second stimulus fully to reverse the memory induced by the first pulse. This stabilization, however, is still incomplete and results in the cancelling of both inverse effects. In the stable phase, the process of the formation of stable memory is complete and the stabilization of deviating polarities is inhibited. This is not caused by limits in the expression of the stimulus in the form of differential growth, since, during the labile phase, much larger curvatures can be observed. There seems rather to be an active pro-

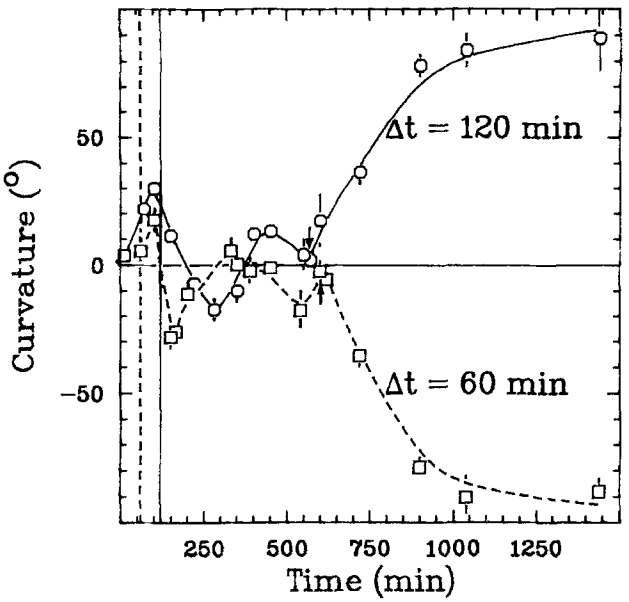

Fig. 10. As **Figs. 8, 9,** but clinostat treatment of the seedlings starting 10 h after the first stimulation. *Solid curve*: time interval 120 min. *Dashed curve*: time interval 60 min. *Solid vertical*: second stimulation for the solid curve. *Dashed vertical*: second stimulation for the dashed curve. *Arrow*: transfer onto the clinostat

cess mediated by stable directional memory. Once it has been formed stable memory remains stable at least several hours (Fig. 6). One is tempted to suggest that this stability might be caused by asymmetric structural changes in components interfering with tropistic transduction and-or differential growth.

Tropistic transduction and stable directional memory. The fact that spatial memory is elicited by tropistically effective blue light makes it probable (but does not necessarily prove) that both phototropism and blue-light-elicited memory formation utilize common perception and, perhaps, transduction elements. It is probable, too, that tropistic curvature as well as memory-mediated curvature result from the same mechanisms of differential growth. There are, however, differences between tropism and the formation of stable memory. Tropistic curvature becomes visible about 1 h after stimulation, i.e. the phototropic transduction is complete. At this time, however, spatial memory is still labile. Assuming common perception and common expression in the form of differential growth one must conclude that at least the step of stabilization and subsequent regulation of differential growth are not elements of the phototropic transduction chain. Consistent with this assumption, a transiently negative curvature is observed during the "first-wins" response (Fig. 4). During this phase, tropistic bending follows the second stimulus, whereas stable spatial memory is determined by the first stimulus, i.e. tropistic and memory transduction are in contradicting states.

Phototropic polarity apparently is produced by integration over the whole coleoptile cross-section (Buder 1920). In contrast, gravitropic polarity is expected to be cell-based. Stable directional memory can be induced by both phototropically and gravitropically effective stimulations. It is likely that the directional memory induced by light is identical to that induced by gravistimulation, although this has still to be tested. Under this assumption and taking into account that there are cases in which tropistic and memory transduction are in contradicting states (see above), one may conclude that directional memory is not identical to tropistic polarity (since the latter is different in its very nature for differing stimulus qualities). Moreover, one would expect directional memory to be of a systemic nature, resulting from integration over the whole organ, because both gravity (producing a cell-based polarity) and light (leading to a systemic polarity) can induce directional memory. It is easier to imagine that a systemic polarity rises from a cell-based precursor than vice versa.

Directional memory determines tropistic bending, not vice versa. The experiments involving stimulation without or with delayed clinostat treatment (Figs. 9, 10) show that spatial memory can be induced even if tropistic bending is connected with gravitropic counterstimulation causing curvature to cease. Directional memory still persists, although it is not expressed as curvature until gravitropic counterinduction is removed by clinostat treatment (Fig. 10). This provides further evidence for differences in tropistic and memory transduction. There appears to be a clear hierarchy between both responses: directional memory is able to determine tropistic growth but not vice versa. It is noteworthy that 30 min of horizontal gravistimulation could induce spatial memory (Fig. 3). In the experiments discussed here, however, counterstimulation by gravity did not disturb the formation of spatial memory, but only its expression as tropistic curvature. This is remarkable because, in the latter case, gravistimulation time is much longer than 30 min, presumably overcoming the smaller stimulation angle (maximal 30° instead of 90°). This could result from the rather gradual appearance of stimulation (the 30-min stimulus was applied in a step-up manner). This would indicate that memory formation involves a differentiation mechanism and possibly an adaptation step.

Directional memory is a stable transverse polarity. Phototropic bending is connected to the appearance of a stable, i.e. irreversible, directional memory. The formation of this stable memory involves at least one step not present in the usual tropistic transduction. It might be that it is caused by a "solidification" of the putative tropistic transverse polarity. Thus, it fulfils essential features of the model implying that polarity could originate from processes leading to tropistic transverse polarity. Consistent with this view, the spatial pattern of directional memory appears to be caused by all-or-none processes as would be expected if self-activation and lateral-inhibition steps, as postulated for phototropism in *Phycomyces* (Hertel et al. 1980) or generally for polarity induction (Gierer 1981), are involved in the formation of stable directional memory.

It appears that directional memory is really induced de novo, at least for light as inducing stimulus (Fig. 7b). The alternative model – an already existing internal asymmetry is only reoriented by the external stimulus – should render a response which is neither towards the first nor the second pulse, but nevertheless shows the same amount of curvature. The observed zero-curvature (Fig. 7b), however, favours the view of two contradicting directional effects cancelling each other, which is not consistent with the idea of reorientation of an already existing directional effect. In analogy to the dispute between Sachs (1980) and Vöchting (1878) one can state that stable directional memory is produced de novo and does not result from reorientation of an already existing internal asymmetry.

Regarding these features of stable directional memory, it thus appears justified to refer to directional memory as stable transverse polarity.

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