

DURATION OF DIVISION RELATED EVENTS IN CLEAVING  
SAND DOLLAR (ECHINARACHNIUS PARMA) EGGS

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A minimal mechanism for cytokinesis comprises a stimulus to surface contraction, a receptive surface and a localized contractile mechanism. The duration of each of these parts appears to be brief and, during the cleavage divisions, the times when they are functional are predictable. The minimum effective stimulus period is about one min, as is the period when the surface must be receptive to its effect. The contractile mechanism in the sand dollar egg cleavage furrow functions for about 8 min ( $8.2 \pm 1.1$ ,  $n = 22$ ) at 17 degrees C. The brief and sequential nature of these events has suggested a chain of on-off actions and interactions coordinated by a complex control mechanism. The purpose of this investigation was to study the nature of the events that begin and end each phase of the division mechanism.

Sand dollar blastomeres during the period from the second to the third cleavages were used for these experiments. Because the early cleavages in a single zygote are synchronous, companion blastomeres served as time controls. By changing a cell's geometry, it was possible to determine whether its capacity to accomplish an activity is restricted to the time when it normally occurs. The time when the furrow first appears was advanced about 5 min ( $4.9 \pm 1.6$ ,  $n = 13$ ) by confining the mitotic apparatus (MA) in a narrow cytoplasmic cylinder. It was prolonged by reshaping the cell into a cylinder and moving the MA each time a furrow appeared. In this way, the MA's capacity to induce furrowing and the surface's capacity to respond was prolonged for about 18 min ( $18.2 \pm 3.1$ ,  $n = 29$ ) after cleavage normally begins. The cycle of the second cleavage requires 48 min, and the minimum period necessary for successful surface stimulation is 1 min or 2% of the cycle, but the results show that the stimulus is effective, and the surface is receptive for a greater proportion of the cycle. The period when active furrowing is possible was prolonged by pushing the MA close to the cell margin with glass needles and then stretching the region through which the unilateral furrow must pass. In this circumstance furrowing persisted for about 25 min ( $25.7 \pm 1.97$ ,  $n = 13$ ). Although the normal furrow lasts for 8 min, or 17% of the cycle, the results show that the surface can actively furrow beginning 5 min before it usually starts and extending 14 min after it usually ends, which amounts to 56% of the cycle.

The normal beginning and end of the principal events of cytokinesis apparently are not determined by the acquisition and loss of functional competence of the participating cell regions. In favorable circumstances, each can operate before and after its normal active period. It appears likely that the normal timing of events may be determined by geometrical factors and by the normal consequences of the activity. The stimulus period may normally start when the elongating astral rays reach the equatorial surface and end when the asters are separated by the intruding furrow. The contractile activity in the furrow begins after astral stimulation and must end when the cell is completely divided. The extended period of competence for each phase and their potential for overlap reduces the chance that delay or prolongation of one phase will block subsequent cleavages and development.

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