Reports

Recovery of Foreleg Placing after Ipsilateral Frontal Lobectomy in the Hemicerebrectomized Cat

Abstract. Forelimb placing recovers in variable fashion after contralateral hemicerebrectomy. In three cats showing poor recovery over periods of 2 to 6 months, and then surviving removal of the ipsilateral frontal lobe, further recovery of placing occurred after the second operation.

Rademaker (*1*) called attention to a number of postural reactions which aid the animal to attain the standing position. Some of these were studied by Bard (*2, 3*) in his work on hopping and placing. Since then it has come to be widely believed that placing reactions are not only controlled by the contralateral cortex, but that they cannot occur in its absence. However, recent experiments occasionally showed return of placing reactions after removal of an entire half of the forebrain (*4*).

We removed cortex, thalamus, and basal ganglia through a wide craniectomy, leaving no brain to the right of the midline above the midbrain. This has been called "total hemispherectomy" by White *et al.* (*5*) and "hemicerebrectomy" by Koskoff *et al.* (*6*). During recovery, placing was tested in various ways, including that elicited by contact of the forepaw and by contact of the chin. Grading was on the basis of quickness and smoothness of best responses, rather than accuracy or consistency from day to day. Later, the remaining frontal lobe was removed back to the ansate sulcus, including the anterior and posterior sigmoid gyri.

Five adult cats were used which had hemicerebrectomy, and which showed poor return of placing in the contralateral forelimbs for periods up to 6 months. Three of these survived the second operation. In all three, there was a period during which placing was present on the left and absent on the right (Fig. 1). In addition, two cats (60-7, 60-21) which showed no placing to contact of the chin previous to the second operation, developed placing to chin contact after the second operation.

In these experiments we have emphasized the maximum performance during each week. This is justified because placing is often variable and may be absent in normal cats when they are distracted, recently fed, or otherwise lethargic. The manner in which the cats are held is important, since stimulation of the skin supplied by the trigeminal and cervical nerves may have a profound inhibitory effect on a variety of postural reactions (*7*).

Placing following contact of the paw depends mainly on tactile stimuli; but even where no motion is observed, there may arise proprioceptive information from slight volar flexion at the wrist or retroflexion at the shoulder. In this connection it is important that the technique used was the same throughout these experiments. Placing may be considered a fractional aspect of the general locomotive pattern: that is a single "step" occuring in isolation. However, placing has been distinguished from "stepping" or similar movements arising from generalized struggling in excited animals. For this reason, we considered the lifting up and setting down of the paw to be "placing" only when it occurred in a quiet animal showing no gross movement until application of the specific stimulus, and occurring as a simple, continuous motion without subsequent repetitive movement.

The return of supposedly "cortical" reactions is not altogether surprising in view of Bard's allusion in his Harvey Lecture (*3*) to a monkey in which hopping reappeared after ipsilateral ablation. Return of placing was seen by Denny-Brown and Chambers (*8*, p. 92). Bard (*3*) mentions the suggestion of McCulloch that the original disappearance could be attributed to the removal of corticifugal facilitation. This view is supported by the present results which we interpret as the effect of a removal of ipsilateral, corticifugal, tonic inhibition. Similar would be an interpretation (following Denny-Brown, *8*) that ipsilateral ablation decreased avoiding tendencies, reestablished a cortical equilibrium, and thus made possible the reappearance of an exploratory response. The restitution of a supposedly lost function increases the ambiguity of the original loss; and it

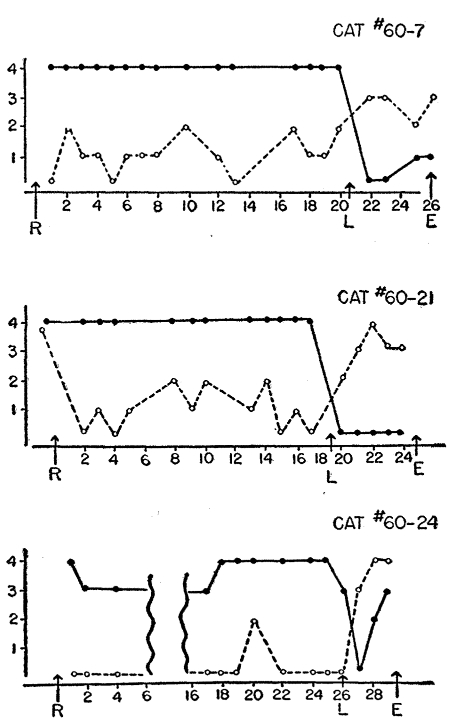

Fig. 1. Performance of foreleg placing to contact of the paw with a table edge. Right-sided operation was hemicerebrectomy. Left-sided operation was removal of frontal lobe. Ordinate shows level of performance in arbitrary units. Abscissa shows elapsed time in weeks. Solid line shows performance of right leg. Broken line shows performance of left leg.

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Type manuscripts double-spaced and submit one ribbon copy and one carbon copy.

Limit the report proper to the equivalent of 1200 words. This space includes that occupied by illustrative material as well as by the references and notes.

Limit illustrative material to *one* 2-column figure (that is, a figure whose width equals two columns of text) or to *one* 2-column table or to *two* 1-column illustrations, which may consist of two figures or two tables or one of each.

For further details see "Suggestions to contributors" [*Science* **125**, 16 (1957)].

would appear to afford an argument against concepts of localization in the brain. On the other hand, experiments that use restitutive ablation may produce particularly persuasive evidence of localization should the restitution be found to depend on the area ablated.

JOSEPH E. BOGEN
BERRY CAMPBELL
Department of Neurosurgery, Loma Linda University, Los Angeles County General Hospital, Los Angeles, California

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Podocoryne carnea, a Reliable Differentiating System

Abstract. The number of nutritive hydranths in a slide-grown colony of this marine hydroid increases exponentially until sexual forms appear in the colony.

Recent studies have emphasized the importance of population factors to cellular differentiation. The size of the cell mass (*1*), its geography, and the effect of metabolic products in controlling subsequent activities (*2*) all play a role in the differentiation of units in a biological mass. It is difficult to evaluate the effects of these factors in embryos because of (i) the size of the units involved—cells, (ii) the difficulty of defining operationally useful end points of differentiation, (iii) the large spectrum of differentiated tissues, and (iv) the fact that cells in an embryo are not end products but on their way to becoming something else.

A reasonable approach would be to find a system that increases in size, originates from a single known unit, and reaches a point where a second distinctly defined type appears. The units of variation in this system should be conveniently visible and analyzable and the gross structure of the system simple enough so that the effect of spatial orientation could be evaluated. In theory it would not be important what the size or complexity of the units in the mass were; they might be as small as cells or as large as multitissue zooids in a colonial population.

The marine hydroid *Podocoryne carnea* (*3*) satisfies these criteria for a reliable system. Colonies can be initiated by placing a single hydranth on a microscope slide in standing sea water. Stolons grow out along the surface of the slide from the base of the hydranth; new hydranths form and increase in size; finally a new type of zooid, which bears medusae, appears. The units, hydranths, are easily visible at $\times$ 10 magnification and the medusa-bearing zooids are recognizable from the time of their first appearance (Fig. 1). The anastomoses of stolons are simple enough up to the time of sexual zooid appearance to allow stolon length to be measured and for the pattern and distribution of hydranths on the stolons to be recorded. Generalizations about differentiation in this simple model should be applicable to more complex embryonic systems.

Important observations have already been made along these lines by Loomis and Lenhoff (*4*), who suggested this approach with the use of hydra as a model system. They showed that sexual differentiation is nonobligatory and is alternative to exponential growth and the nonsexual condition.

However, the hydra as an experimental animal presents certain drawbacks. Its social differentiation ("social" to distinguish this process from the differentiation of cells in a single animal) is not analogous to that of most other animals in which the end product of differentiation is a spectrum of differentiated types. Only two alternatives exist in hydra; the range of differential expression is limited to numerical increase of nonsexual animals on one hand and to gamete formation on the other. Biochemical studies involving nutrient additions or inhibitors can be carried out only with difficulty (*5*), because additives to the medium of this fresh water animal are not taken up by the cells. Although the concept of the unity of an aquarium of hydra is a valid one, the animals are in fact spatially separated and motile, and questions pertaining to the spread of pattern in a differentiating system cannot be asked. Since both sexual and asexual zooids can exist simultaneously in a *P. carnea* colony, it approaches the embryonic situation more realistically than the hydra does. The marine animal will take up small organic molecules from sea water, so that labeling and biochemical studies are easier than with hydras (*6*). Being a sessile animal, *Podocoryne* allows investigations regarding the spread of pattern and spatial distribution of hydranths that are not possible with the fluid hydra system.

Fig. 1. Slide-grown *P. carnea* colony after the appearance of sexual zooids. The medusa-bearing zooids can be easily distinguished from the nutritive hydranths.

An analysis of the factors affecting sexuality in another hydroid, *Hydractinia echinata*, has been published by Hauenschild (*7*). His findings are generally in agreement with those reported here, despite his having had to work with material that, because of the density of the stolon system, could not be studied quantitatively.

The technique for laboratory culture of colonies of *P. carnea* is simple and allows relatively unlimited production

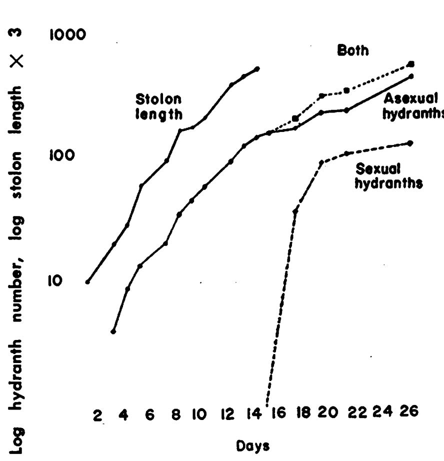

Fig. 2. Relation between time of appearance of sexual zooids and growth rate of asexual zooids in a growing colony of *P. carnea*. Stolon length is measured in arbitrary units.