

Reticular activity and arousal

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Vanderwolf and Robinson (V & R) (1981) hypothesize that reticulo-cortical systems modulate behavior "by influencing the activity of the cerebral cortex, which in turn exerts control over subcortical circuits that co-ordinate muscle activity to produce behavior." They also deal at length with the problems of dissociation of behavior from forebrain EEG variables. I would like to suggest a somewhat different, though not incompatible, model based on our observations of the activity of reticular formation (RF) units recorded in unrestrained cats (Siegel 1979b; Siegel & McGinty 1977; Siegel, Wheeler, Breedlove & McGinty 1980). The central finding of this work is that individual RF cells discharge in relation to directionally specific movements or groups of movements. For example RF cells related either to ipsilateral head movement, neck extension, pinna retraction, tongue protrusion, or eyelid closure have been observed. A small number of cells have somewhat less specific behavioral relations, discharging during any of a number of ;• movements of the facial musculature or to any movement of the forelimbs. However, we have not observed any RF cells that discharged in a way consistent with the usual concepts of arousal. For example, when a noxious stimulus was applied to the cat, the RF unit response was invariably a function of the motor response evoked; for example, if the cat turned toward

the ipsilateral side and the cell was related to ipsilateral movement, the discharge rate increased. If the cat turned to the opposite side, even if vocalizing and showing other behavioral signs of an arousal response, the unit was silent. However, arousing stimuli increased the general level of motor activity and therefore the activity of the RF units.

Furthermore, we have not seen any difference in activity of any RF units in terms of what V & R describe as type I or type II behavior. For example, a cell related to neck extension would discharge when the cat extended its neck during the consumption of food pellets and at equal rates during exploration or play behavior, as long as the neck extension posture was maintained.

These observations suggest that V & R's conceptions should be cast in a somewhat different light. Specifically we propose the following:

1. Arousal is a correlate of activity in a *population* of RF cells, but is not strongly correlated with discharge rate in individual RF cells. Thus, arousal is linked with activity in individual RF cells by the specific movements and changes in muscle tone accompanying behavior commonly described as aroused.

2. Type I and type II behavior patterns are selectively related to activity in forebrain systems, including hippocampus. The RF acts as a final common pathway for the sensorimotor organization of *both* types of behaviors.

3. Dissociations between cortical activity and behavior can be explained by direct RF control of motor activity in the absence of descending influences. These dissociations may be induced by anesthesia or other drug treatment or by lesions, or they may occur in normal behavior. Pontine and medullary medial RF areas have direct as well as oligosynaptic (Peterson 1979) connections with spinal motoneurons. The impressive behavioral capabilities of the decerebrate cat pointed out by Villablanca (1981) demonstrate that brain-stem mechanisms are sufficient to guide many motor activities.

In this model, the arousing effects of electrical stimulation of the RF can be explained by the massive, abnormal recruitment of RF cells and the resulting motor activity. We have found that different cells located at approximately the same point in the RF are often related to movements involving different body parts (Siegel, Nienhuis, Wheeler, McGinty & Harper 1981). Electrical stimulation would therefore be expected to activate widespread cortical regions by corollary discharge, producing cortical arousal.

Inactivation - by lesion, anesthetic, or other drug treatments

Continuing Commentary

- of portions of the RF Conveying this corollary discharge would be expected to depress cortical activity through the loss of a major source of desynchronizing input. However, with the passage of time, other forebrain inputs are apparently able to substitute quickly for the lost RF projections, resulting in a return of cortical "arousal" even in decerebrate preparations. In keeping with this perspective, I would like to distance myself from the conclusion drawn by V & R after their discussion of my review of the literature (1979a) on p. 503. In our analysis we showed that so many different functions have been ascribed to the majority of RF Cells by different investigators, that one must seek a common factor in these relationships. Our conclusion is that this common factor is motor activity, not "arousal," as V & R concluded. Whereas forebrain unit activity may relate to specific classes of behavior, the vast majority of medial reticular units discharge in relation to directionally specific movements regardless of their behavioral context.