Average Evoked Responses and Learning

An interesting area of research on the nervous system deals with averaged electrical transients during learning processes. An important conclusion on this subject was drawn by Pribram, Spinelli, and Kamback (*1*) who stated that "At the striate cortex, the neuroelectric signals encode the influence of experience not only with respect to input differences, but also with respect to the organism's intentions to respond and the outcome of behavior."

We suggest that an additional control is needed in this and similar experiments to establish such conclusions.

In the report by Pribram *et al.*, a difference in the averaged potential, occurring prior to pushing of the right or left panel, is predictive of the direction of the behavioral response. This difference in electrical response does not occur prior to learning and is therefore not produced by panel pushing per se (as Pribram *et al.* point out). However, it is not clear that we can exclude the consequences of other learned responses which might produce the "input difference" to the striate cortex. An anticipatory movement of the head or eye, or both, in the direction of the measured behavioral response could occur reliably after criterion and could, by virtue of patterns in the visual environment, produce an evoked response detectable by the averaging technique. To control for this, the visual environment after stimulus presentation should be entirely uniform—either dark or homogeneously illuminated.

In short, the appearance of the averaged anticipatory potential after criterion could be associated with the development of a consistent orienting response pattern which occurs only after the animal has learned the discrimination. This would produce a change in visual input that is time-locked to the response. Thus, the possibility remains that the observed potential is simply a phenomenon of "input transmission." Similarly, differences in potential relating to the occurrence or absence of reinforcement (*1*) may result from orientation to the food delivery site during reinforced trials. It then follows that variation in an "input pattern," the form of which depends upon stimulus configuration (*1, 2*), could explain both the "intention pattern" and the "reinforcement pattern."

Less at variance with the conclusions of Pribram *et al.* is the possibility that observed electrical responses arise from occipital areas that are involved in the control of conjugate eye movements (*3*). Thus, these potentials could be related to anticipatory eye movements occurring at a relatively fixed interval before occurrence of the measured response or after stimulus presentation.

There are similar experimental situations in which the concern is with differences in averaged evoked potentials other than those evoked by changes in environmental stimuli. Subtle sources of stimulus-locked variation in environmental input must be controlled before we can be certain that they are not responsible for the averaged electrical-response differences. For example, in the Ruchkin and John experiment on stimulus generalization (*4*), we need to know whether the conditioned stimulus would produce identical retinal stimulation regardless of the animal's physical orientation. That is, if orientation toward the manipulandum on generalization trials differed from that on trials not terminated by a response, then a concomitant difference in stimulus action on the retina could account for the different form of the average evoked response in the two conditions. Even if the flash stimulus uniformly flooded the environment, visual attention to the manipulandum could produce a unique stimulus configuration.

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Horel and Vierck point out in their communicaton that the stimulus consequences of learned responses might produce the "intention" and "reinforcement" waves observed in our experiment. They note that the visual system is an input system and that inputs such as those from eye and head movements could become synchronized with the presented stimulus as learning proceeds and thus could evoke the observed responses in the cortex. They suggest as control for this contingency that the visual environment after stimulus presentation should be entirely uniform—either dark or homogeneously illuminated.

We must first admit that few experiments are perfect and that ours suffered from a number of weaknesses due to difficulties usually spoken of as "the state of the art." Having learned a good deal in performing the study, we are now engaged in replicating and extending our observations. However, despite these limitations we did take precautions to the best of our ability. Though absolute darkness or a completely uniform "Ganzfeld" is impractical in a situation where a monkey is to learn to press one of two panels, we did train in an enclosed unlit box located in a room so dark that we had to use a shielded light to record our observations. The monkeys were observed through a slit in the enclosure wall behind them; only during stimulus display could their forms be readily distinguished. In addition, the two panels on which the stimulus was displayed consisted of a large square directly in front of the subject so that there would be as little differential movement as possible when either half of the panel was depressed.

Of course, there exists the possibility that a response is evoked in striate cortex by eye (and even head) movements and that these became sufficiently synchronous with learning to appear in our records. Responses with a latency of 30 msec as a result of eye movement in the alert monkey have been reported; however, these responses disappear in the dark (*1*). Yet these and other types of peripheral orienting responses cannot be completely ruled out. However, we have found that such peripheral responses gradually diminish in amplitude and frequency until they are practically or totally unmeasurable. In such circumstances, we have inferred that the orienting has become "neuralized" and restricted to the operation of a central mechanism. We believe that we now have the tools to tap this central mechanism directly, although our technique is still far from perfected.

Perhaps more to the point is the fact that our "intention" and "reinforcement" waves are locked not to the stimulus but to the response. Thus, "the changes in visual input that is time-locked to the stimulus," referred to by Horel and Vierck, should have appeared in the stimulus-averaged record—and they did not. The importance of finding a process in the striate cortex that is sensitive to response-linked events should not be underestimated, regardless of whether the mechanism turns out to be central or a response-initiated peripheral stimulus. In either case, a mechanism exists within the primary sensory receiving systems for collating information about environment-initiated events with those that are response-dependent.

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Horel and Vierck have raised the question of whether the differences in evoked-response wave shape in generalization trials (CR) and in trials in which no behavioral response (NR) was elicited by the test stimulus might be attributed to changes in head or eye position or movement toward the manipulandum. Of course, this question is relevant to proper interpretation of our observations and was also of concern to us. Our opinion that our findings were not due to such factors is based upon three kinds of considerations.

1) The animals in our study (*1*) were highly trained, having performed these responses consistently for well over 1 year. Recording sessions sometimes lasted as long as 6 hours, with periods during which trials were presented about once a minute. Gross changes in position occasionally occurred but were not accompanied by major changes in evoked-response wave shape. Usually, however, the cats sat relatively motionless in front of the manipulandum, mounted on an otherwise blank panel under overhead lighting which illuminated the entire cage. Little movement of head or eyes could be observed during either CR or NR events. On numerous occasions the cats were carefully observed to establish whether any change in head or eye position occurred as the change in the evoked-potential wave shape took place; no indication of movement was detected.

The early appearance of component II, in the 21 trials resulting in generalization, shown in Fig. 2 of our paper, occurred long before any response was made and did not correlate with the response latency, as one might expect from an anticipatory movement.

2) As illustrated in Fig. 1 of our paper, component II also appeared in nucleus reticularis, which does not map the retina. More intensive analysis of this phenomenon (*2*) shows that, during generalization, component II arises from an apparently endogenous process which appears in the visual cortex and the mesencephalic reticular formation with shortest latency and subsequently propagates to the lateral geniculate. Therefore, this component would appear to have a central, rather than a retinal, origin. Similar potentials have been observed in other cats under comparable conditions, frequently in nonsensory specific structures.

3) These endogenous components of evoked responses seem to be related to the endogenous electrical activity seen in recordings from animals and man in studies that use intermittent rhythmic stimuli. There exists abundant evidence of neural responses which reflect past rather than present stimulation: "assimilated rhythms" at the frequency of an absent stimulus have been observed in many species during intertrial intervals in various laboratories (*3*); "evoked" potentials appear at the time of expected stimuli in man (*4*); frequency-specific responses in various structures can be elicited by a steady tone after pairing with a rhythmic flash (*5*); release of potentials at the frequency of stimuli used during training has been observed during generalization to novel stimuli in various brain structures of the intact cat (*6*) and on the trained but not the untrained side of a split-brain cat (*7*); release of previous temporal patterns of stimulation after change in the stimulus frequency has also been reported in the isolated cortical slab (*8*) and in single cortical cells (*9*). Phenomena of this sort have been reviewed (*10*).

These various findings seem to support the idea that certain components of the sensory evoked response and portions of ongoing electrophysiological activity reflect the release of patterns of neuronal activity which relate to the perception of the stimulus and to the previous relevant experience of the organism.

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Venus: Tectonic Activity

Davidson and Anderson (*1*) proposed that the rate of volcanism and tectonic activity is greater on Venus than on Earth. Actually, the degree of tectonic activity, at least, is likely to be smaller on Venus if tectonic activity is caused primarily by convection currents in the mantle.

Davidson and Anderson's conclusion was based on two assumptions. The first is that the surface temperature of Venus is about 200°C hotter than that of Earth. The second is that the thermal gradient in the crust of Venus is about twice that in Earth's crust