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THE CAUDATE NUCLEUS EGOCENTRIC LOCALIZATION SYSTEM

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Abstract. It is hypothesized that the motor and spatial functions ascribed to the caudate nucleus are actually different aspects of a single system for spatial localization. Within this system movement programs are the code for spatial locations, i.e. the position of any point in space is defined by the head/eye movement necessary to bring that point into focus. This is an egocentric system; points in space are defined solely in terms of their distance and direction from the observer. The experimental finding that caudate lesions in rats impair their performance in an egocentric localization task, but not in another, equally difficult spatial task, demonstrates a caudate role in this system. Since, in an egocentric system, positions in space are defined relative to the observer, every movement of the observer must be accompanied by a compensatory updating of the internal representation of any given point. Studies with Huntington's Chorea patients are consistent with a caudate involvement in this feature of the system also. Electrophysiological experiments with cats indicate that vestibular information, which can be used in the compensatory updating process, is available to the caudate. It is suggested that this system is used by normal animals in delayed response performance.

1. *Historical background*

The central hypothesis underlying the work to be reported here takes origin in two of the themes found in accounts of caudate nucleus function. The more traditional theme, that the caudate plays a role within the motor systems of the brain, developed in the 19th century from demonstrations that caudate lesions (Magendie 1839) and stimulation (Ferrier 1876) had effects on posture and movement. This view was subsequently strengthened by clinical evidence that pathology of the basal ganglia was associated with a variety of movement disorders

(Anton 1896, Jelgersma 1908, Vogt 1911, Wilson 1912, cited by Denny-Brown 1962). More recent experimental study of caudate motor functions has shown that, typically, bilateral caudate lesions lead to an increase in locomotion ("hyperactivity", "obstinate progression", Richter and Hines 1938, Mettler et al. 1957, Turner 1957, Davis 1958, Whittier and Orr 1962) whereas electrical stimulation of the caudate inhibits movement. This inhibitory effect may be demonstrated on a variety of movements ranging from the flexions and extensions evoked reflexly in a single limb of an anesthetized preparation (Mettler et al. 1939, Freeman and Krasno 1940, Hodes et al. 1951) to the locomotion of the awake, intact animal (e.g., Akert and Anderson 1951, Buchwald et al. 1961, Delgado 1964).

Curiously, effects of caudate lesions or stimulation on head and/or eye movements seem to be opposite to the effects on limb movement and locomotion. Electrical stimulation of the caudate, like stimulation of many other areas of the brain, gives rise to eye movement; bilateral caudate lesions lead to a paucity of eye movements (Mettler 1964). Whittier and Orr (1962) and Turner (1957) report a loss of head movement in animals with chronic caudate lesions. The single most characteristic effect of unilateral chemical or electrical stimulation of the caudate is contraversive head turning and circling (Essig et al. 1950, Buchwald and Ervin 1957, Forman and Ward 1957, White and Himwich 1957, Stevens et al. 1961, Laursen 1962). Acute unilateral lesions lead to ipsiversive turning (e.g., Mettler and Mettler 1942, White and Himwich 1954). A persistent problem in the interpretation of caudate experiments is posed by the cortico-thalamic fibers running in the capsular border or passing through the caudate itself. Effects produced by a manipulation of caudate cells proper may be confounded by effects of that manipulation on these corticothalamic fibers. After an extensive investigation in which great care was taken to isolate these confounding effects, Laursen (1962) has concluded that, of the numerous phenomena attributed to caudate stimulation, only the head movements are of truly caudate origin. It is the caudate control of head movement, the oldest, best established and most carefully studied of all caudate-related phenomena, which is the first theme of the central hypothesis.

The second theme has developed more recently from the discovery that lesions or electrical stimulation of the caudate nucleus are sufficient to cause a delayed response impairment (Rosvold and Delago 1956). This finding has since been confirmed by a number of other investigators (e.g., Dean and Davis 1959, Battig et al. 1960). It has been suggested (Teuber and Mishkin 1954, Teuber 1955, Mishkin 1964) that the spatial aspect of the classical delayed response problem is its most essential feature, i.e., the animal must remember *where* the food has been hidden. Stamm (this Symposium) in a demonstration that sulcus principalis stimulation affects delayed-response but not delayed-matching-from-sample, has offered some of the clearest evidence to date that a spatial factor is the key to the deficit following disruption of dorso-lateral frontal cortex function.

In accord with this formulation it appears that surgical destruction or electrical stimulation of the caudate impairs performance in a set of tasks in which the common requirement is a processing of spatil information (delayed response: Dean and Davis 1959, Battig et al. 1960, Teuber and Proctor 1964, Beck 1965, Cianci 1965, Mikulas and Issacson 1965, Kling and Tucker 1967, Divac 1968, Stamm 1969; delayed alternation: Rosvold and Delgado 1956, Migler 1958, Rosvold et al. 1958, Chorover and Gross 1963, Rosvold and Szwarcbart 1964, Gross et al. 1965, Mikulas 1966, Divac et al. 1967, Butters and Rosvold 1968, Borst et al. 1970; spatial reversal: Thompson 1958, Divac 1971). It seems clear that the caudate is involved in spatial, as well as motor, functions.

Divac, Rosvold and Szwarcbart (1967) showed that despite its morphological homogeneity, the caudate is, in some respects, functionally heterogeneous. In contrast to the relatively restricted regions of the caudate involved with spatial functions, head movements can apparently be elicited from sites throughout the caudate (e.g., Forman and Ward 1957, Laursen 1962, but *see* Liles and Davis 1969). This may mean that a single caudate motor mechanism is in service to a variety of other functions distributed at different loci within the caudate. In any case, though the remainder of this paper treats only the spatial orientation aspect of the caudate function, it is understood that there are several, anatomically differentiable caudate functions.

2. *The central hypothesis*

It is temping to suppose there may be a single factor underlying the two classes of function, motor and spatial, with which the caudate has been associated. The writer, in succumbing to the temptation, developed the synthesis which has guided the research summarized in this paper: *the caudate nucleus contains or is contained in a system in which potential orientation movements of the head and eyes are the code for spatial location.* Specifically, the internal representation of any point, P, in space is the set of motor programs which would turn the head and eyes to bring P into focus, given the position of the torso at the moment. In the simplest case, the program would be one which moved the head to bring P into the median plane. It would then generate a vergence movement of the eyes to bring P into focus. Alternatively, if the head were to be kept still, the program might generate a conjugate eye movement followed by a vergence movement. One characteristic of any such system is that all points in space are defined in terms of the observer's position: the head and eyes are the center of the coordinate system. This is an ego-centric system, i.e., a system in which positions in space outside the body are defined by their distance and direction from the observer (Roelofs 1959).

The idea of an ego-centric system based on movement programs is not new; elements of it can be found in many older writings: e.g., Descartes (1962) discussed the role of convergence of the eyes in the localization of objects, Lotze (1852) assigned considerable importance to eye movements in the development of space perception. The concept of spatial localization based on eye movement is, in itself, controversial even without regard to its putative reification within the caudate. Bruell and Albee (1955) have reviewed some older evidence in its favor; Ogle (1962) has raised the objection that convergence by itself is a poor cue to depth. Held and co-workers (Efstathiou et al. 1969) have recently presented new evidence for a system in which head/eye position is the basis for spatial orientation. Gazzaniga (1969*ab*) has reported that reaching movements can be "read out" from head/eye position information. Let us assume as a working hypothesis that this system exists. As described, it has only a limited capacity: it can store only one location at a time. Furthermore, topological relations between spatial locations (e.g., left/rightness) cannot be encoded by the system. Clearly, an ego-centric localization system can only be a short-term component of a more general system of spatial perception.

One of the early indications that the caudate was involved in ego-centric localization developed from a study (M. Potegal, unpublished data) in which it was found that caudate lesions impaired rats' performance in a classical "response learning" task but did not affect classical "place learning". (For a review of "place" vs. "response" learning *see* Restle 1957). Thus, the caudate nucleus is involved when a position in space is defined by the movement necessary to reach that position. Other evidence linking the ego-centric system to the caudate is provided by Teuber and co-workers from experiments in which brain-damaged humans aligned the visual and postural vertical (Teuber and Proctor 1964). These investigators have suggested that the striatum is necessary for an integration of postural and exteroceptive information. Starr (1967) reported that patients with Huntington's Chorea, a disease in which the caudate nucleus is affected, are deficient in a visual tracking and localization task. Bowen, too, has reported (1969) visual tracking deficits in monkeys with caudate lesions.

In a direct test of the hypothesis, the writer has shown that the integrity of the caudate is necessary for an ego-centric localization ability (Potegal 1969). The experiment employed an elevated maze with 12 arms radiating from a central disk; goal boxes were located at the end of each arm. In this set of experiments, the rat always started from one of the goal boxes; the food reward was located in another goal box in a position that was determined solely by the position of the rat's starting box. Thus, the location was, for the rat, ego-centrically defined. In the first experiment, the correct goal box was always at a 30° turn from the rat's "straight ahead"; all other goal box doors were locked. Various procedures precluded the use of other intra- or extra-maze cues. In this 12-choice situation, it was found that rats with caudate lesions were impaired in finding the correct goal box compared to sham-operated animals; the performance of rats with medial thalamic lesions was intermediate between these two groups.

In a second set of experiments, in which task difficulty was controlled, rats searched for a food reward which was hidden according to one of two equally difficult spatial schemas. On each trial nine goal boxes were covered and the food was placed at one of two possible sites. For half of the rats it was always located ego-centrically. For the remaining group, it was located in the leftmost (or rightmost) of the two choices regardless of the left–right relation of those choices to the rat's position (relative position task). To illustrate the latter task assuming that the leftmost goal was correct: if both choices were to the animal's left, then the one furthest to his left was correct; if both choices were to his right, then the near right one was correct. (For further references to the distinction between ego-centric and relative schemas *see* Harrison and Nissen 1941, Bruell and Albee 1955, Ogle 1962). It was found, as predicted, that partial destruction of the caudate nucleus impaired performance on the ego-centric task but not on the relative task, supporting the hypothesis that the caudate is part of an ego-centric system.

3. *An implication of the hypothesis:*
The need for movement compensation

As an observer moves about, the head/eye movement appropriate for bringing a particular object into focus obviously changes. For example, the position of a particular object directly in front of an observer may be represented by him as "straight ahead". If the observer were to move one yard to his right, the target would then have to be represented as "one yard to my left". Thus there is a logical consequence entailed by an ego-centric localization system: since every change in the orientation and position of the observer changes his spatial relation to any given target position, every self-produced movement must be accompanied by a compensatory updating of the internal representation of the target location. It is now appropriate to ask: is the caudate involved in this compensatory updating also?

An answer to this question is provided by a test in which a subject sees a target, commits its location to memory, and then shifts his position without being able to see the target. From his new position he must then point to the target; to do this accurately requires a compensation for his self-produced movement. To discover if the caudate might be involved in such compensation, this experiment was performed on patients with Huntington's Chorea (Potegal 1971). The patient stood in front of a horizontal white table top which had a single black target dot at its center; after the patient had viewed the dot, his vision was occluded by lowering the opaque shield of the goggles which had been placed over his eyes. The patient then took a single step to the side and, from his new position, marked the remembered position of the dot with a stylus. It was found that the accuracy of patients with Huntington's Chorea in this situation was significantly worse than that of normal subjects. The patients were unimpaired on other spatial-motor tasks of equal difficulty which did not involve compensation for movement, making it less likely that the dementia or involuntary movements associated with Huntington's Chorea could account for the impairment.

4. *The role of vestibular information*

What information modalities are used by the compensatory mechanism to determine the observer's displacement and, therefore, the new location of the object relative to himself? In the foregoing experiment, the general accuracy of the vision-deprived subjects in pointing to the target after movement (mean error approximately 1 cm) is consistent with the commonplace observation that it is possible to find one's way in the dark, i.e., in the absence of information from the distance receptors. There are only a few sources of such internal information adequate for monitoring movements, and these can be divided broadly into outflow and feedback categories.

Outflow (feed-forward) refers to information derived from movement commands, i.e., efferent signals generated at some level of the nervous system (*efferenzkopie* — von Holst and Mittelstaedt (1950), *corollary discharge* — Teuber (1960)). Bossom (1965), has reported that caudate lesions, while not affecting ordinary visually guided reaching in monkeys, do interfere with their adaptation to the lateral displacement of the visual field produced by prisms placed over their eyes. Since it has been shown that adaptation to prisms requires an efferent component ("self-produced movement", Held and Bossom 1961, Abplanalp and Held 1965), Bossom's work suggests that the caudate does process outflow information. Several years ago the writer had an opportunity to study a human patient with a unilateral surgical lesion of the caudate. In accord with Bossom's report this patient manifested difficulties in prism adaptation (see Milner and Teuber 1968).

Alternatively, evaluation of displacement through space may be based on the monitoring of the sensory consequences of movement. Perhaps the most obvious sources of this feedback are the kinesthetic senses. Konorski's (1967) proposal that the prefrontal areas are the "locus for kinesthetic gnosis of spatial relations" may, perhaps, be interpreted in this light. Feedback information may also be provided by the vestibular system. The semicircular canals yield a feedback from head or torso movements involving linear and/or rotational acceleration which could be used to find displacements. Jones and Milsum (1970) have demonstrated that, within the velocity range of normal movement, the firing frequency of vestibular nerve fibers are related to the velocity of rotation. Angular displacements could therefore be computed in higher structures of the nervous system by an integration (in the mathematical sense) of the vestibular nerve signal over time.

There is, in fact, behavioral evidence that this integration can be performed, i.e., that vestibular information can play a role in guidance of movements through space. Beritoff (1965) has found that humans and animals deprived of vision can quickly learn to orient themselves and navigate, guided solely by labyrinthine information. He argues that quite general spatial abilities may be supported by labyrinthine cues: in his experiments blindfolded humans and animals were able to take a short cut from the end to the beginning of a path along which they were passively moved. Similarly, Douglas (1966) has reported that rats can keep track of their orientation while being passively moved when the only information available was labyrinthine feedback. This work has since been replicated (Rosen and Stein 1969).

The suspicion that striatal and labyrinthine functions are related is at least 50 years old (Muskens 1922): a brief review of this literature can be found in Potegal, Copack, DeJong, Krauthamer and Gilman (1971). It may now be hypothesized that this striatal-labyrinthine relationship is one in which the labyrinths produce feed-back information from movement on the basis of which the caudate updates its ego-centric representation of objects in space. However, before accepting such a conclusion it is necessary to examine critically the evidence that an input to the caudate from the vestibular system actually exists. Spiegel, Szekely and Gildenberg (1965) have offered some electrophysiological evidence in support of such an input. Unfortunately, their study leaves some doubt about the modality specificity of the responses they recorded because of the anesthetic and method of stimulation which were used. Therefore, a study was undertaken in which the vestibular and cochlear nerves were stimulated electrically, in isolation from one another, in encephale isolé cats (Potegal et al. 1971). By comparison of effects of vestibular and cochlear stimulation it was found that modality specific vestibular responses with latencies of 4–15 msec could be recorded in the dorsolateral caudate contralateral to the nerve being stimulated. Responses could also be detected in the dorsomedial region of the caudate ipsilateral to the stimulated vestibular nerve. These results cannot, of course, be interpreted as support for the existence of a caudate nucleus ego-centric localization system. They merely indicate that the system has vestibular information available to it. It appears that, in all likelihood, the system makes use of the three relevant forms of information — outflow and kinesthetic or vestibular feedback — for computing displacement.

5. *The egocentric system in delayed response*

Normal squirrel monkeys and marmosets solve delayed response problems by visually fixating the foodwell being baited and then maintaining a steady, unmoving, overt orientation toward it during the enforced delay between the baiting of the foodwell and their approach to it (Miles 1957, French 1959). This could be described as an "overt egocentric orientation". In contrast, dogs and rhesus monkeys may typically wander about the testing area during the delay period or retreat to some favorite corner. These latter species may be maintaining an "internalized" orientation to the goal; i.e., may be using their ego-centric localization system. This implies that, as the animal moves about in the delayed response situation, it is continuously keeping track of the head/eye movement necessary to bring the baited foodwell into focus. Caudate nucleus lesions or stimulation would, on this account, impair delayed response performance through interference with the anatomical substrate of this system.

It should be possible, according to this reasoning, to demonstrate the presence of an ego-centric strategy in the delayed response performance of normal animals. One relevant observation can be found in French's (1959) report that the delayed response performance of normal monkeys is affected by placing a screen in front of the baited foodwell but unaffected by covering the unbaited foodwell. This is exactly what would be expected from an ego-centric localization system in which the location of the baited foodwell is encoded but the position of the other foodwell is ignored.

The possibility that the ego-centric system uses vestibular information has been discussed. This raises a problem in the context of the classical delay tasks since Orbach (1962) did not find a delayed-response impairment after labyrinthectomy and P. S. Goldman and M. Mishkin (personal communication) did not find a delayed-alternation deficit after VIII nerve section. However, this existence of several forms of displacement information available to the caudate may allow elimination of a single input without adverse effects on performance.

A great many factors have been shown to influence the delayed response performance of normal and brain-operated animals (Meyer, this Symposium). In the following paragraphs only one of the phenomena associated with the caudate/frontal cortex delayed response deficit will be discussed. A number of the experiments cited below employed subjects with frontal lesions. It is a assumed that similar results would have been obtained with caudate subjects. In fact, however, the parallel between frontal and caudate function needs more investigation (Divac, this Symposium).

A number of techniques have been reported to facilitate, with varying success in the hands of different investigators, the post-operative delayed response performance of frontal and caudate *S*s. Depending upon the species under study, the specific testing situation and the prior experience of the subjects, improved performance of frontal animals may follow drug administration (reviewed by Weiskrantz et al. 1965), pre-delay reward (Finan 1942, Blake et al. 1966), reduction of delay period illumination (Malmo 1942, Orbach and Fischer 1959, McDowell and Brown 1960, King et al. 1968), use of an automatic apparatus (Battig et al. 1960, Stamm and Pribram 1960, Gross 1965), titration of delay (Battig et al. 1960, Divac and Warren 1971) and indirect baiting (Cianci et al. 1967, Pinsker and French 1967, Buddington et al. 1969). It may be that at least some of these special experimental conditions encourage overt orientation or "response chaining" which "bridge the delay" and permit solution.

Direct evidence to this effect has been reported by Orbach and Fisher (1959) and Orbach (1962) for monkeys and by Konorski and Lawicka (1964) for dogs. Wilson, Oscar and Gleitman (1963) and Gleitman, Wilson, Herman and Rescorla (1963) report, however, that at the beginning of the delay period both frontal and normal monkeys adopt a position in front of the baited foodwell but for neither group is this necessary or sufficient for solution. Further analysis is necessary, but assuming that post-operative solution requires overt orientation, the question then arises: why are special conditions necessary to elicit this solution? One obvious proposal is that the hyper-activity of frontal or caudate *Ss* results in movements for which they can no longer compensate and which prevent them from maintaining an overt orientation. All the manipulations in question may reduce these delay-period movements and permit an orientational "pseudo-solution".

Evidence for the view of movement as a post-operative interference factor is provided by experiments with monkeys (Malmo 1942) and gibbons (Fletcher 1964) in which a high correlation between movement during the delay period and error scores, was found. Gross (1963) has found that the sulcus principalis is the focus for both the hyperactivity and the delayed response deficits in rhesus macaques. Gross and Weiskrantz (1964) argue, however, that hyperactivity is neither necessary nor sufficient for the classical deficit. Their claim may be disputed or qualified on three grounds: (i) in some cases, activity was not measured in the testing situation. Since activity in frontal or caudate animals is a function of the situation (Issac and DeVito 1958, Denny-Brown 1962, Gross 1963) measures not taken during testing will not be representative of activity during testing (*see* French 1964, p. 64). (ii) Even if the normal compensatory mechanisms are damaged, head/eye position is the most important aspect of the overt orientation maintained by brain-damaged animals. Thus, many of the activity measures, e.g., the number of crossings from one cage quadrant to another, were inappropriate. Head and/or eye movement during this delay period would be quite sufficient to impair the overt head/eye orientation to the target. (iii) Therefore, an increase in activity, measured in the usual way, is not necessary for producing a deficit. The unchanged low-level post-operative activity of squirrel monkeys (Miles and Blomquist 1960) would, on the present hypothesis, be sufficient to produce a deficit. The report of Dean and Davis (1959), that administration of phenidylacetate improved delayed response performance without modifying hyperactivity, presents difficulties for this interpretation but their study may be open to criticism (i), i.e. that activity was not measured in the test situation.

Whether or not the spatial character of the delayed response deficit can finally be understood as a disturbance of an ego-centric localization mechanism, the next few years might profitably be devoted to bringing our comprehension of these neuropsychological functions on a par with our knowledge of their anatomical locus. As a first step Pohl (1970) has found that dorsolateral frontal lesions, in contrast to parietal lesions, do not affect a two-choice task in which the location of the baited food-well was indicated by an "external landmark". However, frontal animals were impaired relative to parietal animals in a spatial task which was learned in the absence of external cues. In this effort of teasing out the exact nature of caudate and frontal cortex spatial functions, the transfer techniques of Harrison and Nissen (1941) might prove very valuable indeed.

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