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Classification and Naming of Cat Retinal Ganglion Cells

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Abstract

Many schemes of ganglion cell classification seek to classify the cells by some particular characteristic, such as the time course of the cells' physiological responses or their dendritic morphology. It is here argued that such schemes are based on the Aristotelian concept of 'essences' and raise the same difficulties as have arisen with the essentialist approach to animal taxonomy. A better approach to the classification of neurones, it is proposed, is to base the classification on as many features of the cells as possible, and to regard the classification as an hypothesis, subject to testing and modification by experience, about the 'functional niches' occupied by the cell types distinguished.

that 'many classifications attempt to be both identification schemes and classifications' and that 'much of the development of modern taxonomy has been toward the clearer and clearer separation of these entirely different operations.'

Choice of Nomenclature

A number of problems are involved in the choice of nomenclature, and it is important to discuss them separately.

Avoidance of Essence-Indicating Names

It has been argued at some length, above, that the issues of nomenclature and classification are not separate, and that an important step in avoiding the difficulties raised by the essentialist approach to classification is to choose a nomenclature which does not draw attention to a particular feature or features of cells being classified. In practice, this has meant the avoidance of descriptive labels and the use of alphabetical or numerical labels. As table I shows, various workers have used Roman and Arabic numerals, and Latin and Greek letters, to name groups of ganglion cells. The problem with purely descriptive labels such as 'brisk-sustained' is not simply that they are descriptive, but also that they are essence-indicating.

Avoidance of Role-Indicating Names

Just as terms which refer to a particular descriptive feature are to be avoided, it is important to choose labels which do not attribute to a group a particular functional significance or role. Names such as 'local-edge detector' or 'uniformity-detector', for example, describe a particular opera-

tion which these cells are deemed to perform, and imply that this operation is of primary importance. They are no less essentialist than the essence-indicating names discussed above and raise the same difficulties. Such names also tend to confuse the neuronal groups themselves with the operations which they perform; this problem is discussed further in the following section.

Parallel Terminologies

As different groups of workers study and classify the same group of cells, alternative non-committal terminologies commonly arise; table I is an example of this for retinal ganglion cells. After eliminating essentialist terminologies, three of the terminologies in table I remain, two of which

(Y/X and types I/II are apparently equivalent and SAITO and FUKADA [1975] have subsequently adopted the Y/X terms. Even after these simplifications, however, two terminologies remain (Y/X/W and *alfly*) and seem likely to remain in separate use for some time. Parallel terminologies such as these are likely to arise whenever two classifications of the same population of neurones are based on types of observations which are difficult or impossible to make on the same individual cells. Although there is very considerable evidence that the two sets of three cell groups correspond very closely [BOYCOTT and WASSLE, 1974; CLELAND and LEVICK, 1974a; CLELAND *et al*, 1975; FUKUDA and STONE, 1974, 1975; STONE and FUKUDA, 1974b], there is presently very little overlap in the sets of observations on which the two classifications are based, the Y/X/W classification being based on physiological data, the *alfly* classification on morphological data. Except under very specific experimental conditions [CLELAND *et al*, 1975; FUKUDA and STONE, 1975], both types of data cannot be obtained from the same individual cells. Thus, in most cases, an individual ganglion cell cannot be readily categorized in both schemes. As our understanding of these cells increases, one set of terms will presumably come to be preferred. For the moment, however, it seems necessary to retain the two terminologies, using each in its appropriate context.

Naming of Subgroups

There is generally a certain amount of descriptive variation contained within any natural group. Indeed, if all natural groups were homogeneous in their properties, many of the problems of classification and nomenclature would not have arisen. Basically, such variation can be handled in two different ways: (1) the use of descriptive prefixes, and (2) the formal delineation of subgroups. Each represents a different level of organization within the group, and the two should not be confused.

(1) The W, X and Y cell groups are all more or less heterogeneous in their properties. Among Y cells, for example, those found at the area centralis have slower conducting axons and smaller receptive field centres than peripheral Y cells, give more tonic responses to standing contrast, and are less markedly responsive to high stimulus velocities [CLELAND *et al*, 1973; CLELAND and LEVICK, 1974a; STONE and FUKUDA, 1974a]. This variety of properties has generally been handled by referring to 'area centralis Y cells' as against 'peripheral Y cells'. A similar central-peripheral gradation of properties is apparent among X cells and has been handled

in the same way. Both X and Y cell groups also include cells with On-centre receptive fields, and cells with Off-centre receptive fields, and these subtypes are distinguished simply as On-centre X cells, Off-centre X cells, On-centre Y cells, and so on. W cells, while having many features in common and rather less variation with retinal location than X or Y cells, have a greater variety of receptive field types. This variety has also been handled with descriptive names, so that various subtypes of W cells were called 'tonic Off-centre W cells' or 'phasic On-centre W cells', and so on.

The use of descriptive prefixes to distinguish variations within the Y, X and W cell groups is common to all workers who have published on these cells, and might seem to impose an essentialist crust on a non-essentialist loaf, i.e., to introduce the Aristotelian concept of 'essences' into classifications otherwise non-essentialist in their presuppositions. We would argue, however, that this is not the case. The problems of the essentialist approach to cell classification have been identified above. The approach implicitly or explicitly deems one or a few properties to be essential to the grouping and other properties to be accidental or at least of lesser importance; the approach cannot easily handle diversity within a group, and so tends to produce a large number of groupings; the approach commonly leads to quite unnecessary controversy as to which properties of cells comprise their essence. None of these problems are raised when descriptive prefixes are added to non-descriptive group labels. In the term phasic Off-centre W cells, for example, the use of 'W cells' keeps the polythetic, non-essentialist basis of the classification, while the terms 'phasic' and 'Off-centre' simply describe the properties of the cell along a single parameter (receptive-field organisation). Such prefixes refer to particularly useful identifying characteristics of the cells, and their use has not tended to downgrade interest in other properties of the cells or to create controversies about 'essential' features, nor has it lead to the creation of large numbers of cell groups. In brief, prefixes such as 'phasic Off-centre' when used with a term like W cell, although descriptive, are not 'essence-indicating'.

(2) Whenever some of the members of a group display a feature not common to all members of the group, and particularly when the appearance of this feature is correlated with the possession of one or more other characteristics also not common to all members of the group, it may be appropriate to give these individuals the status of a functional subgroup. The principles involved in the establishment of such categories are the

same as those involved in the establishment of any other category, and have been set out in some detail above. With regard to nomenclature, if subgroups are to be formally distinguished, non-descriptive names should be devised for them. For example, STONE and FUKUDA [1974a], writing without a full appreciation of taxonomic theory 'classified' the common varieties of W cells into tonic and phasic types and regarded the less common varieties (e.g., direction-selective On-Off cells, suppressed-by-contrast cells) as separate small subgroups. In that paper and subsequently, a clustering of other properties has emerged around the two major 'types'. For example, the tonic cells have (on average) faster axons than phasic cells [STONE and FUKUDA, 1974a; CLELAND and LEVICK, 1974b] and probably larger somas [STONE and FUKUDA, 1974b], and have a principally uncrossed projection from temporal retina [STONE and FUKUDA, 1974b; KIRK *et al.*, 1976b]; phasic cells have slower axons, smaller somas and a principally crossed projection from temporal retina. Moreover, evidence has emerged that some of the less common varieties of W cells show a similar clustering of properties. For example, direction-selective On-Off-centre cells give phasic responses, have slow axons and probably small somas, and a principally crossed projection from temporal retina [KIRK *et al.*, 1976b] resembling the phasic 'type' of W cell. Conversely, colour-coded W cells (first distinguished by CLELAND and LEVICK [1974b]) and suppressed-by-contrast cells have faster axons (within the W cell range), are tonic in their responses to standing contrast (some suppressed-by-contrast cells are an exception) and probably (from fig. 2 in KIRK *et al.*, [1976b]) have a principally uncrossed projection from temporal retina. They seem therefore to resemble the tonic 'type' of W cell distinguished by STONE and FUKUDA [1974a].

These clusterings of properties may indicate some functional distinction between the two groups, and seem sufficient to justify a division of W cells into two subgroups. We suggest that these subgroups be given the non-descriptive names W_1 and W_2 . As shown in table III, the $\sim W_X$ group would include tonic On- and Off-centre, colour-coded and suppressed-by-contrast W-cells; the W_2 group would include phasic On-, Off- and On-Off-centre, and both On-Off-centre and On-centre directionally selective W cells. STONE and FUKUDA'S [1974a] data indicate that, overall, the W_1 and W_2 subgroups would each comprise about half the W cell population. ROWE and STONE'S [1976b] data indicate a limited difference in the relative frequencies of W_1 and W_2 cells between peripheral retina and the visual streak.

Table III. Suggested subgrouping of W cells

Subgroups suggested	Response to standing contrast	Axonal velocity (extraretinal)	Soma size	Projection from temporal retina	Receptive field organisations recognised	Relative numbers and retinal distribution
W_1 mostly	relatively fast tonic	mean 11.7 m/sec	relatively large	principally uncrossed	Off-centre, On-surround On-centre, Off-surround suppressed-by-contrast colour-coded	approximately 50 % of W cell group; relatively more common outside visual streak
W_2 phasic	relatively slow	mean 6.6 m/sec	small	principally crossed	Off-centre, On-surround On-centre, Off-surround On-Off-centre, inhibitory or On- or Off-surround On-Off-centre, direction-selective On-centre, direction-selective	approximately 50 % of W cell group; relatively more common in visual streak

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The reason for choosing names such as W_1 and W_2 for the subgroups is the same as for using non-descriptive names generally; names should be avoided which suggest that any particular property is essential to the subgrouping. BOYCOTT and WASSLE [1974] also followed this principle when they distinguished a variety of y-cell, which they termed <5-cells. We would stress, however, that while W_1 and W_2 cells differ sufficiently in their properties to suggest some degree of separate functional specialization, they also share a number of features, particularly their patterns of retinal distribution and central projection [WILSON *et al.*, 1976; FUKUDA and STONE, 1974; ROWE and STONE, 1976b], which indicate a degree of functional communality comparable to that found within the X and Y groups. Hence, for the present, it seems appropriate to also retain the single W cell category at the same taxonomic level as the X and Y categories.

To summarise the critique of ganglion cell classifications presented above, it is not meant to suggest that any particular scheme of classifying ganglion cells, whether by morphology or physiology, is *the* correct one. We do mean to suggest that certain schemes are simpler, more adaptable to new findings and less likely to be a source of confusion than others. In the following, more theoretical section, an attempt is made to set out principles by which such schemes of classification might be devised for neuronal populations.

Towards a Theoretical Basis for the Classification of Neurones

The above discussion of schemes of ganglion cell classification, and TYNER'S [1975] discussion of similar problems encountered in classifying motor system neurones, point to the same need, for some understanding on the part of neurobiologists of the issues involved in the classification of nerve cells. Two propositions are therefore set out below which might be considered by neurobiologists confronted with the need to classify. Neither proposition is original; both stem from taxonomic theory. Together with TYNER'S discussion, however, they may contribute a step towards establishing a theoretical basis for classifying neurones. The two propositions are: (1) that any classification should be viewed not as a definition of cell groupings, but as an hypothesis that the cell groupings being delineated fulfill distinct functional roles; and (2) that the functional roles referred to by the classification should be defined in terms quite independent of the properties of the cells being classified.

Classification as an Hypothesis

Darwin recognized that classification should not be regarded as an end in itself and that the theory of evolution provided a much needed functional basis for the classification of plants and animals. 'Expressions such as that famous one by Linnaeus, ... that the characters do not make the genus but that the genus gives the characters, seem to imply that some deeper bond is included in our classifications than mere resemblance' [DARWIN, 1872, p. 569]. HENCE DARWIN [1872, p. 576] suggested '... that community of descent is the hidden bond which naturalists have been seeking, and not ... the mere putting together and separating objects more or less alike.' Thus, the theory of evolution made it possible for classifications of animals to be regarded as hypotheses about phylogenetic or cladistic relationships between them, and the aim of taxonomy became, in the words of J. S. HUXLEY [1940, p. 2], 'the discovery of evolution at work'.

This view of classification has at least three major advantages. First, as an hypothesis, a scheme of classification is a testable proposition, intended to be modified or even discarded if necessary, and therefore inherently adaptable to new accumulations of data. Second, because observations used to generate hypotheses cannot validly be used to test them, the testing process itself results in the collection of new data. The classification thus has the effect of generating new observations, rather than of formalising old ones. Third, this view of classification requires that a distinction be made between the description of a group and the definition of the category to which it belongs. The biological species for example, is a *category* of animals, and is defined as a group of animals whose members interbreed freely with each other, but which is reproductively isolated from all other groups [BOCK, 1973; MAYR, 1963]. This definition is independent of any particular description of the properties of the animals. In general, the assignment of any described *taxon* (group of animals) to a category is an hypothesis about the evolution of that taxon. Methods of classification which incorporate this separation of description from definition can readily accommodate the descriptive variation which often exists within a natural group, for example a species, due to factors such as age, sex, social status, or ecological situation (for fuller discussion, see MAYR [1970]).

The essentialist approach to classification shares none of these advantages. The membership of any group is determined entirely by the possession of a certain essential feature and the description of this feature then becomes the definition of the group. Such schemes are not constructed as or intended to be hypotheses and, in so far as they are not, have no heu-

ristic value. Since groups are both named and defined according to an essential feature, new information about the things being classified can be incorporated only by the creation of new categories or the division of old ones. Because no distinction is drawn between description and definition, essentialist schemes cannot easily accommodate the diversity which may exist among individuals within a group.

Functional Basis for Classifying Neurones

If a classification is to be regarded as an hypothesis, what should the hypothesis be about? The theory of evolution provided a functional basis for the definition of various categories, and hence for the classification of all organisms, and taxonomy came to be regarded as an attempt to elucidate the processes of evolution. Clearly, some analogous basis is needed for the classification of neurones.

Evolutionary History of Neurones

All neurones and groups of neurones presumably have evolved and the differentiation of the brain of any animal into various divisions, subdivisions and nuclei, and the presence of morphologically distinct cell types within nuclei probably reflect the processes of brain evolution. Indeed, it could be argued that different groups of neurons have different evolutionary histories in the sense that their properties have developed in response to different subsets of the selective pressures acting on the animal, i.e., they are each becoming specialized to perform a unique function. Any classification of neurons into groups should be capable of eventually incorporating knowledge of the different evolutionary histories of those groups. However, of more immediate concern to most neurobiologists is the delineation of groups of neurons according to the functional roles which they play in the operation of a neuronal system. Consequently, the basis of classification which we are proposing is not primarily intended to reflect the evolutionary histories of various groups of cells, although we recognise the importance of understanding that history. It is rather designed to reflect the unique functional contributions of those groups to the overall operation of the neuronal system to which they belong.

Functional Niche

Sympatric species of plants and animals (species which share an environment) generally interact in such a way as to provide an optimal parti-

tioning and utilization of resources, forming a fairly stable balance, or ecosystem. Each species plays a particular role in the ecosystem, and can be said to occupy an ecological niche within it. Analogously, groups of neurones within a neuronal system also interact with each other in order to perform certain operations. Each group of neurones contributes a particular component to the overall function of the system and can be tentatively said to occupy a functional niche within it. We would suggest that the functional roles played by various neurones do provide a basis for their classification into groups; and that the classification should be regarded as an hypothesis that particular groups of neurones fill particular functional niches.

This approach makes the necessary distinction between neuronal groups and the operations which they perform, a distinction analogous to that between taxa and categories in animal taxonomy [BOCK, 1973; see above]. By the same token it allows the operations to be defined in terms independent of the description of the neuronal groups. Although these requirements seem obvious and unexceptionable, the use of labels which fail them is very common. For example, in ganglion cell physiology, the classifying of certain cells as 'detectors' for particular visual stimuli (e.g., 'local-edge detectors' or 'uniformity-detectors') might seem to embody an hypothesis about the functional roles or niches filled by the cells concerned, just as we have suggested a classification should do. The problems with this form of terminology are two. First, as already mentioned, the terms commonly refer to a single feature of the cells (in the case of the 'detectors' just mentioned certain aspects of their receptive field organisation) and have the same tendency as descriptive, essence-indicating names to concentrate attention on that feature. The second is that the names confuse the cells being studied with the functional niche they are supposed to fill; the operations which the cells are postulated to perform are *not* defined in terms independent of the description of the cells. Clearly, it is circular and difficult to refer to a cell as a local-edge detector (for example), while still testing the hypothesis that it fills this functional role. The 'detector' terminology tends therefore to become a definition of the cells concerned, rather than a suggestion or hypothesis about the roles they perform.² Once the above requirements are met, however, classifica-

² A similar problem has arisen in visual cortical physiology. The 'simple-complex-hypercomplex' classification of cells in cat visual cortex of -HOTEL and WIESEL [1962, 1965], was set up as an hypothesis about the functional relationships between the cell groups being distinguished (just as we here suggest a classification should

tion can be regarded as an attempt to delineate groups of neurons which are specialized to perform various independently defined operations, and a scheme of classification can be a source of testable hypotheses about the neuronal circuitry underlying those operations.

In this context the Y/X/W grouping of retinal ganglion cells can be regarded as an hypothesis about the functional niches filled by the three cell types, and discussions of what their roles might be have already been set out by IKEDA and WRIGHT [1972], CLELAND and LEVICK [1974a] and STONE and FUKUDA [1974a]. In reading these discussions it will be noted that the functional role suggested for X cells (pattern vision) is indeed defined in terms independent of the properties of X cells, but that the roles suggested for Y and W cells are less satisfactorily defined. STONE and FUKUDA [1974a], for example, comment that since W cells appear to form 'the major retinal input to the superior colliculus, it seems logical to suggest that they subserve a variety of midbrain visual functions. More specific suggestions are still to some degree speculative, partly because the range of visual functions performed by the midbrain has still to be established, and partly because the midbrain... also receives input from Y cells and the division of function between Y cells and W cells has still to be established.' Clearly, we need to know more about the visual sense before independently defined functions can be postulated for Y and W cells. In the meantime, their classification into groups separate from each other and from X cells can be regarded at least as an hypothesis that the three groups fulfill substantially *different* functional roles in vision, even though we cannot yet satisfactorily define those different roles. This situation does not satisfy the ideal conditions set out in propositions 1 and 2. However, it is often a necessary approach in the face of limited knowledge, and is then a useful approximation to the ideal. Indeed, formulation of such limited hypotheses can be of heuristic value in that it draws attention to gaps in our knowledge, in this case of the visual sense.

As already noted, a good example of an independently defined operation or functional niche in the visual system is that of pattern vision. The group of cells which occupies this functional niche need not be a collection of neurones with identical properties, but might be expected to share

be). But because the cell groups were given relationship-indicating names, their different positions in the cortical hierarchy have, in subsequent work, become synonymous, or at least identified, with the properties of the cells themselves. Ensuing problems of terminology in this area are still unresolved.

a number of properties consistent with their hypothesized role. As noted previously [IKEDA and WRIGHT, 1972; CLELAND and LEVICK, 1974a; STONE and FUKUDA, 1974a] the cells most likely to fill this niche in the cat visual system are the X cells, because of their small receptive fields, their concentration at the area centralis and because they form a high proportion of the cells which project via the lateral geniculate nucleus to the visual cortex. Nevertheless, the great majority of cells included in the X group are located in peripheral retina, and have much larger receptive fields and are much more responsive to fast image movement than area centralis X cells; compared to area centralis X cells, peripheral X cells do not seem specialised for pattern vision. Despite this variation in their properties, X cells at all retinal locations have smaller receptive fields than neighbouring Y or W cells, are less responsive to fast image movement and have more tonic responses to standing contrast than Y cells, and have the same unique pattern of central projection. At all retinal locations, therefore, a characteristic gap exists between the properties of X cells and those of Y and W cells. X cells seem to occupy the same functional niche throughout the retina, and are thus considered to constitute a single functional group.

The concept of a functional niche is also of considerable value in comparative studies. Because of its functional basis this approach to classification could facilitate the recognition of cell groups which occupy similar functional niches in different species, even though they may differ considerably in certain descriptive properties.³

DREHER *et al.* [1976], for example, have described Y like and X like relay cells in the lateral geniculate nucleus of the monkey, cells which presumably reflect the activity of Y-like and X-like retinal afferents. The names were not chosen because the Y like cells were identical with cat Y cells, or the X like cells with X cells. Many X like cells in the monkey were colour-sensitive, for example, while cat X cells are not, and many lacked an antagonistic surround, which cat X cells invariably have. With

³ One word of caution should be added here. The hypothesis that groups of cells in different species occupy the same functional niche is not to be equated with the suggestion that these groups are homologous. The problems involved in the establishment of homology have been discussed elsewhere [BOCK, 1969; CAMPBELL and HODOS, 1970; HODOS and CAMPBELL, 1969] and we do not wish to further complicate the situation here. The criteria for the establishment of homology are independent of (although they overlap with) the considerations involved in defining a functional niche. Groups of cells in different species could occupy the same functional niche as a result of either homology or homoplasy.

an essentialist approach, these differences might distract attention from and even obscure any functional similarity between cell groups in the two species. Nevertheless, it was shown that in the monkey, X like cells differ from Y like cells in many of the ways that cat X cells differ from Y cells; namely, they are capable of greater spatial resolution, have slower-conducting axons and more tonic responses to standing contrast, and are less responsive to fast image movements. They also greatly outnumber the Y-like cells and have been shown by others [DE MONASTERIO and GOURAS, 1974] to concentrate at the fovea. Clearly X-like and Y-like cells occupy functional niches in the monkey visual system similar in many ways to those of X and Y cells in the cat. Recently, it has also been proposed that relay cells in the lateral geniculate nucleus of the owl monkey [SHERMAN *et al.*, 1976] and tree shrew [SHERMAN *et al.*, 1975] can be divided into X and Y groups on the basis of a number of their properties, and that many of the ganglion cells in the retina of the rabbit can be divided into Y, X and W groups [CALDWELL and DAW, 1976]. Thus, some features of the functional groupings described in the cat may be found in a number of mammalian lineages.

Once it has been established that parallel cell groups in different species, e.g., X cells in the cat and X-like cells in the monkey, occupy the same or very similar functional niches, it becomes worthwhile to examine descriptive differences that exist between them, such as the colour-specific properties of monkey X-like cells. These differences can be a rich source of information about the various ways in which the visual system can and has adapted to meet different requirements. Such analyses should generate a very broad and integrated picture of visual system function based on a full appreciation of its many adaptive variations and provide a context into which data obtained from any species can be usefully placed, and from which a better understanding of the unique combination of features found in any species, including man, can be realized.

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