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Review

Thirty years of collaboration with Gabriel Horn

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ABSTRACT

All the collaborative work described in this review was on the process of behavioural imprinting occurring early in the life of domestic chicks. Finding a link between learning and a change in the brain was only a first step in establishing a representation of the imprinting object. A series of overlapping experiments were necessary to eliminate alternative explanations. Once completed, a structure, the intermediate and medial mesopallium (IMM), was found to be strongly linked to the formation of a neural representation of the object used for imprinting the birds. With the site identified, lesion experiments showed that it was necessary for imprinting but not associative learning.

Also the two sides of the brain responded differently with the left IMM acting as a permanent store and the right side acting as a way station to other parts of the brain. The collaborative work led to many studies by Gabriel Horn with others on the molecular and cellular bases of imprinting, and also to neural net modelling and behavioural studies with me on the nature of category formation in intact animals.

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Contents

1. Introduction

Gabriel Horn was a superb scientist. He was also a dear friend with whom I worked for many years. This article describes our long collaboration which began by chance at a dinner in King's College Cambridge. After Gabriel had qualified as a doctor at Birmingham University, he was appointed as Demonstrator in the Department of Anatomy in Cambridge. Faculty members were expected to teach students in small groups and Gabriel supervised medical students from King's for several years, before being made an Official Fellow in 1962. In 1965, I returned from a 2 year Harkness award in California to a Research Fellowship also at King's. In those days the traditional Cambridge Colleges still operated something like monasteries as though they were filled with resident bachelors. Those of us who were married were expected to dine with other fellows at least several evenings each week. Over the years as more and more fellows had young families and partners who were working, this practice has dwindled. Even so, meeting fellows from other disciplines was rewarding and sometimes had major benefits. It

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certainly did for me because it was in this way that I met Gabriel. For my PhD I had worked on behavioural imprinting by which young animals such as domestic chicks rapidly form a social preference for a conspicuous visual stimulus (Bateson, 1964a,b, 1966). Gabriel had had a longstanding interest in the brain going back to his student days at Birmingham where he had written a brilliant essay on the neurological basis of thought. As Gabriel and I talked animatedly over dinner, we realised that imprinting in naïve chicks would be an excellent form of learning in which to study the neural basis of memory. Any effects of experience should stand out more prominently in an animal that had come straight out of the dark for the first time. We agreed to work together.

2. The nature of imprinting

Behavioural imprinting is undoubtedly startling. The learning process occurs early in the lives of many birds and mammals and, in some cases at least, can have profound and lasting effects on the sexual preferences of adults. The image conjured up by the term is vivid and simple. At a certain stage, the wax of the young animal's brain is soft and it receives the imprint of the first conspicuous thing which the animal encounters. The German term Prägung (translated as "imprinting") was first used by Heinroth (1911), although Spalding (1873) had used a very similar metaphor, namely "stamping in". Lorenz (1935), who did so much to make the phenomenon famous, liked the image because it suggests, as he believed to be the case, an instantaneous, irreversible process. It also led to strong claims that imprinting is quite different from other forms of learning (see Hess, 1973). As more evidence became available, the claims were disputed and the term was held to be misleading (Bateson, 1966; Sluckin, 1972). Nevertheless, Lorenz (1981) continued to treat the process as special and "imprinting" has been retained in the literature by advocates and critics alike.

When characterising classical conditioning, Dickinson (1980) argued that the learning process serves to uncover the causal structure of the environment. The jobs of learning to predict and to control the environment are not, however, the same as that of learning to categorise it even though attempts have been made to explain both forms of learning in the same terms (e.g. Hall, 1991). Detecting causal structure may require classification, but establishing a classification does not involve an association of cause with effect.

In the real world, a complicated object often presents a substantially different set of features from one view than it does from another. In many circumstances, an animal would benefit from treating these different sets as though they were equivalent (Bateson, 1973). Consider the problem facing the bird which has to gather information about the front, side and back views of its mother. All these views are physically distinct and they may also take on different appearances when viewed at different distances. Information from two separate arrays of features may be combined into a single representation when the two arrays occur in the same context or within a short time of each other (Bateson and Chantrey, 1972). Chantrey (1974) varied the time between the onset of presentation of one imprinting object and the onset of presentation of another and subsequently required domestic chicks to discriminate between the two familiar objects in order to receive a food reward. If the objects were presented five or more minutes apart, the birds learnt to discriminate between the two objects more quickly than those in the control group that had not been exposed to these two objects. However, when the two objects were presented 30 s or less apart, the imprinted birds took longer than the control group to learn the discrimination. Honey et al. (1993), using a different technique from Chantrey, double-imprinted chicks and then required them to discriminate between the two imprinting stimuli in order to receive a heat reward if they approached one of them but not the other. In the imprinting regime, the birds were either given alternate exposures with a mean inter-exposure interval of 14 s—the mixed condition. Alternatively, they were exposed to periodic exposures to one stimulus and then after a gap of two hours to periodic exposures to the other—the separate condition. The pattern of imprinting was otherwise the same and the total exposure to the two stimuli was identical in the two conditions. The birds imprinted in the mixed condition took significantly longer to learn the heat-rewarded visual discrimination than the chicks exposed to the separate condition. The explanation is that, when stimuli are presented in alternation close together in time, they are classified together; if subsequently the birds are required to learn the discrimination, they first have to disaggregate the two representations before they are able to distinguish between them.

3. Biochemical studies

In the early stages of the work that Gabriel and I did together we cast around for various biochemical measures that we could use as correlates of imprinting. We initially collaborated with Les Iversen using measures of neural transmitters but did not find anything. After a seminar in London, we had the offer of help from Steven Rose who was then at Imperial College London but later moved to the Open University. He was, first and foremost, a biochemist, but he had great interest in the effects of visual experience on the brain. In our early work with Steven we soon found that measures of protein synthesis and RNA synthesis in the roof of the forebrain were associated with imprinting (Bateson et al., 1969, 1972; Rose et al., 1970). The job at the Cambridge end was to run the experiments, remove and roughly dissect the brains into different regions and send the coded samples packed in dry ice to Steven who, not knowing the code, would analyse them. This early collaborative work among the three of us led to a review in Science (Horn et al., 1973a).

Collaborators in Steven Rose's laboratory found that imprinting was involved in enhancing RNA polymerase (Haywood et al., 1970, 1975) and lysine uptake (Hambley et al., 1977) in the forebrain roof of the chick. The problem in all these studies was to rule out various alternative explanations to the possibility that the biochemical change was related to the storage of a specific representation. It was not good enough simply to show that a particular part of the brain was biochemically active when the bird was learning about the imprinting object. We were all aware that such associations could be explained in many ways.

4. Eliminating alternative explanations

As one of his many interests in the brain, Gabriel had examined how repeated stimulation with light led to a gradual waning of activity in stimulated neurons in the brain of anaesthetised rabbits. He wrote later "I suddenly realised that we were dealing with a neural counterpart to behavioural habituation." As a result of this insight, he had discussed his interest with Robert Hinde who had worked on the waning of a mobbing response to an owl by the chaffinch. Together Gabriel and Robert organised a conference in King's on the behavioural and neural aspects of these short-term process with a stellar cast of international speakers. They subsequently published the proceedings in book form (Horn and Hinde, 1970). My contribution to Gabriel's and Robert's book was entitled "Are they really the products of learning?" (Bateson, 1970). It was a critical review of studies by those scientists who had claimed to have discovered the neural basis of learning and memory. The claims were based on correlations and, of course, a correlation does not establish causation. Gabriel, Steven and I were faced with

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