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Gravity as a Zeitgeber: The Mechanism[1]

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It has been postulated that gravity is not only a physical vector providing organisms with a Spatial Reference Frame, but that it may also be utilised to provide a Temporal Reference Frame, thereby acting as a synchroniser. The mechanism inherent in this is traced to the Arousal I system of Routtenberg's Two Arousal Hypothesis. Consequently it is deduced that there may be no single centre for the biological clock, nor that sensing thereby is continuous.

Das Gravitationsfeld als Zeitgeber: Der Mechanismus

Die Gravitation ist nicht nur postuliert als physikalischer Vektor, der dem Organismus ein räumliches Referenznetz verleiht, sie kann auch als zeitliches Referenznetz benutzt werden, und in diesem Sinne als Zeitgeber operieren. Der dabei inhärente Mechanismus wird als erstes Arousal-System der Routtenberg'schen Zwei-Arousal-Hypothese hinzugefügt. Daraus wird gefolgert, dass es kein singuläres Hauptzentrum der biologischen Uhr gebe, und dass die Zeitabnahme einer solchen Uhr nicht andauernd sei.

1 Introduction

It does not seem to be a quirk of nature, but a matter of fact that life has its ups and downs, the most obvious rhythmical changes being circadian in nature. Numerous of these have been documented (J. Aschoff, 1963; E. Bünning, 1973). In order to explain how these rhythms individually keep in phase to one another, synchronisers, or Zeitgebers, have been postulated. Various agents have been implicated as synchronisers, such as light, temperature or magnetism (E. Bünning, 1973), from which it has been concluded that some agents are better synchronisers than others (light is more effective than temperature), and that coinciding synchronisers are more effective than either of these on an individual basis (light plus temperature is better than light alone), suggesting an additive effect. To the list of exogenous synchronisers has recently been added the gravitational vector (H.-G. Tittmar, 1973).

Evidence has been accumulated by Schneider (F. Schneider, 1975a) that at least one organism *(Melonlontha melolontha L.)* is able to respond to nuances in the gravitational environment. These nuances are related to the distribution of masses in the proximate environment (F. Schneider, 1964, 1974), as well as temporal fluctuations of circadian changes in the Earth's gravitational field (F. Schneider, 1972, 1977). From these results, it has been postulated (H.-G. Tittmar, 1978) that the gravitational vector may provide not only a Spatial Reference Frame (as in orientation), but also a Temporal Reference

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I am indebted to Prof. N. Birbaumer's integrative view of physiological Psychology, which stimulated much of the thinking behind this article.

Frame (in the guise of a Zeitgeber) for the organism. This conclusion rests on the dual foundations of Schneider's empirical findings, and the discussion (H.-G. Tittmar, 1978) that daily gravitational fluctuations are within the detectable range of biological transducers. It was further argued (H.-G. Tittmar, 1978), that since temporal fluctuations in the gravitational field are slow and finite, a continuous sensing mode would be inefficient, whereas a gated sensing mode becomes more practical. Periodic up-dating of circadian fluctuations in gravity ought to result. Indeed, not only has Schneider observed orientation in his cockchafers to be time dependent (F. Schneider, 1974, 1975 b, 1977), but also that cockchafers will make more or less step-wise, progressive and periodic adjustments (F. Schneider, 1977).

2 Elements of gravitational sensing

2.1 Autocentric sensing

Such sensing, and correcting, as observable in Schneider's cockchafers, by Schachtel's definition (E. G. Schachtel, 1959), has to be an autocentric sensory experience. The stimulus (smell, temperature, pain, proprioception) is primarily integrated by the local sense organs, eliciting direct, often reflexive, behavioural controls. In contrast, an allocentric sensation (odour, heat, touch, acceleration) is one that draws on memories and conceptualisations: i. e. this is equivalent to Piaget's argument (H. E. Gruber and J. J. Voneche, 1977), concerning the course of behaviour being depending upon existing schemata. Newborns do, however, have few, if any, schemata concerning their external environment and much of their early years seem to be devoted to their building and accruing. Newborns do have, however, circadian-type rhythms (E. Bünning, 1973). Ignoring the possibility of an endogenous Zeitgeber, any exogenous timing can therefore only be measured in an autocentric mode. It has further been argued, that allocentric experience exists only in species high on the evolutionary ladder (E. G. Schachtel, 1959), and hence for all species, any exogenous Zeitgeber can only be sensed in an autocentric mode. An experiment exists (J. R. Cannon et al., 1976) which affords some support to this premise.

Newborn quokka exhibit a negative geotropic response, by means of which gravity is utilised as the sole navigational aid. Since, at birth, their vestibular apparatus is still undifferentiated, the authors suggest that a righting reflex is involved, making the animal negative geotropic. This reflex may be mediated by muscle stretch receptors, particularly in the neck, and had disappeared in 65–70 day olds. Such tropic behaviour not only underlines Schachtel's categorisation of autocentric behaviour, but also brings into focus the replacement of an autocentric by an allocentric response (cf. M. Lewis and J. Brooks-Gunn, 1979, p. 243). It further underlines, and reminds us, that the vestibular apparatus is not the sole sensory system from which information concerning our Spatial Reference Frame is utilised, but that additionally there are those sensory systems, namely the stretch receptors in muscles, and stretch receptors in joints, which aid in the maintenance of static equilibrium (G. J. Tortora and N. P. Anagnostakos, 1975).

Attending to stimuli has been classified by Hernandez-Peon into sensory and intellectual activity (R. Hernandez-Peon, 1966), which mimicks Schachtel's distinction, where the sensory attention is equivalent to an autocentric experience. Such sensory attending is involuntary, passive, reflexive and externally elicited. Because of this, and not being "ruled" by schemata, autocentric experiences tend not to be remembered, or, at best, are hard to describe (E. G. Schachtel, 1959). A notable example of this is the vibrations of the head being linked to the cardiac cycle, particularly the carotid pulse (T. Gualtierotti, 1971), movements of which are well within the threshold of detection, and yet subjects found hard to describe. Since such vibrations affect the visual system, they must be compensated for reflexively to preserve a steady signal. Changes in carotid pulse rate will induce equivalent changes in the frequency of head vibrations, thus clarifying that even if the brain treats such vibrations as "noise", it is still an autocentric experience since a "steady" visual image is maintained, despite changes in head vibrations. Perhaps, using Freudian terminology (cf. N. Birbaumer, 1975), an autocentric experience is not so much a sub-conscious, but a pre-conscious experience.

2.2 Reticular formation

Whatever the terminology adopted, it appears to be a fact that autocentric experiences are directly controlled by the Reticular Formation (R. Hernandez-Peon, 1966). Furthermore, since the Spacial Reference Frame seems to be deduced from at least two, if not three, gravity sensing systems, a multi-sensory information organisation is precluded. Multi-sensory information integration exists within the CNS not until the Reticular Formation (N. Birbaumer, 1975). Hence, again, the Reticular Formation is implicated.

Having posited the Reticular Formation to be involved in the autocentric experience of gravity sensing, it arises that if a stimulus attains importance, then conditional attention is facilitated by attention to it being enhanced by the Reticular Formation. This tends to be reflected by an increase in potential amplitude (N. Birbaumer, 1975), and is somewhat analogous to Broadbent's filter model (A. Treisman, 1967).

Supplementary evidence exists (see N. Birbaumer, 1975) that filtering, or inhibition, of irrelevant material occurs at still higher levels, and may not occur until reaching the cortex. More important, attention to a sensory experience precludes the participation of the Arousal I system from Routtenberg's Two-Arousal Hypothesis (A. Routtenberg, 1968). The occurrence of a response (approach/avoidance) is probable when the Arousal I system is active. Since the two arousal systems inhibit each other reciprocally, there is a dynamic balance between the two systems. Thus inhibition of the Arousal I system (Reticular Formation) is characterised by hippocampal theta activity. While the Arousal I system reflects the expressiveness of drives, the Arousal II system is a reinforcement-motivated system through which drive reduction is attained (i. e. reciprocal inhibition exists). This switching between the two arousal systems by reciprocal inhibition, is, no doubt, the biocybernetic gate alluded to earlier (H.-G. Tittmar, 1978), the closure of this gate being typified by hippocampal theta activity (Birbaumer has postulated that alpha acts as a barrier to incoming insignificant stimuli, N. Birbaumer, 1975).

Activation of the Arousal I system is indicated by hippocampal beta activity (gate open). Hippocampal beta activity is present with automatic and organised activity as in the execution of habits. (In contrast, Arousal II dominates in the planning and preparation of active behaviour). The modulation of the two electrophysiological cortical reactions result from a complex interaction between cortical analytical- and storing systems, and subcortical activating and inhibiting structures (N. Birbaumer, 1975). The following working hypothesis has been developed and is described by Birbaumer. An incoming stimulus is transmitted within milliseconds to a localised cortical area, where the stimulus pattern is compared with a simple neuronal model (Sokolov, 1963) of earlier inputs. This comparison is, no doubt, non-conscious, and if a mismatch arises, this will lead to corticofugal activation of the Reticular Formation, which, in turn, activates the cortex (arousal). Only then, more complex models from stable memory circuits may be incorporated into subsequent comparisons. If the mismatch still persists, the (re)orientation response is evoked. The activated cortex is thus a precursor for reaction. This preparative phase is characterised by alpha free intervals and a desynchronised spontaneous EEG, both of which seem to allow a greater degree of attention. Also, if at this stage the integrating mechanism is preparing the whole body for a response, it must "know" the body's attitude. A positive response by the organism to a gravitational stimulus (as in reorientation) leads to corticofugal activation of the limbic systems (hippocampal theta emerges), which, in turn, inhibits Reticular Formation activity (Arousal II dominates), shown by EEG synchronisation (consolidation) and facilitating the storage of S-R event. Reorientation results (Arousal I steering a routine task), to be followed by Arousal II for evaluation and consolidation. Thus periodic updating of neuronal models (as opposed to schemata) is attained. A more explicit expression may be derived from Birbaumer's discussion of stimulus processing (N. Birbaumer, 1975), from which it may be deduced that matching between stimulus and neuronal model will produce immediate consolidation.

3 Implications from arousal theory

It arises, that the orientation mechanism described here involves semi-reflexive behaviour patterns, reflexive ones, and also cortical areas. Since not all species have evolved the cortex, and even those that have, may, in the infantile stage, act reflexively (e. g. newborn quokka – J. R. Cannon et al., 1976), even for complex (human) social behaviour patterns (M. Lewis and J. Brooks-Gunn, 1979), then autocentric experiences imply a subcortical system of neuronal models. Since many of the basic diurnal rhythms are largely representive of autonomic functions, synchronisation of the same has to be at the subcortical level. Thus, the medial hypothalamus seems implicated along with the Arousal I system.

From these assumptions several observations arise, which may be utilised as foundations for testing these assumptions. During a vigilance task, beta and theta may predominate; i. e. Arousal I and II oscillate. External stimulation is only recalled when alpha or beta activity is prominant.

Acoustically evoked potential can be recorded in all sleep stages and may increase three to four times in amplitude during sleep stages two and three. During stage two, low beta activity with spindles predominates. Such increased amplitude may be caused by inhibited inhibition, or by amplification.

Since the gravitational stimuli are essentially a "steady" signal, its encoding may be altered to that of a summed potential, which, of course, will reflect in an increase in evoked potential amplitude. Indeed, is this what spindles are? For the enhanced acoustically evoked potentials found by Weitzman and Kremen, 1965 (shown in N. Birbaumer, 1975) approximate to the EEG spindle pattern. Are the spindles, therefore, an expression of the Zeitgeber stimulus having leaked through the beta gate? If so, this may preclude the occasions when any such message is decoded, and therefore becomes open to experimental verification.

4 Discussion

Additional structures implicated in gravity sensing are those through which proprioceptive information has to pass, namely the medulla and pons, being part of the Reticular Formation, and the cerebellum. Indeed, it may be that autocentric experiences may incorporate, and reach as far as the cerebellum, whereas allocentric experiences always involve the cerebrum. Bünning (E. Bünning, 1973) quotes Brady (1971) as saying that locomotory rhythms are stopped by lesions between the optical lobes and the brain, or between the brain and the thorax. While Brady's argument does hinge upon experimental evidence (that of J. Nishiitsutsuji-Uwo and C. S. Pittendrigh, 1968a, 1968b), others have assumed the subesophageal ganglia in the cockroach to be the mantlepiece for the master clock (J. Harker, 1960), while the corpora allata has been implicated in insect studies (V. B. Wiggelsworth, 1950). It is true that lesions, e. g. in the cerebellum, may grossly interfere with postural and/or movement functions (asynergia), but complete cerebella removal appears to produce less disturbance (S. W. Ranson and S. L. Clark, 1959). With partial removal, not only seems there to be an imbalance between signals set up within the cerebellum, but it itself is now in imbalance with its associated structures, such as the inferior olivary nucleus and cerebellar peduncles, and their subsequent connections.

Implied is that not only is proprioception a multi-channel system, but also involves a multi decoding system. A mismatch between sensory channels may lead to disorientation, and, at its worst, travel/motion sickness (J. Reason, 1974). A mismatch between sensory decoding may lead to faulty orientation. Thus, no single clock location is proposed, but, and previous studies are not at variance to this, that subsidiaries of the Arousal I system and its associated autonomic regulatory structures are all integrated with one another.

Several advantages accrue. If one structure (Clock) is damaged, the others can maintain the correct time. If one runs fast, or slow, it may be reset by the remainder on a majority deductive principle. A gross analogy to the second property exists in the Space Shuttle computer system (R. Edgar, 1975), where three computers have to be in agreement before a decision is implemented.

It may be concluded that gravity, as a Zeitgeber, operates as an autocentric sensory experience, which, if being attended to, is measured during hippocampal beta activity. Since beta activity is not continuous, a gated sensing mode is implied. Postulated is a multi centre integrating and synthesising system, which acts as an elaborate system of homeostats. A necessary consequence of sensing an exogenous synchroniser is that the organism is not sensing a signal per se, but fluctuations in background noise. It should also be appreciated that while the argument here is based upon gravity as a synchroniser, other exogenous synchronisers are not excluded. Indeed, not only would the same mechanism be inherent, but by adding additional sensory channels, e. g. light, temperature, the multi logic decision system may become enhanced.

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