HOW THE HIERARCHICAL ORGANIZATION OF THE BRAIN AND INCREASING COGNITIVE ABILITIES MAY RESULT IN CONSCIOUSNESS

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Abstract

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Defining perception, awareness, consciousness and reflexive or self-reflexive consciousness is difficult. I will not linger on definitions of fuzzy concepts but will attempt to put forward evidence for the rationale that awareness is likely to emerge as a consequence of how the brain processes information. Efficiency in information processing has resulted in a limited number of preferential (motivational) states of the brain and, in fact, of the whole organism. In addition, animals have the ability to internally represent external conditions and, through interactions with the motivational state, generate expectations.

It is argued that optimal decision-making requires that possible sequences of behaviours each activate their associated neuronal networks representing cue- and context-related information. Prior to the initiation of an action, the consequences of each possible scenario are estimated. An efficient animal must have the ability to anticipate, weight and choose. This weighting occurs at a hierarchically higher level and results in signals which possess a coordinative function in activating the appropriate motivational state, response selection, activation of associated networks and maintenance of attention.

Higher cognitive executive centres perceive and recognize such signals and integrate ongoing behaviour with internal representations about the past and expectations within the context of the signal induced state. Humans experience these simultaneously-occurring processes as awareness. The nature of the subjective experience may vary from an emotional state to reflexive consciousness depending on the cognitive abilities of the species and the stage of development and the level of arousal in the individual.

Keywords: *animal welfare, anticipation, attention, awareness, efficiency*

Behaviour is efficient

Living animals in general, and vertebrates in particular, have achieved a remarkable efficiency in using environmental resources and avoiding potentially harmful stimuli and situations. Behavioural ecologists (see Krebs & Davies [1993] for a review) have captured such efficiency in models which are partly derived from and related to the field of human economics: the relationships between the investment of an organism on the one hand, and the consequences of its actions on the other, can be represented by equations used in or derived from micro-economic theories in terms of costs and benefits (economy of behaviour: eg Dawkins [1988, 1990]; Houston [1997]; Mason *et al* [1997, 1998a, b]). For instance, food items are collected by many animals in such a way that a minimum amount of energy is spent to get a maximum benefit (see Krebs & Davies [1993]; McFarland [1993]).

It should be noted that these studies have predominantly been focussed at the level of function or ultimate causation of behavioural patterns. However, here I will outline those principles of brain behaviour organization which reveal something about the proximate causation of this efficiency.

I will not unequivocally prove consciousness from organized neuronal systems, although I will put forward evidence that an efficient brain must contain supervising systems which receive the signals of lower levels of analysis. The brain has the capacity to evaluate various scenarios as a response to certain events and then make an optimal choice. It uses signals representative of the internal state and external conditions.

In general, the following cognitive abilities are required to solve issues of efficiency:

i) the ability to estimate the 'cost:benefit ratio' prior to or during the activation of a given motivational system and take its actual state and previous experience with the commodity into account (*maximizing profit of ongoing behaviour*); and

ii) the ability to solve conflicts between motivational systems (*setting priorities for ongoing behaviour*).

Thus, the animal must be able to monitor its own status with respect to a certain commodity and it must be able to assess the value of this commodity using previously acquired knowledge and taking into account the energy it requires to collect it.

Both for assessing the cost of obtaining a certain commodity vs its value, and for comparing different commodities belonging to different motivational systems, items of different dimensions (food, water, social contact, safety, etc) have to be compared.

Emotional states: an old way of information processing

Preferential states

If the question of whether animals have emotional states such as anxiety, euphoria, etc is raised, the answer is usually yes. Such states are characterized by a coherent set of behaviourally and physiologically integrated responses which each apply to a broad, but specific, category of environmental challenges. For instance, danger, whatever the nature, requires a certain number of responses which are relevant to all potentially aversive stimuli, eg enhanced attention, increased heart rate and blood pressure, etc.

The necessity to be able to react promptly to a variety of stimuli – for instance, dangerous stimuli – with a common set of responses promotes the likelihood of pre-programmed (genetically anchored) concerted actions by different functional units of the central nervous system (CNS).

Emotional states are defined as those concerted actions which must be readily elicited by, usually, external signals and mediated by internal signals: subsequently these internal signals have an organizing effect on other brain structures, including cognitive structures, and induce an internal state. Emotional states may thus be indirectly recognized by observing behavioural patterns and by the presence of internal organizing signals (hormones, releasing factors, neuropeptides, etc). In particular, stress and reward systems seem to have such signals, which coincide in humans with subjective experiences such as the (in)ability to experience pleasure – (an)hedonia. If such states have an organizing effect by integrating physiological (autonomous) and behavioural aspects to give the final response – including cognitive functions – this implies that emotional states affect cognitive centres in such a way that relevant information for a specific state is stored and retrieved in association with such a state.

There is abundant evidence that learning is influenced by the emotional state of the animal (state dependent learning). In addition, it is known that the internal state of an animal can be used as a discriminative stimulus. An animal can be trained to recognize its own emotional state such as anxiety, euphoria, etc. These techniques have been used extensively for studying the subjective effects of potential medicines, for instance the detection of possible addictive (unwanted) properties of medicines (Andrews & Stephens 1990; Colpaert 1995; Van Ree *et al* 1999).

Anxiolytic, addictive or antidepressant properties of drugs can be, and have been, identified in this way because the animal recognizes them and can be trained to perform a certain behaviour to indicate the internal state that has been induced by the drugs (drug discrimination).

Theoretically, it would make no sense if an animal could not recognize its own state, as acquired knowledge has to be integrated with other levels of information processing especially when this processing occurs in parallel. This recognition is no proof of awareness, but it shows that brain structures involved in the final response selection not only integrate cue- and context-related information in the response, but also the emotional state.

The above-mentioned states bear similarities to motivational systems which refer to a coherent set of behavioural and physiological reactions dealing with a specific need of the organism. A motivational system can be defined as a set of behavioural patterns which are activated by a certain class of (internal) stimuli and deactivated by specific events or behavioural patterns: they can be described as feedback systems (Wiepkema 1985; Hughes & Duncan 1988; Jensen & Toates 1993, 1997; Jensen 1996). For example, the search for food (appetitive behaviour) can be triggered by an internal condition (a lowered blood glucose level or an altered leptin level, which is representative of the metabolic state of the individual), after which food consumption leading to increased levels of blood glucose and leptin will terminate the activation of the system. Every response which diminishes the difference between the actual (the current state) and the expected (genetically or ontogenetically determined reference) state can be regarded as having a rewarding property (pleasure; positive affective state) and will reinforce ongoing behaviour: failure to diminish this difference is defined as having no rewarding property (displeasure; stress; negative affective state) and will lead to the termination of ongoing behaviour and a search for alternatives (Wiepkema 1985; Jensen 1996; Fraser & Duncan 1998).

Food or water deprivation will induce hunger or thirst depending on the motivational system involved. More intense deprivation of food or water induces anxiety in both cases, because both forms of deprivation imply loss of control. Some states may reflect common characteristics of other underlying motivational systems at a higher level. Success and lack of success in obtaining a commodity or meeting a challenge are such common characteristics and may activate reward and stress systems, respectively.

The brain: a hierarchically organized set of parallel feedback systems

The main function of the brain is to control the internal and external input (sensory information) by regulating behavioural and physiological reactions (controlling the output). In the hierarchical organization of the brain, higher structures receive input from lower structures and each layer generates output aimed at maintaining the input within certain reference signals (Powers 1973). Hierarchically organized systems with parallel information processing mean that different features of incoming stimuli can be processed separately and simultaneously.

The results of these separate processes must eventually be integrated into a final response. Quick responses can be generated by reacting to specific features from the input, inducing a state relevant for those features which limits the number of possible reactions and facilitates a prompt reaction. For instance, autonomous, emotional and cognitive aspects seem to be processed parallel to each other before being integrated into a coherent response.

As mentioned above, different motivational systems may be interfaced at a higher level with more general systems that monitor their status in terms of being in or out of control. A motivational system for which the actual state does not fall outside the expected state is in control. A comparison of different motivational systems along the same dimension is possible if reward systems are positioned at a hierarchically higher level than motivational systems. Reward is then defined as a reduction in the difference between the actual and expected state of any motivational system. Of course these latter states are represented by physiological signals.

The reduction of the difference between an actual state and the expected (reference) state must be estimated prior to the execution of any action. This expected reduction in the difference between the actual and expected state results in the activation of a reward centre or centres and subsequently in the display of appetitive behavioural patterns; at least if costs do not exceed benefits, ie when a profit remains. Aversive stimuli increase the difference between the actual and expected states and will suppress such activation (distress).

To accomplish a comparison of various cost:benefit ratios, it is sufficient to compare the *degree* to which the difference between an actual and expected (reference) state can be reduced irrespective of the *nature* of that difference. When a decision has to be made as to which behavioural system is to be activated, the ability of each motivational system to reduce the difference between the two states pertaining to that system has to be compared. I argue that, to rank the expected consequences of behavioural responses that are different in nature (for instance eating vs drinking), it is essential that the consequences be translated into a common currency. Studies on humans and rats show remarkable similarities in the organization of behaviour, and the human verbal ratings of pleasure strongly indicate that 'pleasure', or whatever the animal equivalent should be called, is this common currency. Such a common currency could be the activation of reward centres by each motivational system. (Cabanac's maxim [Cabanac 1992; Balasko & Cabanac 1998]: 'pleasure is the common currency').

Thus, each motivational system has not only specific physiological consequences for initiating and finishing activities aimed at a specific goal (as already mentioned, blood glucose or leptin levels may determine whether food consumption will be started, continued or ended) but there must also be common consequences, which allow the comparison of metabolic state vs osmolality state, or hunger vs thirst.

If both systems also measure the degree of pleasure ('satisfaction'), then they allow the comparison of the common currency at a higher level by a structure which is connected to both motivational systems. Thus, the internal state of motivational systems and the costs they require in a given situation to satisfy them must be weighed in order to set a priority. Such evaluations are normally taking place continuously because of the continuously changing internal physiological environment and the continuously changing external environment resulting from external events or activities of the animal itself.

I assume that the motivational system with the largest possible reduction in its actual vs expected (reference) state, in comparison to the effort it requires to achieve this reduction, acquires or maintains control over behaviour.

An efficiently behaving animal is an anticipating animal

Economy of behaviour requires that the rewarding properties of an activity to be executed are estimated beforehand and that costs vs profit must thus be estimated a priori. This is exactly what most animals demonstrate: they display anticipatory behaviours when a reward is announced (also when an aversive stimulus is announced). It is proposed here that 'anticipatory behaviour' includes general characteristic behavioural patterns such as short abrupt movements and enhanced activity as well as incomplete and accelerated displays of exploratory behaviours. Anticipatory behaviour is thus characterized by general motor excitement, and orientating and searching behaviour patterns (Konorski 1967): for example, rats become alert, groom and are highly active (Schallert *et al* 1982). The distinction between preparatory behavioural patterns and consummatory behavioural patterns bears similarity to the distinction between sign tracking and goal tracking in appetitive classical conditioning (Davey *et al* 1982; see also literature on autoshaping cited in Cleland and Davey [1983]).

Anticipatory behaviour may be defined as a maintained state of attention elicited by environmental challenges – possibly rewarding stimuli – leading to and facilitating consummatory behaviour. Although the distinction between appetitive and consummatory behaviour is not clear-cut, it has proven to be useful in ethological (Tinbergen 1951; Eibl-Eibesfeldt 1975), neurobiological (Sherrington 1906; Wilson & Soltysik 1985) and theoretical analyses of behaviour (Zernicki 1968). These two categories of motivated behaviour differ substantially in several dimensions. Consummatory behavioural patterns can be readily identified and described. In contrast, anticipatory behavioural patterns are more flexible and sometimes have less immediate objectives.

Anticipatory behavioural patterns are not completely invariable, apart from the common general characteristics (Jenkins *et al* cited in Davey *et al* [1982]). They also depend on the modality of the conditioned stimulus (eg visual vs auditory [Cleland & Davey 1983]).

The neural substrate underlying anticipation

The analogy between economics and the principles underlying the organization of behaviour (investing is anticipating, consuming is collecting the commodity which is paid for) is not limited to behaviour, but can also be found in the organization of underlying neural structures.

The distinction between these two behavioural systems (anticipation and consumption) both in time and in function becomes clearer by considering apparent differences in the underlying neural substrate. Dopaminergic systems have been proposed as a neural substrate of incentive motivation (Crow 1973). Dopamine antagonists and the destruction of dopaminergic cell bodies selectively suppress anticipatory behavioural patterns while leaving consummatory responses intact (Blackburn *et al* 1989). From previous studies it has become apparent that an elevation in locomotor activity is often seen prior to circadian food delivery (Hooks *et al* 1994) and prior to sexual contact in a cage with different floor levels (the bi-level box; Pfaus & Phillips 1991; Balthazart *et al* 1995). This elevation in activity has been interpreted as anticipatory behaviour. It is this enhanced activity that is defined as characteristic for the forthcoming reward. The ventral tegmental area is the source of dopaminergic innervation of the ventral striatum and the frontal cortex. Opioids modulate dopaminergic activity, have been implicated in all motivational systems and have been described as counteracting stress-induced activity (Hayden-Hixson & Nemeroff 1993).

These two systems together form the neural substrate of reward (and addiction) and their complex interplay and the plasticity of their respective receptor (sensitivity and tolerance) systems are crucial for evaluating ongoing behaviour. Elasticity in price – what the animal wants to do for an incentive – may somehow be related to sensitivity/tolerance of reward centres or even to underlying receptor systems in the mesolimbic brain structures.

Anticipation requires the ability to internally represent expectations

Behavioural patterns revealing the intensity of anticipatory behaviour may not be the only relevant tools for assessing the animal's perception of environmental demands and commodities: in addition, operant techniques may be, and have been, applied for this purpose. Providing animals with resources and ranking them based on what the animal is prepared to pay (do) in order to obtain them has been proposed by Dawkins (1988, 1990) as a means of assessing the animal's motivational state and, indirectly, its welfare. At a behavioural level, elasticity in demand, prices, necessities and luxuries have been described and used in experimental settings, preferentially in a closed economy (Mason *et al* 1997, 1998a, b). Consumer demand approaches have been recommended and applied, for instance in studies on hens (Faure & Lagadic 1994; Cooper & Appleby 1995) and pigs (Matthews & Ladewig 1994; Ladewig & Matthews 1996). The measurement of anticipatory responses is complementary to operant techniques. If an operand is the price the animal pays for a commodity, then the anticipatory response reflects the willingness to pay.

In an experiment on anticipation, the focus is on the phase preceding the operant and consummatory behaviour. In fact, paying can be skipped when the incentive is provided without paying a price or when the incentive is not actually given, but close contact with the incentive is provided. For instance, when one wants to measure the need for social interactions, a conspecific can be provided behind bars so that interactions cannot take place but 'access to' is allowed. This prevents consummatory responses affecting the rewarding properties. The fact that similar anticipatory activity is observed for different incentives provided indicates that the display of enhanced activity reflects the state of the animal rather than properties of the incentive.

Another practical difference is that consumer demand approaches when operant responses are measured have to be conducted in a closed economy situation, where the price for all commodities can be assessed and compared (Mason *et al* 1998a, b), whereas an anticipatory response can be elicited in the home cage. The fact that operant techniques reflect so clearly the efficiency of behaviour means that ongoing operant behaviour is continuously evaluated.

Thus, the activities leading to collecting a reward, from the moment it is anticipated to actually conducting the necessary behaviours to obtain it, requires a continuous evaluation of progress. This implies that the internal representations of the own state and the representations about the goal and the series of actions leading to the goal have to be maintained. In order to integrate cue- and context-related information into the programming of behaviour, environmental stimuli have to be analysed to retrieve information stored about them or to assess novelty. This requires complex attentional processes and comparisons of the environment with stored information.

The role and function of reward centres and mechanisms underlying attention are phylogenetically old and seem to be present in all vertebrates.

Emotional states, attention and cognition together form the template for awareness

Monitoring ongoing and already performed behaviour is a necessity for organisms that have the ability to learn and adapt. This ability is a prerequisite for economic behaviour. The more the CNS has the capacity to internally represent sequences of behaviours resulting in a specific goal and to evaluate them a priori with respect to their consequences, the more efficient behaviour will be. Cues and context can be associated with aversive or rewarding properties and may activate these centres to enable evaluation of behaviours associated with these cues and within a particular context. How much, and over what time-span, planned behaviours can be evaluated by reward centres strongly depends on the cognitive abilities of the animal.

Anticipation supposes selective activation of neuronal nets representing cue- and/or context-related contents and integrates this in the final response. As already explained, the execution of a response in relation to the environment must be evaluated a priori. An animal anticipating a reward or a challenge is doing this. Thus, a state of selective attention is observed prior to choosing a response, during which all relevant information is retrieved. Not only must a goal be chosen, but also the most efficient way of achieving this goal. Decision-making requires that sequences of acts must be composed and evaluated, adapted, re-evaluated, etc. This requires the internal representation of the own state, position in space and time and maybe even the position in relation to others (socially). Internal representations of the own state have to be combined with a number of possible actions that can be performed.

This combined set of activated neuronal networks is then evaluated. This process requires advanced cognitive abilities, including memories, that can be accessed at any time in an associative way. If behaviour is defined as a continuous stream of actions, and if this ongoing behaviour maintains a high degree of efficiency, then a continuous stream of behaviour must continuously activate neuronal networks representing the own state, acquired relevant knowledge and possible behavioural scenarios. Activation of networks representing the own state have to be maintained and combined with alternative networks representative of different behavioural options (see also Singer [1998]). Such a process of activating neuronal networks of which some (representing the own state) are more permanent than others (different responses) and evaluating the consequences inevitably requires maintaining their activation over time.

The role of maintained attention for awareness has appeared from experiments on trace conditioning, which involves inserting a time gap between a conditioned stimulus and the unconditioned stimulus in a Pavlovian procedure. Clark and Squire (1998) have shown that only subjects who became aware of a simple relationship between a tone and an air puff could learn the relation. Interestingly, animals can also be trained according to a trace-conditioning paradigm (Clark & Squire 1998).

In order to detect relationships between environmental stimuli, animals also have the ability to internally represent those stimuli for a while in a way that in humans coincides with awareness. The hippocampus appears to be pivotal for selecting and supervising what should be attended to and has been assigned a role as supervisor, comparing incoming information with what is expected and thus detecting novelty: it therefore has a role in memory (Eichenbaum 1999). Although no specific brain structure can be pinpointed as the sole centre of awareness, human consciousness has been related to, for instance, inferior temporal lobe (see Taylor [2001]) and prefrontal cortex for its capacity to capture and evaluate numerous possibilities in order to plan behaviours in time. Differences in such structures between different vertebrates are gradual.

To restrict the number of options that have to be evaluated, motivational states may limit the number of possibilities by their organizing effect on associative networks. In a particular motivational state, only relevant associations for that state are retrieved. A further reduction in time-consuming analyses can be achieved by ensuring that this only takes place when a challenge (unexpected event) is met. This is in agreement with the general notion that reward centres are only activated when challenged.

It is also in line with the notion that arousing stimuli affect the degree of attention and, subsequently, awareness. In this context, individual variability in awareness is often illustrated by describing differences between a highly active state of arousal and the various stages of sleep. Humans experience a lack of clarity of consciousness during dreams. They can be very vivid and emotional but often lack appropriate context and self consciousness and can be described as a stream of scenes or images with emotional reactions. Maybe the world of an animal with fewer cognitive abilities is comparable to such experiences.

Anticipation in animals can be maintained for minutes or even longer when confronted with a challenge. It requires a certain level of attention, the presence of signals representative of reward or aversion, and the activation of networks linking the past to what is to be expected. Thus, anticipation, decision making and evaluating are not continuously going on at the same level. Likewise, the quality and the intensity of activity of hierarchically higher neuronal nets, especially those representative of the own state, depend on the nature of signals representing different states. This complex description of what could be going on concomitantly with every change in behaviour initiated could be the description of the underlying neural substrate of a variable stream of experiences.

Humans experience these simultaneously-occurring processes as awareness. The nature of the subjective experience may vary from an emotional state to reflexive consciousness depending on the cognitive abilities of the species and the stage of development and the level of arousal in the individual.

I define awareness as the result of cognitive abilities operating simultaneously at different levels. The inevitable selection from a vast number of possibilities requires an organizing function. This appears already at the level of motivational systems, which affect stress, and reward systems, which then affect higher brain functions.

Animal welfare implications

If the anticipatory state reflects, amongst other things, the need of an animal for an incentive, then this offers an approach to welfare from the perspective of the animal. If anticipation coincides with enhanced attention and activated reward or stress centres, it appears to be an appropriate moment for the presence of a sort of subjective awareness of the animal's own state. It also appears to be the appropriate moment to address an animal when one wants to assess its state in terms of welfare. Although in this paper the emphasis has been on reward, it should be emphasized that, likewise, aversive stimuli induce anticipatory responses and accompanying states.

The intensity and quality of subjective experiences, in terms of awareness or consciousness of animals, is relevant for the moral rules that are applied concerning animal welfare. In that context, the question of whether consciousness can be attributed to animals is often asked. Although even invertebrates have the ability to form simple associations, I have emphasized here that the hierarchical structure of information processing results in states representative of the appraisal by the animal of its external (and also internal) conditions. I also propose that emotional states such as anxiety and satisfaction have an organizing effect on the brain: they can be associated with cues or context and can be recognized by the animal as an important factor governing behaviour. It is this interaction between information processing at an emotional level, mainly dealt with by limbic systems, and the resulting signalling of these structures to higher cognitive structures with the ability to remember and expect that gives rise to forms of subjective experiences. Primates may even recognize such states in other individuals and react accordingly.

In my opinion, if the presence of subjective experience is a decisive argument for animal welfare issues, then animals which have all the necessary hardware and which show signs of knowing their own state should be treated with care. The assignment of subjective experience as the logical consequence of the main principles of brain functioning implies that welfare is not equally important across all animal species. It is suggested that the differences between vertebrates are not so much determined by essential differences in brain functioning, but rather as a result of differences in the contents of networks in what can be represented about the past and the future.

This implies huge differences in quality and intensity of subjective states which should be taken into account and which have consequences for the degree we consider the welfare of different species. This implies, for instance, that the welfare of primates deserves more consideration than that of fish, although the welfare of the latter cannot be neglected.

Theoretically, subjective experiences are not the sole privilege of mammalian brains. In completely different hierarchically organized decision-making systems that have to integrate past experiences into optimal choices for expected events, a development of similar phenomena cannot be excluded.

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