General Organizational Principles of the Brain as Key to the Study of Animal Consciousness<1>

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ABSTRACT: In this paper a framework to study consciousness in animals is proposed which is based on (i) a hierarchical organizational feedback model of the central nervous system, (ii) the separation of a given mental state into two components, i.e. an invariant part, and a variant part, which are separately related to the organization of the central nervous system, i.e. 'a neural network' and 'momentary active connections within the neural network determined by in- and output of this neural network' respectively, and (iii) phylogeny based on the invariant part or the presence of a neural network. Consciousness is defined as a property of neural networks of self-organizing systems dedicated to dealing with rapidly changing environments affording flexibility of behavioural patterning.

1. Introduction

Consciousness is one of the most intriguing, hotly debated and elusive phenomena in science. Especially so when consciousness is discussed in the context of the study of animal behaviour or in the context of animal ethics (see, e.g., volume 1 of the series

Animals in Philosophy and Science, edited by Dol et al. 1997). As Tinbergen made clear in his 1951 classic *The Study of Instinct,* ethology as a (natural) science cannot deal with consciousness or mental states (see Van den Bos, 1996, 1997). In this respect ethology followed the methodological tradition of comparative psychology, i.e., methodological behaviourism. Although Tinbergen clearly saw that study of the central nervous system could contribute to the study of animal behaviour, i.e., neuro-ethology, he was silent -- for whatever reason -- about the role of the study of the central nervous system in the study of consciousness or mental states, even in humans (Tinbergen, 1951). Yet, it is exactly through study of the central nervous system that the study of consciousness may find its footing in ethology and -- for that matter -- in the study of humans as well, i.e., in psycho-neuro-ethology (Van den Bos, 1997). To substantiate this let us consider the following experiment which appeared in a recent issue of *Science* (1998, vol. 280, pp. 77-81).

2. What Brain Research Tells Us About Consciousness

In this issue of *Science* Robert Clark and Larry Squire published the results of a classical Pavlovian conditioning experiment in humans. Two different test conditions were employed both using the eye-blink response to an air puff applied to the eye but with different temporal intervals between the air puff and a preceding, predictive stimulus (a tone): in one condition the tone remained on until the air puff was presented and both coterminated (delay conditioning); in the other a delay (500 or 1000 ms) was used between the offset of the tone and the onset of the air puff (trace conditioning). In both conditions experimental subjects were watching a silent movie while the stimuli were applied and questions regarding the contents of silent movie and test conditions were asked after test completion.

In the delay conditioning task subjects acquired a conditioned response over 6 blocks of 20 trials: as soon as the tone appeared they showed the eye-blink response before the air puff arrived. This is a classical Pavlovian response in which a shift is noted from reaction to action, also known as specific anticipatory behaviour. This shift occurred whether subjects had knowledge of the temporal relationship between tone and air puff or not: both subjects who were aware of the temporal relationship -- as judged by their answers to questions regarding this relationship after test completion -- and subjects who were unaware of the relationship learned this experimental task. One could say that this type of conditioning occurs automatically, reflex-like or implicitly.

In contrast, the trace conditioning task required that the subjects explicitly knew or realized the temporal relationship between the tone and air puff. Only those subjects knowing this relationship explicitly -- as judged by their answers to questions regarding this relationship -- succeeded in performing the task; those that were not, failed. In other words, subjects had to be explicitly aware or have conscious knowledge of the task at hand in order to bring the shift about, that is, to respond after the tone and before the air puff. This is called explicit or declarative knowledge. Clark and Squire (1998, p.79) suggested that "awareness is a prerequisite for successful trace conditioning": (i) when explicitly briefed before trace conditioning about the temporal relationship between tone and air puff, all subjects learned the task, and faster than those without briefing; (ii) when performing an attention-demanding task, subjects did not acquire trace conditioning.

Interestingly, amnesia patients could perform the delay conditioning task, but not the trace conditioning task. These patients suffer from damage to the hippocampal formation or medial temporal lobe, suggesting that such an intact structure is a necessary condition for trace but not for delay conditioning to occur.

Now what do animals do in this task? Interestingly, the same difference in task procedure and effects of hippocampal lesion is found in, for instance, rabbits: intact rabbits acquire both tasks, hippocampal lesioned rabbits only the delay conditioning task (Clark & Squire, 1998; Wallenstein et al., 1998).

So, this would suggest that rabbits -- like humans -- are aware of the temporal relationship between the stimuli or have conscious knowledge of this temporal relationship and act on this. In other words, it would seem that a classical Pavlovian task might reveal aspects of awareness or consciousness in animals and "raise[s] the intriguing possibility that delay and trace conditioning could be used to study aspects of awareness in nonhuman animals" (Schacter, 1998, p.60; cf. Clark & Squire, 1998; see Van den Bos, 1997, for a review of how another classical task -- operant conditioning -- from another angle might prove fruitful in studying consciousness in animals).

The results of this kind of research fit in with the broader notion that the hippocampus is not involved in tasks requiring procedural or implicit knowledge, but is involved in tasks requiring declarative or explicit knowledge (Schachter, 1998); "this structure is involved most critically in learning and memory tasks in which discontiguous items must be associated, in terms of their *temporal or spatial positioning, or both*" (Wallenstein et al., 1998, p. 317; italics added). Finally, it would appear that this function is critically dependent on the function of the prefrontal cortex for its expression, as lesions in this area may block the occurrence of trace conditioning (see Clark & Squire, 1998).

Now what do these observations reveal? First, it is clear that a (cor)relation exists between (neural activity in) brain structures and (aspects) of consciousness in humans. Second, that such a relation might hold true in animals as well. How strong is this relation however in animals, and where does this lead to scientifically? An often used, straightforward, but minimal, approach is to apply the analogy postulate.

The scientific study of animal consciousness in this case reduces to the application of the analogy postulate, which is based on the following two premises: (i) the homology of brain-structures of humans and animals (the hippocampal-(pre)frontal areas) and (ii) similarities in behavioural patterns between humans and animals (delay and trace conditioning) in situations in which humans report conscious or explicit knowledge. These two premises make it plausible -- *and no more than that* -- that animals have such conscious explicit knowledge in such situations as well. This "ejective mentalism" (Romanes, 1883) does not bring us closer to the question of animal consciousness, however, for reasons which I have outlined elsewhere (Van den Bos, 1997).

The outcome of the postulate itself (either a "yes" or a "no" based on whether the premises apply) escapes by definition further scientific analysis, more specifically, *the question of animal consciousness itself escapes further scientific analysis.* It is only the premises -- comparative neuro-anatomy, similarity in response between human and animal behaviour, as well as the relation between response and consciousness in humans -- which are under scientific study and discussion. These premises are framed in terms of continuity in *degrees* of mind between humans and animals or in a *scala naturae* view of evolution (cf. Darwin's programme as worked out by Romanes, 1883, in the psychological domain; see Bermond, 1996, 1997, for a consequent application). However, as has become clear, such a view of (neuro-anatomical) evolution is false as it does not take phylogenetic relationships through common ancestry into account, i.e., a *branching tree* view of evolution (see, e.g., Hodos & Butler, 1996, and Preuss, 1995, for reviews). The *scala naturae* view compares presently living species directly and frames the results hereof in terms of higher and lower (developed) species. It misses thereby that species may -- indeed -- have evolved differently after their ancestral split but, at the same time, share certain features exactly through common ancestry. Accordingly, there is no universal yardstick against which to measure minds in terms of degrees. In fact, this opens the possibility that different *kinds* of mind may -- in principle -- exist in different species which could, however, still be based on similar organizational principles due to common ancestry (Van den Bos, 1997; Preuss, 1995). In order for animal consciousness to be studied scientifically I therefore propose the framework described in the next part.

3. Outline for a Study of Animal Consciousness

3.1. General

Recently, I have proposed a theoretical framework which consists of three different domains each encompassing organizational principles (Van den Bos, 1997): the psychological (or consciousness) domain comprising the organization of consciousness or mind, a neuronal domain comprising the organization of the central nervous system, and a behavioural domain comprising the organization of behavioural patterns. Each domains conforms to abstract rules of organization. Powers' (1973) notion that behaviour is the control of input (or perception; cf. Cools, 1985) in a hierarchically organized negative feedback system (an extension of Von Uexkuell's functional circles; Von Uexkuell & Kriszat, 1934) is the key element which binds these domains: behaviour is goal-maintenance of a self-organizing system or transitions of neural states (in organisms with a nervous system) expressed as changes in muscular activity -- visible as transitions of (arbitrarily delineated) behavioural patterns -- and changes in conscious activity -- transitions of (arbitrarily delineated) mental states visible in goal-directed behavioural patterns or intentional action (defined further below). In other words, behaviour expresses, or manifests, itself as transitions of behavioural patterns and mental states. More precisely, *consciousness* is the transition of mental states in the same sense as *motion* is the transition of behavioural patterns (cf. James's notion that consciousness is a process). Mind is defined as the sum of different classes of mental states and their interrelationship.

The hierarchically organized feedback system is subordinate to a reorganizing (motivational) system which deals with the physiology of the organism (critical systems for survival; see Van den Bos, 1997, for elaboration).

Reduction in this framework means a relationship between theories of organization in each domain or intertheoretic reduction (cf. Churchland, 1986): T_R (reduced theory) stands in a specified relation to T_B (basic theory). Accordingly, phenomenon P_R which is characterized by T_R can be reduced onto phenomenon P_B which is characterized by T_B. At present reduction of a theory (T_R) of the organization of consciousness (P_R: mental state) onto a theory (T_B) of the organization of the brain (P_B: neural state) is not within reach. Research has, however, shown *that* a relationship exists between mental states and neural states (activity in brain-structures); the *how* of this relationship is unclear. What follows in the next section is an attempt to search for a way to bridge the gap in the future.

3.2. Mental States and Neural States

Whereas all people may feel pain and adjust their behaviour thereupon, the feeling of pain itself may both vary within one's own life (depending upon previous experiences) and between different individuals (depending upon, e.g., different histories). Mental states therefore have two different components: they consist of an *invariant* part (symbolized as "shape") which is the same for all individuals of a given species and throughout one's life, and they consist of a *variant* part (symbolized as "contents") which is different for individuals of a given species and throughout one's life (upper parts of Figures 1, 2 and 3).

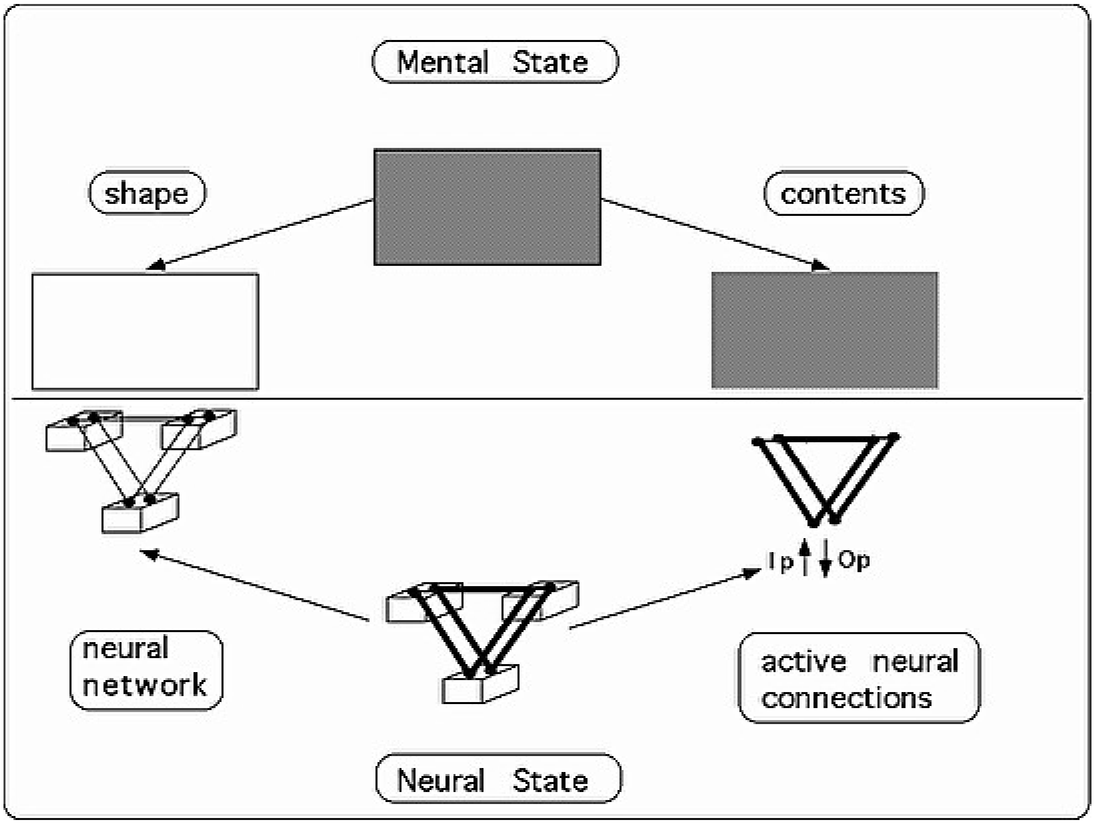

Figure 1

Relation between mental states (upper part) and neural states (lower part). Mental states have two components: an invariant part (left side, symbolized by "shape" (rectangle)) and a variant part (right side, symbolized by contents (patterning)). These are differently related to neural networks (left side, the neural network per se) and neural activity therein (right side, active neural connections within the network at a given time point depending on Input (Ip) and Output (Op) relationships). Blocks represent brain structures (or parts thereof), dots represent neural groups, lines represent active connections between neural groups of brain structures or parts thereof.

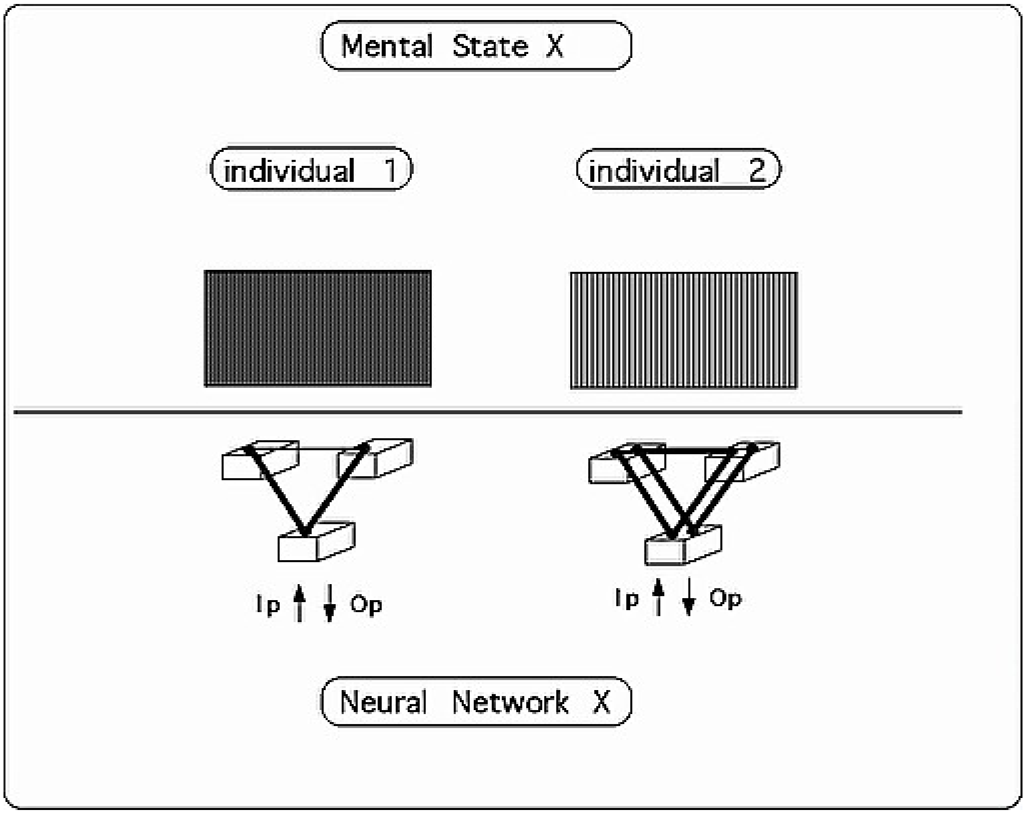

Figure 2

Difference between mental states and neural states of individuals: differences do not exist in the invariant component (the neural network per se) but in the activity of neural networks (symbolized by different neural groups and different active connections; only active connections are shown) dependent on (slightly) different input-output (Ip-Op) relations.

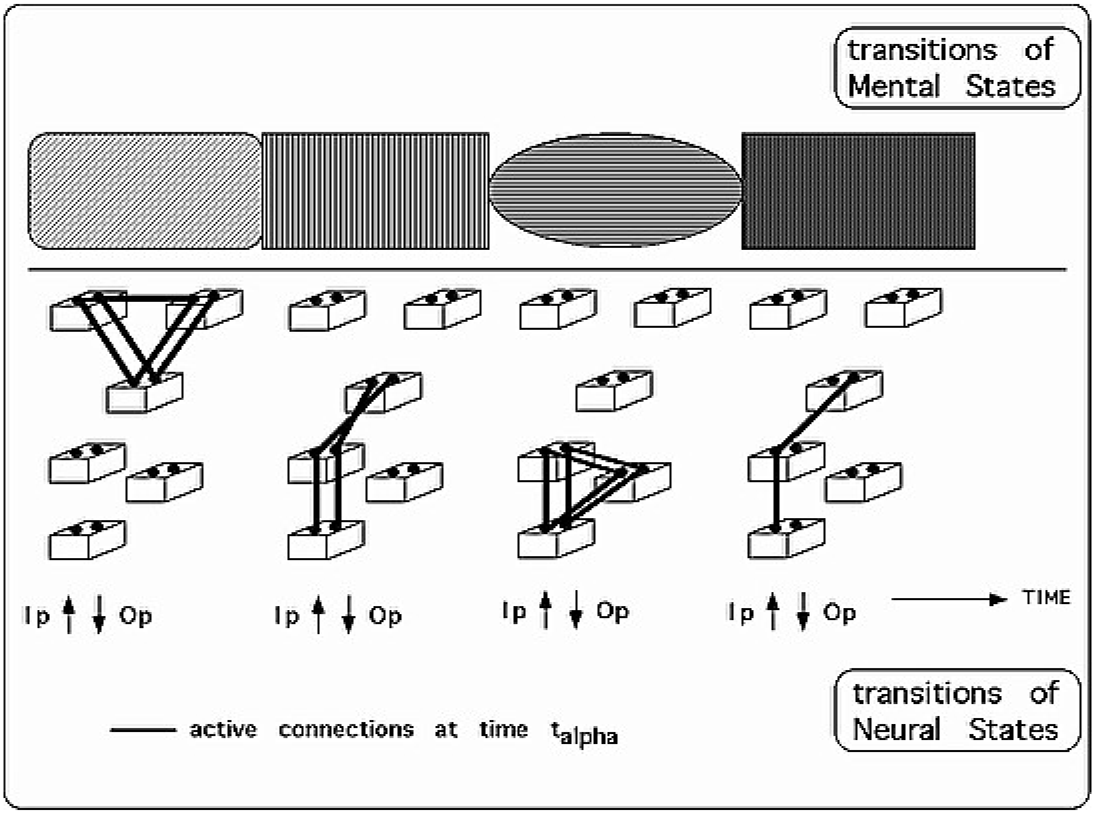

Figure 3

Transitions of mental states (upper part, consciousness) and neural states (lower part) or behaviour in a self-organizing system. Different classes of mental states are symbolized by different shapes, which are related to different neural networks. The contents of the same mental state may differ over time due to experience, symbolized by different patterning of the rectangle and different active connections in the neural network at different time-points. For sake of clarity only *active* connections at each time-point are shown.

So, in formal language: a given mental state, say MS^X, is characterized by two different components: (i) an invariant part, I^X, which as such is shared by individuals of a given species (*that* individuals have MS^X) *and* (ii) a variant part, V^X, a specific contents which is unique to each individual of a given species or at any point in one's life (*how* MS^X is of the individual), or $MS^X_{1..n} = I^X_{V1...n}$ with n the number of individuals or life-time points.

Given the foregoing, the relation between mental states and neural states is hypothesized to have two sides: (i) a relation between the *invariant part* of mental states and neural states *and* (ii) a relation between the *variant* part of mental states and neural states. The presence of a mental state is hypothesized to be dependent on the presence of a given neural network, i.e., (parts of) brain structures which are interconnected and form a functional unit (lower parts of Figures 1, 2 and 3). The specific contents of a mental state at a particular time point is dependent on momentarily active neural connections within the specific network and the information encoded in these connections (Figure 1). The encoded information is formed by the specific input (through the sensory organs) and output (the movements which are made) relationship in the hierarchical system.

The contents of a mental state, or how a mental state looks, at a given time-point (formally, the binding problem) varies over time as the result of differences in active connections in the neural network at different time-points and the changes in connections due to previous events (Figure 3; cf. Edelman, 1992). These neural networks include at least parts of the neocortex such as the (pre)frontal cortex (see below). It is beyond the aim and scope of this paper to discuss which neurotransmitters and sub-cortical structures are involved in regulating transitions between, and actual contents of, mental states.

With this separation of the invariant and variant part of mental states we can now turn to questions concerning phylogeny of mental and neural states.

3.3. Phylogeny of Mental States and Neural States

Continuity between minds of different species is hypothesized to depend on the continuity of the invariant part of mental states and not of their variant part. In other words the "shape part" of mental states is the potential invariant across species. This means that neural networks are potential invariants across species (Figure 4). The minds of different species may differ in terms of the number of different classes or their interrelationship depending on the differences in (the organization of) neural networks. Furthermore, the contents of their states are different since the encoded information differs between species (due to differences in sensory organs and movements). Therefore, different kinds of mind in all likelihood exist (cf. the different Umwelts of Von Uexkuell & Kriszat, 1934, Preuss, 1995).

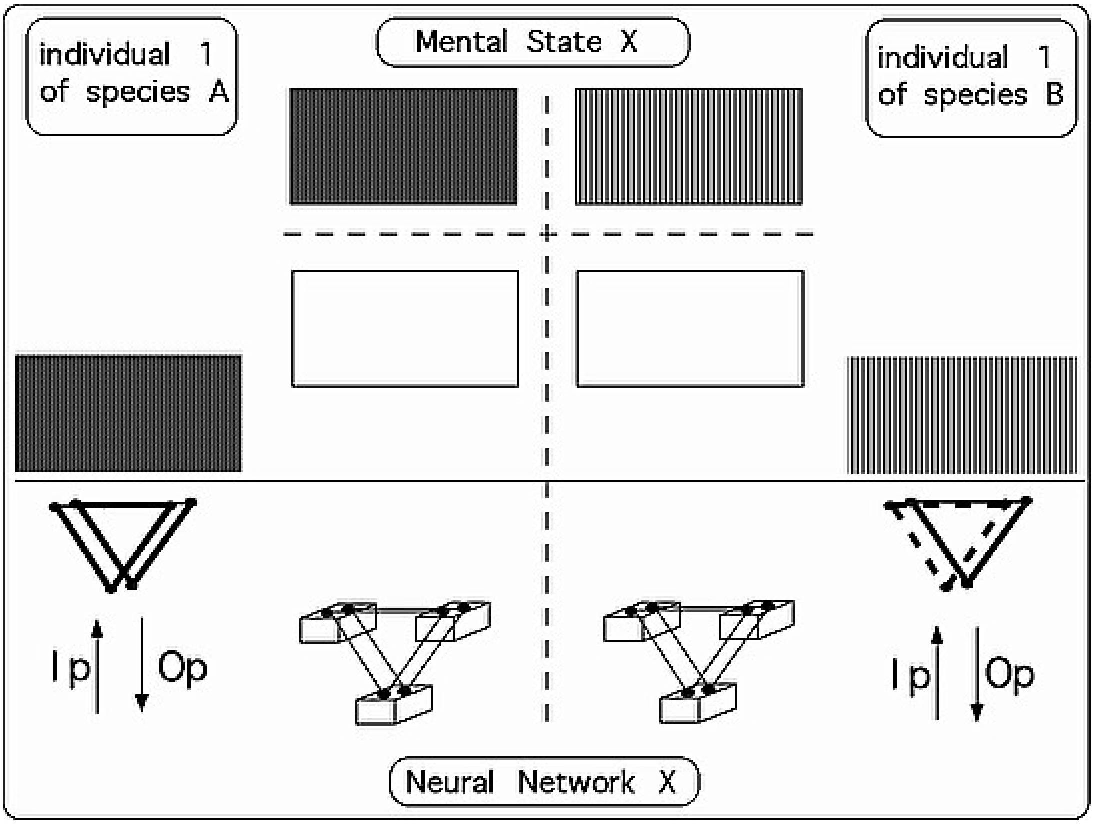

Figure 4

Phylogeny of mental states (upper part) is basically phylogeny of the invariant component of mental states (rectangle sec) or neural networks (lower part, the neural networks per se). The contents are different (represented by different patterning of rectangles) related to different activity in neural networks due to different Input-Output (Ip-Op) relationships of these networks (symbolized by the presence of the dashed line on the right hand side).

More formally, the phylogeny of a mental state may be characterized by the evolution of I, or the evolution of connections between structures of the neural networks as such. Since the contents depend on the specific input-output relationships with the environment, the variant part of a mental state therefore differs between (individuals of) species ($V^X_{A1..n}$ =/= $V^X_{B1..n}$, with X a given mental state, A & B different species and n=number of individuals), whereas the invariant part may not ($I^X_{A1..n} = I^X_{B1..n}$) or species may share the same connections between structures of the neural network. If continuity exists between a mental state, it is therefore in the invariant but not in the variant part. To study consciousness in different species, therefore, in this framework is to study mental states primarily in terms of invariant and not variant parts.

The next step in the argument now is to specify mental states more precisely.

3.4. Mental States: Intentional States

Folk belief-desire psychology offers a suitable initial framework to separate mental states into various major classes, i.e., feelings, desires, (instrumental) beliefs, intentions, reasoning and reflection, with a clear cut interrelationship (see Astington, 1993; Heyes & Dickinson, 1990, Figure 5). Belief-desire psychology is framed in intentional states or mental representations of the relation between the world and the individual. A system acting on these intentional states can be labelled an intentional system. It is of less relevance whether humans and animals truly are such intentional systems (i.e., reason along the lines outlined below) rather than that this intentional framework makes it possible to predict their behaviour accurately. In this sense I adopt an instrumental rather than a realist approach to the study of consciousness. This is the intentional stance of Dennett (1991) in the study of intentional action (see Van den Bos, 1997). Applying strict criteria allows for studying intentional action (when and if behaviour may be classified as intentional; cf., Heyes & Dickinson, 1990). It is beyond the aim and scope of this paper to consider whether this approach effectively sets the subject of phenomenal consciousness or experience (the hard problem of the science of the mind according to Chalmers, 1996) aside or not. It suffices to say here that as long as in humans it is not clear whether phenomenal consciousness has a special ontological status or not (absent: Dennett, 1991; present: Chalmers, 1996) I consider it to be wiser (or more pragmatic) to start with the Dennett-ian -- albeit minimal -- approach to study animal consciousness.

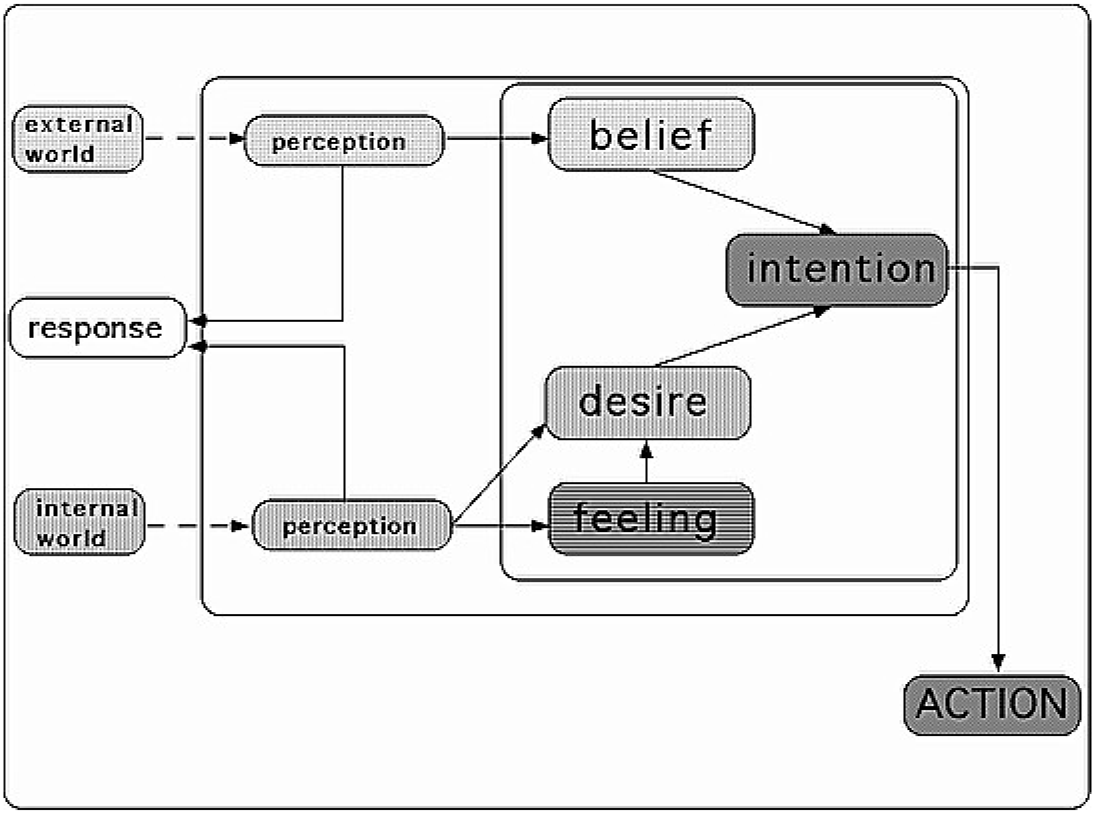

Figure 5

General model of stimulus-response and intentional action. The latter is of the form: CAUSE [PERFORM (A): -- CAUSE (A, ACCESS(O)), ACCESS (O,L_O)] for second-order intentional systems

and PERFORM (A): -- CAUSE (A, ACCESS(O)), ACCESS (O,L_O) for first-order intentional systems.

Two major classes of intentional systems may be described (Van den Bos, 1997): first-order and second-order. Second-order refers to the fact that organisms learn the representational character of mental states, i.e., they gain insight into the properties of mental states *as* relating to the world. This is described as developing a "Theory of Mind": to have insight into one's own mental states and those of others and to act upon that knowledge (Astington, 1993).

Desires reach from the organism out into the outside world, are based on feelings (desires are beliefs about values [feelings] of commodities in relation to physiology [internal world]) and can be fulfilled or not. As such, the direction of fit is from mind to world (see Bartsch & Wellman, 1995). (Instrumental) Beliefs on the other hand reach from the outside world into the organism, describe relationships in the outside world (if X happens than Y will follow) and are true or not. Accordingly, the direction of fit is from world to mind.

In formal language (cf. Heyes & Dickinson, 1990, Van den Bos, 1997) intentional action can be described as:

CAUSE [PERFORM (A): -- CAUSE (A, ACCESS(O)), ACCESS (O,L_O)]

in which L_O stands for *liking* (or not liking, i.e., feelings) commodity O, ACCESS(O,L_O) for the *desire* to obtain commodity O based on liking O and CAUSE (A, ACCESS(O)) for the (instrumental) *belief* that behavioural pattern(s) A will cause commodity O to be in reach or give access to commodity O. The combination of desire and instrumental belief lead by a process of practical reasoning or practical inference to the third mental state, PERFORM(A), the *intention* to perform the action, that it is appropriate to perform behavioural pattern(s) A in the present context given the present desire and present belief. CAUSE [..] stands for *reflection* of this kind of reasoning, i.e. this represents the second-order part of intentional action.

Intentional systems assure a fast match between physiological needs and the behaviour of the individual such that future behaviour is appropriate under similar conditions, whereby predictable relationships emerge. The final step is to relate intentional states to neural states.

3.5. Intentional States and Neural States

Intentional action (first-order & second-order) is dependent on the presence of specific neural networks. Networks crucial in this respect are (pre)frontal cortex, amygdala and hippocampus (temporal lobe), as shown in Figure 6. Beliefs are dependent on the hippocampal formation and (dorso-lateral) prefrontal cortex (Clark & Squire, 1998; LeDoux, 1996; Wallenstein et al., 1998), whereas desires and feelings are dependent on the amygdala -- orbitofrontal cortex (Damasio, 1998; LeDoux, 1996). Theory of Mind (or reflection) seems to be dependent on the orbitofrontal cortex, amygdala and temporal cortex (Baron-Cohen, 1995) and/or medial frontal cortex (Frith, 1998).

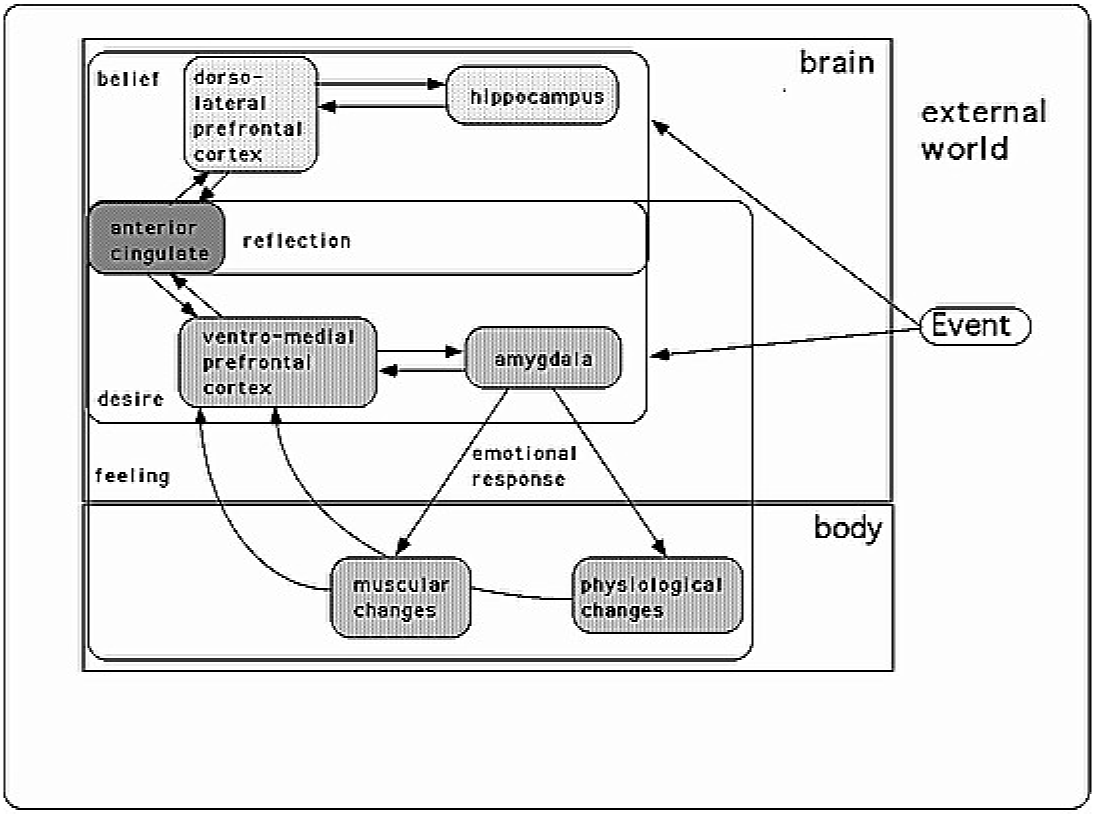

Figure 6

An attempt to relate the model presented in Figure 5 to neural substrates. This is of course only a starting point (based on Damasio 1998; Frith 1998; LeDoux 1996).

Intentional neural networks are pre-programmed networks that contain the ability to form mental states. They are a product of natural selection and give the opportunity to deal with variable environments in which it is impossible to program relationships between stimuli and responses, but possible to program the ability to form beliefs about events in the external world. On the other hand non-intentional neural networks are pre-programmed neural networks that contain sequences of behavioural patterns in relation to stimuli (S-R; lower levels in the hierarchical organization, Van den Bos, 1997): they have emerged over many generations within species, families, orders, classes, etc. in relation to stimuli in an environment (micro, macro) that have been stable enough to allow selection and be maintained.

4. Closing Remarks

The hypotheses on the relation between mental states and neural states can be tested by (i) phylogenetic reconstruction of the evolution of mental states (intentional action) in relation to neural networks (evolutionary neuro-psychology; we have recently shown how such an analysis might develop for Theory of Mind in nonhuman primates; see Van den Bos et al., 1998), (ii) the ontogeny of mental states (Intentional Action) and neural networks, (iii) the deterioriation of mental states and neural networks as, for instance, happens in autism (Baron-Cohen, 1995) and (iv) experimental tests to show the relationship between mental states and their relation with neural states and their ontogeny (Van den Bos, 1997).

Returning to Clark and Squire's (1998) experiment, this viewpoint frames comparison between humans and rabbits on delay and trace conditioning in terms of acting as first-order intentional systems (it does not seem to be related to Theory of Mind or second-order intentionality): the phenomenon of trace conditioning (or similar kinds of conditioning) is at least dependent on forming instrumental beliefs about external events (tone and air-puff) which in turn seems dependent on a neural network comprised of at least the hippocampus and (pre)frontal cortex. This opens the question of studying the phylogeny of this phenomenon in terms of common ancestry related to neural networks. Moreover, following this line of reasoning it becomes possible to search for the origin of this phenomenon in terms of neural networks. Finally, it leads to the question what second-order intentionality adds to this phenomenon, which role language plays in this phenomenon, and how this might lead to differences between rabbits and humans.

Only the integration of Psychology, Neuroscience and Ethology or the integration of Mind, Brain and Behavioural Patterns (Psycho-Neuro-Ethology) leads to a successful further step towards understanding consciousness. Neuroscience allows for integrating Psychology (through neuro-psychology) and Ethology (through neuro-ethology) into one coherent conceptual framework. Only a theoretical framework which contains behavioural patterns, mental states and neuronal events leads to progress in the study of animal consciousness: (i) separating mental states into two components (an invariant part and a variant part) with the invariant part open to study in relation to the species' Umwelt; (ii) placing different invariants in a coherent theoretical framework; (iii) connecting invariants and the presence of neural networks (and variants with active connections within networks).

To maintain that ethology and psychology have different agendas, aims and methods is a sterile point of view based upon historic demarcations (Bermond, 1996). Likewise, to maintain that ethology and cognitive ethology have different agendas, aims and methods is a sterile view, based upon misunderstanding and confusing levels of interpretation (causal and functional analysis and the difference between selection of behavioural patterns and selection of mental patterns). In both cases selection has been on neural networks that allow, on the one hand, certain patterns to be performed and, on the other, mental capacities to arise.

Notes

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