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978-1-107-05368-7 — Beyond Evolutionary Psychology
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Introduction

1.1 THE ISSUE

One of the key issues in human biology is the nature/nurture debate: which aspects of our bodies and behaviour are genetically determined, and which are environmentally shaped? As regards the human brain, what innate modules are there in the brain, producing behaviours that are hard-wired rather than learnt through our life experiences (Carruthers et al. 2004)? Or to put the issue another way, where does human knowledge come from (Elman et al. 1998)? Even more fundamentally, what is the nature of human nature (Buller 2005, pp. 420–480)?

Many evolutionary psychologists propose, in reply, that there are a variety of genetically determined brain modules – our evolutionary heritage – which provide innate knowledge from the day we are born: modules for language, folk psychology, folk physics, folk biology, cheater detection, and so on (Chomsky 1965; Tooby and Cosmides, 1992, p. 13; Pinker 1994, pp. 419–427; Cartwright 2000, pp. 193–211; La Cerra and Bingham 2002, pp. 179–187; West-Eberhard 2003, p. 81; Buller 2005, pp. 127–200; Geary 2005; Carruthers et al. 2005, 2006, 2007). A full set of possible cognitive modules is listed by Cartwright (2000, pp. 195–196). Other ways of talking like this are to propose a language instinct (Pinker 1994), or refer to innateness (Carruthers et al. 2005), nativism (Pullum and Scholz 2002), or domain-specific modules (Laland and Brown 2004; Carruthers et al. 2005). These authors propose that key aspects of human knowledge are innate; that is where much cognition comes from and how much human behaviour is determined.

The evidence brought forward in support of these proposals is, on the one hand, the evidence of 'poverty of stimulus' (Carruthers et al. 2005, pp. 6–7) and, on the other, data concerning the behaviour of young children (Carruthers et al. 2005, pp. 8–10). In particular, the poverty of

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stimulus argument has been strongly supported by Chomsky in the case of language (Chomsky 1965): the developing child does not have sufficient input data to deduce the rules whereby language is constructed. Hence, that knowledge must be innate.

There are a number of problems with this argument. In particular, it is based on a view of language as a rigidly *rule-based* system (Chomsky 1965) – which is not the natural way the mind works. The mind is grounded not so much in rules as in pattern-recognition and prediction (Hawkins 2004; Frith 2007; Friston 2010; Churchland 2013; Clark 2016) based in connectionist principles (Elman et al. 1998). While it can be trained to operate in a rule-based way, that is not the basic way it functions. This applies specifically to language, as can be demonstrated, for example, by documenting how learning to read actually takes place (Bloch 1997) and how reading actually happens in a meaningful context (Flurkey et al. 2008). One can argue that lexis is complexly and systematically structured, and that grammar is an outcome of this lexical structure (Hoey 2005), as evidenced by collocation studies (Biber et al. 2006). Learning actually occurs via Latent Semantic Analysis (Berry et al. 1995; Landauer and Dumais 1997).

Theoretical arguments for the 'poverty of stimulus' proposal pick up on the linguistic view that an infinite number of sentences are possible; therefore, there is no way the required understanding for reading all sentences could be learnt from available stimuli. See Kamorova and Nowak (2005) for a formal 'proof' that is supposed to show that innate language modules exist. This is hopelessly unrealistic; the longest sentences that can occur in the real world are strictly bounded, because you must remember the start of the sentence by the time you reach the end (see Appendix). Furthermore, the poverty of stimulus argument is undermined by empirical assessment of its criteria (Pullum and Scholz 2002). Lastly, it disregards the effects of the intense emotional bond between the infant and its mother (Greenspan 1997; Greenspan and Shanker 2004).

In any case there are a number of problems with all these cognitive innateness proposals, arising in essence from the fact that they do not take physiological and developmental issues seriously enough. Behavioural or brain imaging data may be able to establish that domain-specific modules exist in developed or developing brains, for language for example, but that does not establish that such modules have a genetic origin. Genes determine outcomes to some extent, but a key feature of brain development is plasticity in response to interactions with the environment (West-Eberhard 2003; Fernando and Szathmary 2010). This shapes neural networks at the higher level (Elman et al. 1998)

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and gene regulatory networks at a lower level (Kandel 2006; Wagner 2011), resulting in a simultaneous evolutionary origin of regulation and form (West-Eberhard 2003). An adequate investigation of the nature/nurture issue must take such biological effects into account; it cannot proceed simply on the basis of behavioural outcome data. That data must be carefully unpicked to analyse what kinds of innate modules it might actually support, when developmental and physiological issues are also taken into account. In particular, we should recognize that cortical modules can be adapted to quite different roles if the sensory input to the cortex in question is rewired (Roe et al. 1992) or if it is damaged (Johnson 2007, pp. 132–137; Chanraud et al. 2013). Perhaps, the most dramatic example of this is the experiment in which Sur and colleagues (Roe et al. 1992; von Melchner et al. 2000) reconfigured newborn ferret brains in such a way that their visual pathways were directed to the cortical region where hearing normally develops; these ferrets developed visual functions in the supposedly auditory parts of their cortex. In other words, they saw the world with brain tissue that was supposedly genetically specialized for hearing sounds. If this can be done for sounds in general, how much more must the principle be true for language sounds in particular?

As regards the behavioural data on infants and young children, this must be carefully related to which specific brain modules the data are supposed to support. In particular, it must distinguish between sensory modules, cognitive modules, and emotional modules. As discussed in the subsequent passages, these form very different categories.

This book sets out a developmentally based view that challenges ideas proposed in the name of evolutionary psychology regarding the genetic origin of neocortical brain modules. It will propose a much narrower, more biologically based set of innate modules underlying development of the brain, which are not in themselves cognitive modules but play a key role in cognitive evolution.

The fundamental point here is that there *are* innate modules in the brain, but they do not perform cognitive functions; they perform affective ones. A growing body of research shows the guiding role of affect (emotions) on both behaviour and cognitive development (see e.g. Greenspan (1997) and Damasio (1994, 1999)). This research suggests that emotion must have played a key role in evolutionary development – it must both have been selected for by evolution and affected evolution. So what then are the genetically determined affective systems that have been selected for? They are the 'primary emotion command systems' investigated in particular depth by Jaak Panksepp (Panksepp 1998; Panksepp and Biven

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2012), based in the ascending activation and limbic circuits of the mammalian brain (Kingsley 2000) releasing dopamine, norepinephrine, and many other neuromodulators in the cortex.

These ancient systems have an important role to play in the function and evolutionary development of the human brain. The case will be made that *these affective systems are the innate modules that shape both cognitive development and behaviour* and are the lynchpin between evolution and psychological development. This link is what is missing in standard discussions of evolutionary psychology. The role of this book is to make good the hiatus.

1.2 GUIDING PRINCIPLES

Why should there be modules in the brain in the first place? It is a basic principle of complex systems that the only way to create true complexity is via modular hierarchical structures (Simon 1962; Flood and Carson 1990; Booch 2007). As stated by Nelson in Schlosser and Wagner (2004, p. 17):

> Modularity pervades every level of biological organisation, from proteins to populations, biological units are built of smaller, quasi-autonomous parts. This type of organisation is essential to much of biological function. In particular, modular design enables evolutionary change. To quote Raff, 'It is the property of modularity that allows evolutionary dissociation of the developmental process and thus makes the evolution of development possible.'
>
> (Raff and Sly 2000)

Thus, modularity is a key to evolutionary processes (Simon 1962). But how do evolutionary and developmental processes lead to modularity?

As famously pointed out by Dobzhansky, 'Nothing in Biology Makes Sense Except in the Light of Evolution' (Dobzhansky 1971). However, that is hardly the whole story, as one might believe from some evolutionary psychological writings. It is equally true that nothing in biology makes sense except in the light also, firstly, of epigenetic developmental processes (Gilbert 2006; Gilbert and Epel 2009), secondly, of physiological structure (Rhoades and Pflanzer 1989), and, thirdly, of biological function (Hartwell et al. 1999; Campbell and Reece 2005). These interlocking issues are the foundations on which a sound understanding must be built.

Principle 1: Evolutionary origin: A theory of brain modules must be based in an account of evolutionary processes whereby they could have come into existence.

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This will of course be a Darwinian process of natural selection over geological timescales. It is based on survival of the fittest (in some suitable sense). While many genetic variants ('genotypes') may be neutral in the sense of not affecting reproductive survival rates, others are crucial because they lead to behaviours or functions ('phenotypes') that are better adapted to the local physical, ecological, or social environment. It is these better adapted phenotypes that preferentially pass on their genes to succeeding generations and so lead to environmental adaptation (Corning 2005; Ayala 2012). But they must be sufficiently important to compete as survival criteria with all the other biologically compelling issues impinging on animate life, such as the search for food and for safety from predators.

Principle 2: Behaviour/function: A theory of brain modules must include an account of behaviour or function whereby reproductive survival rates are enhanced.

It is a further principle of biology that structure underlies function, and this applies in particular to the brain (Nicholls et al. 2001; Clark et al. 2012). Hence, physiological structures are selected biologically on the basis of the functions that they enable.

Principle 3: Structure/physiology: A theory of brain modules must identify physiological structures whereby behaviour or function that enhances reproductive survival rates is enabled.

The structures that occur come into being by developmental processes (Johnson 2007) based on the information contained in the genotype but adaptively controlled via gene regulatory networks (Wagner 2017) and epigenetic effects (Gilbert and Epel 2009). These change outcomes in an essential way in response to environmental conditions (West-Eberhard 2003) and so are not pre-set developmental programmes (Buller 2005, pp. 123–126, 133–137).

Principle 4: Adaptive development/neural plasticity: A theory of brain modules must identify viable developmental processes whereby the needed physiological structures can be brought into being. These processes involve developmental plasticity in response to the environment; this shapes neural connectivity.

Principles 1–4 are the basis on which we develop our proposals. It is important to note that these principles will apply to all the interlocking scales involved in a living organism. Figure 1.1 represents the basic causal chain we have outlined here.

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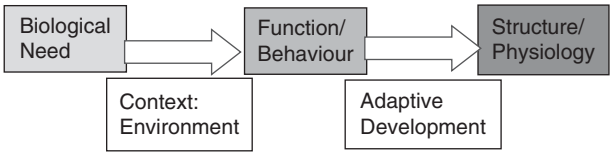

FIGURE 1.1 The chain of causation. The basic needs are survival, involving in particular the continual search for energy (metabolism), and reproduction with inheritance

1.3 PROBLEMS WITH INNATE COGNITIVE MODULES

There are problems with innate cognitive modules in regard to each of these principles.

Principle 1: Evolutionary origin: The issue here is the following: suppose there is some cognitive behaviour that enhances survival prospects, for example an effective understanding of physics or biology. There is no plausible mechanism whereby this behaviour can get written into DNA. Firstly, because developmental issues strongly suggest DNA cannot encode the needed neural network details (see the following). Secondly – supposing we ignore that issue – because it is unlikely that emergence of such modules would lead to sufficient enhancement of survival prospects, in competition with all the other variables that affect survival, as to control which genes get passed on to later generations. Thirdly, because the massive early developmental expansion of human neocortex – beyond what is found in living anthropoid apes (chimps, gorillas, and orangutans) – is largely controlled by a single gene (Florio et al. 2015), which leaves little room for hard-wiring of intrinsic human neocortical functions.

Principle 2: Behaviour/function: The modular argument is often phrased in terms of survival advantage in the context of an environment of evolutionary adaptedness (EEA) (Laland and Brown 2004), usually taken to be an African savannah. But there is not a single relevant environment; what is actually needed is the ability to adapt to whatever environment is encountered. This is stated by La Cerra and Bingham (2002, pp. 186–187) as follows:

> We agree that your brain is composed of neural adaptations that resulted from evolution. but these adaptations did not take the form of well-defined, inherited information processing circuits that were designed to generate predetermined adaptive solutions to Stone Age problems. Rather, they took the form of components of a system that could

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construct adaptive information processing networks – individualised circuitries that generated behavioural solutions that precisely fit the specific environmental conditions, bioenergetic needs, personal experiences, and unique life history of an individual.

Principle 3: Structure/physiology: This principle is related to the previous one: if our cognitive processes were based in cortical modules adapted to the EEA, we would not survive for a day in New York or Johannesburg. We need an *adaptive* modular system rather than an *adapted* modular system (Buller 2005, pp. 127–200).

Principle 4: Development/neural plasticity: If we ignore the previous problems and suppose the needed information could get written onto DNA, there is no way it could get read out in developmentally plausible terms. The point is that it is difficult enough seeing how the modules that certainly do need to be hard-wired (the homeostatic brainstem and instinctive limbic systems, the primary sensory and motor systems) can be generated by developmental processes through reading DNA. In these cases (as in the case of c elegans) the networks and synaptic connections are well defined and can be 'hard-wired' by reading DNA with suitable positional indicators guiding the process. But the forest of detailed synaptic connections in cortical columns (Plate 2(a)) is a completely different story. Reading out DNA with precise enough positional information to uniquely specify these connections just does not seem possible.

The conclusion is that we need a process whereby one lays down specific connections in the brain and sensory-motor organs that perform precise predetermined functions and are more or less invariant through life, which in turn prime instinctual learning systems that can respond and adapt to changing local circumstances. The kind of adaptive developmental processes described by West-Eberhard (2003) will do the job nicely. What happens is that random synaptic connections are initially set up, and then on the one hand pruned and on the other hand strengthened or weakened, on the basis of experience.

Thus, 'precise patterns of environmental stimuli to which the developing cortex is exposed play an essential role in shaping brain circuits, and the functional properties of those circuits . . . Environmental inputs to the brain shape the more fine-grained cortical structures by determining the outcome of cell competition' (Buller 2005, p. 133).

This is a process of adaptive selection whereby 'neurons compete with each other for the sort of information processing structure they

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are going to be, and brain activity, guided by environmental inputs, determines which neurons win this competition, hence which processing roles they end up playing' (Buller 2005, p. 135). This is a form of neural Darwinism, as discussed by Edelman (1989, 1992). At the molecular level, this happens because of top-down control of gene regulatory circuits through the activity of the mind (Kandel 2005, 2006). This process sets up *Adaptive Representational Networks* (ARN) in the cortex (La Carra and Bingham 2002), which are the basis of pattern recognition and prediction through learning (Hawkins 2004; Friston 2010; Churchland 2013).

1.4 HARD-WIRED AND SOFT-WIRED CONNECTIONS

To proceed, it is useful to distinguish between what we will refer to as *hard-wired* and *soft-wired* connections in the brain. Here,

- *hard-wired connections* refer to neurons where genetically based developmental programmes produce a fairly tightly prescribed set of connections to other neurons in a specific domain; they will be affected to some extent by contextual variables, but nevertheless the outcome is connections with a very specific set of predetermined functions. This leads to the kind of innate modularity envisaged by the authors cited above.
- *soft-wired connections* refer to neurons where genetically based developmental programmes produce an initially random set of connections to other neurons in a specific domain, which then get pruned and altered in strength in response to experience so as to produce specific connections that are essentially the product of learning processes, with broad functions that are an outcome of this process (Buller 2005). This is the kind of developmental plasticity described in detail by West-Eberhard (2003).

Given this distinction, hard-wired modules exist in brain areas where specific pre-prescribed functions are required. Such hard-wired connections occur in two contexts:

- *targeted connections* that connect neurons in specific local brain domains to other neurons (specific post-synaptic targets) which are also in specific local brain domains;
- *diffuse systems*, which are the topic of the next section.

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The hard-wired targeted connections are (see Plate 1 (see colour plate section)):

1. The spinal cord and peripheral nervous system (Kingsley 2000, pp. 22–30).
2. The autonomic nervous system (Kingsley 2000, pp. 471–487) and cranial nerves (Kingsley 2000, pp. 337–380).
3. The subcortical sensory systems, ultimately leading to the cortex: specifically, the somatosensory system (Kingsley 2000, pp. 165–208), the auditory system (Kingsley 2000, pp. 393–415), and the visual system (Kingsley 2000, pp. 433–465), mostly excluding in each case the associated cortical areas, as well as the gustatory and olfactory systems.
4. The subcortical motor systems, ultimately leading from the cortex: specifically, the spinal mechanisms of motor control (Kingsley 2000, pp. 209–238), descending motor systems (Kingsley 2000, pp. 239–283), and basal ganglia connections (Kingsley 2000, pp. 285–310).
5. Much of the connectivity of the limbic system.

By contrast, soft-wired connections exist where brain plasticity is required in order that flexibility and learning be possible; this is the case in

- all intrinsic cortical areas associated with cognition: the cerebral hemispheres and lobes (Kingsley 2000, pp. 7–15) – which are structured in terms of columns and layers;
- the cerebellum (Kingsley 2000, pp. 311–336);
- some aspects of the limbic system (certainly hippocampus and amygdala).

Outcome 1: *There are no hard-wired cognitive systems within the cortex. There are, however, soft-wired, developmentally shaped cognitive modules arising from interaction between individuals and their social, physical, and ecological environments.*

Neurons in specific layers of the sensory cortices may all have a common property, but that does not amount to the kind of detailed neural network weighting system that is required for coding cognitive information (Churchland 2013).

In more detail, it is crucial that the connections from the primary sensory systems (from the eyes, ears, tongue, nose, skin) be hard-wired through neuronal migration, so that the sensory input ultimately leading to the cortex is directly related to incoming signals – such as the synaptic connections in the retina (Plate 3(b) (see colour plate section)) and from there to the visual

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cortex (the optic tracts via the lateral geniculate nucleus, Plate 3(a) (see colour plate section)) – must be tightly prescribed, and so must be hard-wired. However, the connections into and within the visual cortex itself (Plate 3(b) (see colour plate section), bottom) can only be soft-wired, according to the above outcome. This is why we have to *learn* to see cortically.

Similarly, the descending cortical motor systems must be connected to muscles via hard-wired subcortical connections, in order that the cerebrum can accurately control our actions. But this must be flexible, so their connections in and from the cortex itself are soft-wired. This is why we have to learn to perform voluntary movements.

As to the cortex itself, this outcome excludes the possibility of language modules, folk physics modules, and so on, on developmental grounds. Such modules could not be pre-wired, even if the needed data could somehow be stored in DNA (or even in gene control networks). The specificity required of the wiring process is simply too high.

1.5 DIFFUSE SYSTEMS AND THE CRUCIAL ROLE OF EMOTION

Our second key point is that a family of diffuse projections from the upper brainstem and limbic system nuclei to the cortex are hard-wired. Here,

- *diffuse connections* refer to neurons that do not link specifically to other neurons in a small domain (no obvious postsynaptic targets are seen) but rather link to widespread cortical and subcortical areas, their function being to modulate synaptic activity across such large areas (Nicholls et al. 2001, p. 282).

The relevant modules here are the so-called *ascending systems* (Plate 2(b) (see colour plate section)) which include

- the *noradrenaline (norepinephrine) system* originating in the locus coeruleus complex (Kingsley 2000, p. 132; Nicholls et al. 2001, p. 283);
- the *dopamine systems* originating mainly in the substantia nigra and ventral tegmental area (Kingsley 2000, p. 132; Nicholls et al. 2001, pp. 284–285);
- the *serotonin system* originating in the raphe nuclei (Kingsley 2000, p. 133; Nicholls et al. 2001, p. 278);
- the *cholinergic system* originating in the basal forebrain nuclei (Nicholls et al. 2001, p. 278);
- the *histamine system* originating in the tuberomamillary nucleus in the hypothalamus (Nicholls et al. 2001, pp. 284–285).

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