



Review

Top-down effects in the brain

George Ellis

Mathematics Department, University of Cape Town, Rondebosch 7701, Cape Town, South Africa

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Abstract

The purpose of this investigation is to demonstrate that one is unable to understand the operation of the brain without taking top-down effects into account. This is demonstrated by looking in turn at evolutionary and developmental aspects, then at functional aspects related to sensory systems, learning processes, and motor processes that lead to action on the world. It is also clear in terms of the effects of a society on brains located in that society. The possibility of top down affects exists both because of multiple realisability of higher level processes at lower levels, and because lower level elements are adapted to perform their higher level functions. These top-down processes validate a non-reductionist approach to how the brain works.

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1. The basic idea: all is contextual

A key idea in the emergence of complexity in living systems is that strong emergence [27,107] is enabled by a combination of bottom up and top down effects in the hierarchy of structure and causation [24,101,105,46,44]; that is, contextual effects play a key causal role. This article, following on the discussions in Murphy and Brown [101] and Ellis [44], claims this is true in the brain in particular, which is situated in society and cannot be understood outside of that context [39,41]; for example, social context exerts top down influences right down to synaptic and genetic level.

The article extends the work in those previous writings by considering top-down causation in regard to each of the main specific aspects of brain operation.

1.1. The basic concept

The hierarchy of structure for the brain is shown in Table 1 [122,51,44]. Associated with each level is a set of functions and causal behaviours emergent at that level as shown in Table 2. With a few exceptions, a different vocabulary is used at each level for the entities and behaviours relevant at that level, for the emergent features in biology are quite different than just a summation of the lower level parts or actions: “more is different” (Anderson [7]), “the whole is greater than the parts” (Noble [104,106]). As well as the parts, it is their structuring in terms of higher level patterns of

E-mail address: george.ellis@uct.ac.za.

Table 1
The hierarchy of structure for a brain located in a society.

Level 10	Society	Group
9	Person	Organism
8	Brain, CNS	Systems
7	Brain regions	Assemblies
6	Neurons, astrocytes	cells
5	Dendrites, nuclei, axons, synapses	Sub cellular structures
4	Genome and cell structures	DNA strands, cell structures
3	Proteins, RNA, DNA	Bio molecules
2	Polymers	Polymer units
1	Atoms	Atomic

Table 2
The hierarchy of function for a brain located in a society.

Level 10	Society	Social interactions
9	Person	Psychological actions
8	Brain, CNS	Perception and planning
7	Brain regions	Information processing
6	Neural nets, Neurons, astrocytes	Spike chain processes
5	Dendrites, nuclei, axons, synapses	Signal transmission
4	Genome and cellular systems	Protein synthesis
3	Proteins, RNA, DNA	Cellular processes
2	Polymers	Structural function
1	Atoms	Physical interactions

Table 3
The levels of causation enabled by the combination of bottom-up emergence (left) and top-down realisation (right).

	Level 10	Society	↔ Causation 10	
	9	Person	↔ Causation 9	
	8	Brain, CNS	↔ Causation 8	
	7	Brain regions	↔ Causation 7	
	6	Neurons, astrocytes	↔ Causation 6	
	5	Dendrites, axons, synapses	↔ Causation 5	
	4	Genome	↔ Causation 4	
	3	Proteins, RNA, DNA	↔ Causation 3	
	2	Polymers	↔ Causation 2	
	1	Atoms	↔ Causation 1	
	0	Electrons, protons	↔ Causation 0	

organisation that is crucial in enabling strong emergence to take place [101,44]. That organisation cannot be described in lower level terms.

Causation takes place at each level, as characterised by the kinds of laws of behaviour that apply at that level, using concepts and language appropriate to that level. What about interlevel relations? Firstly, bottom up emergence occurs: each higher level is comprised of entities from the next lower level, and so is emergent from constituent entities at that level. However additionally, each higher level is the context for existence of the next lower level, and so constrains that level in both structural and functional terms. Higher level structures and functions are realised through lower level structures and functions (the upward arrow in Table 3), with numerous lower level realisations possible for each higher level structure or function (the downward arrow).

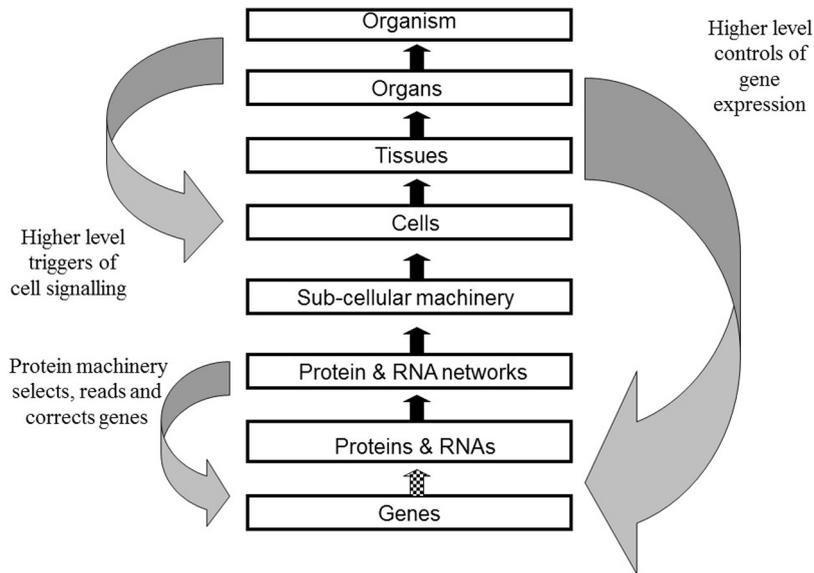


Fig. 1. Top down control of cell signalling and gene regulatory networks (from [105] with permission).

Thus lower levels in biology fulfil higher level functions by operating in a way that is coordinated and shaped via higher level structures and functions [101,44]. These are the top-down effects discussed in this paper. I will often refer to this as top-down causation, because if one alters higher level conditions this leads to changes of lower level interactions, often in a predictable way – that is, in a way that is predictable up to the existence of lower level equivalence classes. This is experimentally testable, because in addition to testing what changes occur at the lower levels when one alters higher level variables, one can also observe how those lower level changes then in turn lead to higher level changes in accord with the higher level structure and function, with its own logic.

This kind of effect is made clear for example in the way genes are controlled by the local and global context through gene interaction networks [109,62,104–106,59,136,71], see Fig. 1.

Proteins are created by reading information from the genome in a contextual way, controlled by gene regulatory networks, and then carry out key sets of biological functions [114,45]. These networks respond to higher level conditions so as to supply the needed proteins at the right place and time, in turn controlling signal transduction networks and metabolic networks to carry out the desired biological functions according to higher level context. This kind of effect takes place in particular in neurons and synapses, and hence for example top-down control of gene expression underlies the way memory works [77,78].

The basic message behind what follows is that reductionism is not fit for purpose, when trying to understand self-organisation in biological (neuronal and social) systems. The emphasis on top down causation resonates with the circular causality that underlies early treatments of self-organisation in cybernetics and subsequent more formal treatments in synergetics (e.g., laser physics). In this setting, there is a necessary separation of temporal and spatial scales that mandates a top-down causality. Often, this is cast in terms of stable, fast microscopic degrees of freedom (in coupled dynamical system) that subtending averages or modes of slow, unstable, macroscopic dynamics – referred to as order parameters. Crucially, while the microscopic states underwrite the emergence of macroscopic order (i.e., order parameters) the order parameters enslave the microscopic ensemble. This is known as the (en)slaving principle that can also be construed as the centre manifold theorem. In short, top-down causality is necessary to complete the circular causality that is a necessary aspect of any coupled dynamical system with a separation of scales.

1.2. Multiple realisability

A hallmark that top-down effects are occurring is when higher level entities or functions are realised via equivalence classes of lower level entities or functions [113,120,8,44]. A specific individual animal (a particular cat, dog, human, etc.) has a specific atomic and electronic make up at any instant, and so is realised in a unique way at the lower levels

at any particular time. However a class of animals of a particular type (cats, dogs, humans, etc.) can be realised in a huge number of ways at the lower levels. An equivalence class of lower level entities correspond to a higher level type of entity, where the equivalence class will contain huge numbers of entities at the lower levels. Similarly, a specific higher level type of action or function will correspond to an equivalence class of lower level actions or functions. For example a plan (at the psychological level) for an action (such as making a cake) can be realised at the neural net level by a great many different network structures and excitations (spike trains), which in turn can be realised by a great many more detailed neuronal realisations, in turn based in a huge number of possible molecular configurations – which all correspond to the same higher level thought. The notion of equivalence classes can also be – at least conceptually – related to the notion of exchangeability in statistics. In other words, if it makes no difference exchanging one molecule with another in a gas, one can formally analyse their density dynamics – leading to statistical mechanics and stochastic thermodynamics. In short, in the absence of equivalence classes or exchangeability, we would not have statistical mechanics or much of physics as we currently know it.

It is this multiple realisability at lower levels of higher level structure and function that is at the core of emergence of new properties at higher levels [127,120,44,16,72] characterising when top-down causation is taking place [8], because it is only at that higher level that the core causal pattern emerges. It is not possible to specify the action at a lower level in a way that reveals the causal patterns that drive what is happening; in philosophical terms, the attempt to do so results in descriptions that are not natural kinds (Fodor, see [11]: 403–407; [44]: 374). Descriptions that are natural kinds (“The eagle swooped down in order to catch its prey”, “The aircraft departed at 12h00 because that was the scheduled time of the flight”) emerge at higher levels. A key point here is that in philosophical discussions (e.g. [101]: 19), the specific individual representative of a class is called a *token*, while the class is called a *type*, so one can distinguish token identity and type identity. Thus multiple realisation takes place as regards types, not tokens. Higher level emergent principles refer to classes rather than individuals; they are realised in individuals because the individuals are members of the class. Object oriented programming makes such class-member relations explicit [18].

In a modular hierarchical structure, the tight internal binding of modules relative to the weaker inter-module binding allows higher levels to have greater causal power than lower levels [70], and allows abstraction: inner variables are hidden from external view, except for passing of control variables through a precisely fashioned interface [18]. Higher level causation occurs by black boxing lower level interactions rather than coarse graining them [45]. Indeed, one could even treat the variational calculus and the notion of a variable x , which underlies mathematics, as a statement that x is a class that stands in for token numbers or variables. In other words, mathematics is interested in, and only in, class member relations.

1.3. Room at the bottom?

There is a complex philosophical discussion of the issue of emergence and supervenience, querying whether strong emergence is in fact possible, see [11,107] for surveys. However from the viewpoint of neuroscience, it is clear that such emergence does indeed take place, together with associated top-down causation; for example, ideas demonstrably have real causal powers [44] and thoughts are genuinely emergent [49], [101]: 195–236). How can this occur? There are four key issues:

- One can separate out what does the work, and what decides what work will be done ([135]; [101]: 87–88, 193–237). The nature of what is accomplished by lower level work is channelled by higher level constraints (that is, constraints that cannot be described in lower level terms; for example, which transistor is connected to which in a digital computer, or what algorithm is realised in the software that is running).
- The key point in determining patterns of higher level causation is the nature of the functional organisation at these levels, not what these levels are physically composed of [101,44]. This is another statement of the principle of multiple realisability.
- An invariance under higher level counterfactual perturbations make higher level explanations irreducible to even the most complete possible physical explanations of the same phenomena (Lange 2005); these emergent laws differ from physical laws in terms of the range of counterfactual perturbations under which they are invariant.

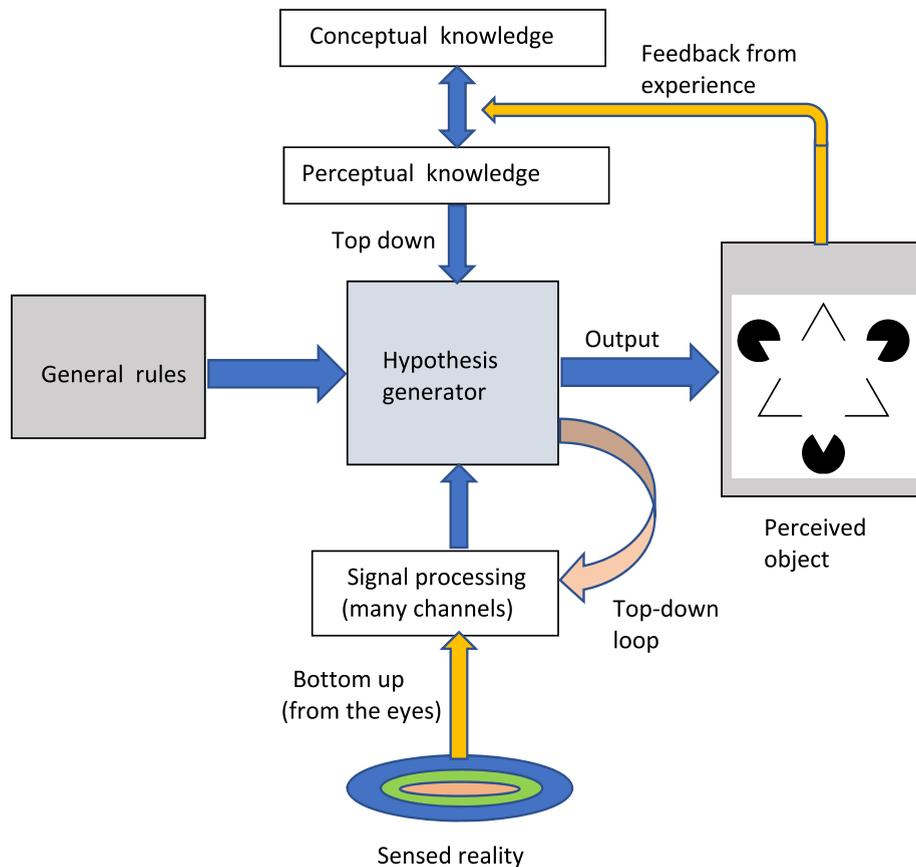


Fig. 2. Black box of vision. As usual, signals from the eyes and the other senses are ‘bottom-up’. Conceptual and perceptual object specific knowledge are shown in separate ‘top-down’ boxes. Knowledge as embodied in the general rules applied to all objects and scenes, is introduced ‘sideways’. Perceptual learning seems to work largely by feedback from behaviour. The top-down circuits involved are shown in Fig. 1 of [55]. Adapted from Figs. 2 and 4 in [67].

- Finally the billiard-ball model of emergence underlying reductionist positions¹ simply does not represent the world of biology, where lower level components are selected so as to be adapted to higher level functions ([101]: 65–70, [44,45]). This model does not even adequately represent the world of physics, where quite apart from issues to do with quantum entanglement and measurement [3], key lower level entities such as phonons only come into existence because of higher level crystal structures [89,134] and associated broken symmetries [7].

The issue is discussed in depth in ([101]: 42–104, [44]). I claim demonstrate by conceptual analysis in this paper and the examples considered here (see particularly Figs. 1–3) that there is indeed occurrence of top-down causation in biological contexts in general [104–106], and in the brain in particular [101,102,44] in all its major functional aspects.

1.4. The major contexts

There are three main inter-related contexts in which emergence, and associated top-down causation, occurs. These are, evolutionary emergence, developmental emergence, and functional emergence.

¹ The idea that atoms interacting in a gas can be modelled as billiard balls with no internal structure so their collisions are just governed by energy conservation and centre of mass momentum conservation. They have no interesting internal structure so the gas properties emerge in a purely additive way. Their properties are completely unaffected by context.

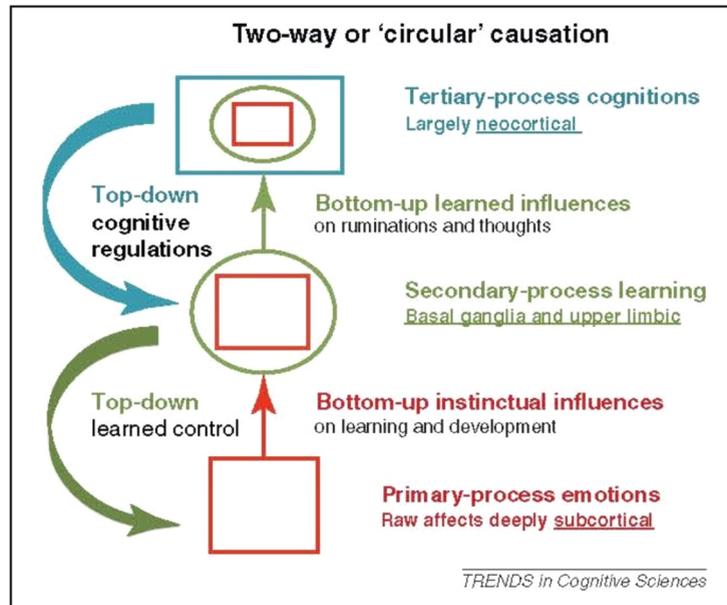


Fig. 3. Top down effects in the brain as a whole. From [110], with permission.

1.4.1. Evolutionary emergence

There was no life 13 billion years ago; now it exists in great variety. This evolutionary emergence takes place over time scales of hundreds of thousands to billions of years. How life came into being is not understood; however once it did exist, it was from then on shaped by Darwinian processes of natural selection [36], which together with genetic drift, mutation, recombination, and migration is the accepted origin of the vast variety of living systems, each adapted to their specific environment. This is discussed *inter alia* in [97,25,116,75]. According to Randall et al. [118],

“The physiology of an animal is usually very well adapted to the environment that the animal occupies, thereby contributing to its survival. Evolution by natural selection is the accepted explanation for this condition, called adaptation... A physiological process is adaptive if it is present at high frequency in the population because it results in a higher probability of survival and reproduction than alternative processes.”

This is a top-down process from the nature of the environment to the detailed structure and function of individual organisms [24,101,44], for example a polar bear has white fur because that is beneficial for its survival in a polar environment, and accordingly its genes (whether they arose by mutation or drift) have been adapted so as to lead to the growth of white fur, rather than the brown fur of other bear families, because this gives selective advantage. Similarly global climate change acts top down on all species and drives global variation in natural selection [125]. According to Stone [132],

“Evolution is essentially a process in which natural selection acts as a mechanism for transferring information from the environment to the collective genome of the species.”

Examples are that at the microscale, the proteins that underlie brain function are determined by natural selection [45], as are the DNA sequences that specify the proteins needed for cell function [137] and in particular for existence of gene regulatory networks, signal transduction networks, and metabolic networks [136] as well as associated developmental systems [109]. At the macro level, major aspects of the brain are innate, see Ellis and Solms [47] for a thorough discussion.

A key point here² is that group level evolutionary processes take place [19,108,140,141]; otherwise for example one could not have selection for a social brain [40–42,124], which exists only because living in groups is good for survival. Indeed major evolutionary transitions reflect group level selection processes [96,140]. Furthermore it is unlikely that language would otherwise have emerged because social interactions play a key role in this development [41], which then alters evolutionary processes in key ways [119], in particular by facilitating development of technology that has fundamentally altered human evolutionary history *inter alia* by enabling our victory over the other hominids.

1.4.2. Developmental emergence

Each living animal starts as an individual cell, and then grows by developmental processes [146,58] to an adult organism over time scales of weeks to decades, in the case of human beings developing to 10^{13} cells, of which 10^{11} are in the brain. But this always takes place in a contextual way: outcomes are environmentally dependent [109,59,104,106]. This developmental process varies with context (‘developmental plasticity’, [138,139,115]) and interacts with evolution over long time scales to give “evo-devo” processes [60,26,98].

These top-down processes from the environment shape macro and micro brain structure – for example, determining what languages we can speak at the macro level on the basis of specific neural connections at the micro level. Thus experience driven brain plasticity [85,94] is a key feature of development and learning as we interact with our physical, ecological, and social environment. This plasticity underlies our ability to adapt to our environment, whatever it may be, and underlies health and the ability to recover from injury. As stated by Johnston [74],

“Neuronal plasticity allows the central nervous system to learn skills and remember information, to reorganize neuronal networks in response to environmental stimulation, and to recover from brain and spinal cord injuries. . . . Basic mechanisms that are involved in plasticity include neurogenesis, programmed cell death, and activity-dependent synaptic plasticity. Repetitive stimulation of synapses can cause long-term potentiation or long-term depression of neurotransmission. These changes are associated with physical changes in dendritic spines and neuronal circuits. Overproduction of synapses during postnatal development in children contributes to enhanced plasticity by providing an excess of synapses that are pruned during early adolescence. Clinical examples of adaptive neuronal plasticity include reorganization of cortical maps of the fingers in response to practice playing a stringed instrument and constraint-induced movement therapy to improve hemiparesis caused by stroke or cerebral palsy.”

Thus this plasticity is a key aspect of brain function [47], and is an adaptive response to our context, shaping brain structure and function. A different environment will result in different outcomes, for example speaking Spanish instead of English (based in different synaptic connections and weights).

1.4.3. Functional emergence

We are made of electrons and atoms shaped into biomolecules and systems (Table 1) so that brain function emerges on a moment by moment basis from these physical foundations [122,79]. This functional emergence takes place over timescales of milliseconds to minutes, and is again enabled by top-down causation [102], as will be discussed below, this is enabled at the micro level by biomolecules and particularly proteins [45], and at the macro level by neural network structures and brain macro-organisation [101]. However it must be emphasized that this kind of emergence is closely tied to developmental emergence: from our viewpoint the difference between them is that developmental emergence changes neural network connectivity and synaptic strengths, thus enabling learning, while functional emergence notionally refers to emergence of behaviours and thoughts from a brain with a fixed neuronal structure. In practice learning takes place all the time so both take place in an intertwined way.

² There are major controversies over this issue, as well as over the relative importance of drift as opposed to selection. However the view taken here will be that, as stated clearly by Mayr [97], selection has to take place at the level of the organism, as evolutionary processes have no direct purchase on genes: any such purchase can only occur as a consequence of survival of organisms that house those genes. Consequently selection at the gene level occurs as the top-down result of selection at higher levels. Because of the multiple realisability of phenotypes in terms of genotypes, the adaptive outcome of the process of selection, which is perfectly clear at the organism and physiological levels [25,97,118], is much less clear at the genotype level.

Table 4

The three levels at which any machine carrying out an information processing task must be understood. Adapted from ([95]: 25).³

Computational theory	What is the goal of the computation, why is it appropriate, and what is the logic of the strategy by which it can be carried out?	1
Representation and algorithm	How can this computational theory be implemented? In particular what is the representation for the input and output, and what is the algorithm for the transformation?	2
Hardware implementation	How can the representation and algorithm be realised physically?	3

1.5. The major aspects

At the macro level, brain function is divided into three major aspects [5,6,100]:

- Perception and analysis of incoming data, including written and spoken language and internal states of the experiencing subject, leading to learning;
- Prediction and planning, relying on theories of the world and memory of past events;
- Action controlled by feedback processes so as to attain the desired goals, including engaging in written and spoken language.

This all takes place within an environment with physical, ecological, and social aspects. The brain responds and adapts to all three such aspects at the psychological level, and this adaptability is based in brain plasticity at each of the lower levels.

One should note here that in fact these processes take place in a highly integrated way, with the mind as “modulator and regulator of ongoing embodied activity, and this requires abandoning the dividing lines among perception, cognition, and action” ([30], quoted in [101]: 37). Nevertheless, in practice one cannot discuss them all at once. This article will deal in turn with perception and top down effects (Section 2), learning, memory, and the predictive mind (Section 3), planning, motor control, and action leading to the causal efficacy of thoughts and intentions (Section 4), and the situated integral brain: social neuroscience and psychiatry (Section 5), leading to a holistic view of the brain and top-down action (Section 6).

2. Perception and top down effects

I will focus here on vision, as it is the most studied perceptual mode. One can look at it at any of the levels shown in Tables 1 and 2. It has computational and psychological aspects.

The way vision occurs in computational terms is explored by David Marr in his classic text [95]. He represents the three computational levels underlying vision as in Table 4. This is a logical hierarchy for what happens [44], enabled by the implementation hierarchy of Tables 1–3. This illustrates how, just as in the case of a digital computer ([44]: 35–82), the task at hand (Level 1) drives the algorithm used to solve that task (Level 2) which then determines what specific operations will take place at the physical Level 3. Physics enables this logic to take place, but does not decide what the logic will be that is implemented in the computation. How physics enables this logic to emerge via specific biomolecules is discussed in [45].

But what is the goal of these computations? It is perception ([117]: 131), which is not simply related to vision because in order to comprehend what one is seeing, one must solve the visual inverse problem identified by Helmholtz, and “*the visual system cannot logically analyse the retinal image to decide how these factors have actually been combined to generate a particular luminance . . . given that the visual system cannot determine the nature of objects by logical operations on image features, the most likely . . . alternative would be to do so empirically*” ([117]: 129). That is, we learn how to see through experience, which shapes how our brains interpret incoming data. Object perception can be formulated, in probabilistic terms as inference or Bayesian prediction . . . This is illustrated by Fig. 2, adapted from Gregory [65].

³ With the table switched around to represent the top-down nature of what is going on.

Excellent descriptions at the psychological level are by Gregory [65–67], Frith [53], and Purves [117], all going back to Helmholtz, who proposed ([53]: 41) that perception of the world is not direct, but depends on unconscious inferences. That is, before we can perceive an object the brain has to infer what the object might be on the basis both of information reaching the senses, and information stored in memory. Vision as it occurs in practice is an outcome of a combination of top-down influence from knowledge and expectations, and bottom-up influences from spike trains conveyed by the optic nerve from rods and cones in the eye reaching our visual cortex after processing in the lateral geniculate nucleus in the thalamus ([117]: 106).

Gregory [66] expressed this as follows:

“Are perceptions like hypotheses of science? . . . It may be said that hypotheses structure our accepted reality. More specifically, it may be said that hypotheses allow limited data to be used with remarkable effect, by allowing interpolations through data-gaps, and extrapolations to be made to new situations for which data are not available. These include the future. . . . I shall hold that all of these statements are true, and that they apply to perception. In addition, both the hypotheses of science and the perceptual processes of the nervous system allow recognition of familiar situations or objects from strictly inadequate clues, as signalled by the transducer-instruments of science and the transducer-senses of organisms. This is at least true for typical situations: in atypical situations the hypotheses of both science and perception may be dangerously and systematically misleading. Errors and illusions can be highly revealing for appreciating the similarities – and the differences – between perceptions and the conceptual hypotheses of science.”

Kveraga et al. [88] state similarly,

“The human brain is not a passive organ simply waiting to be activated by external stimuli. Instead, it is proposed that the brain continuously employs memory of past experiences to interpret sensory information and predict the immediately relevant future. This review concentrates on visual recognition as the model system for developing and testing ideas about the role and mechanisms of top-down predictions in the brain.”

Object perception takes place as Bayesian prediction [82,31], which means it is based in previous knowledge and understanding which modulate visual experience in a top-down way [130]. Two key further points:

- A key aspect of vision is paying attention [34] and discarding irrelevant detail. We discard billions of bits of irrelevant information by the minute in order to pay attention to what matters [12,133,87,103]. The issue of what is relevant is related to our current intentions and assessment of our situation, which are higher level psychological variables, which determine how we proceed. Thus top-down effects determine for example where we point our eyes through activating the relevant muscles. There is top-down control of the human visual cortex by frontal and parietal cortex in anticipatory visual attention [21].
- Additionally, attention is guided by affective systems that underlie our emotions [47]. These carry out a sub-cortical assessment of what is important, and emotional tags get attached to each memory so that when we see particular people or places those emotional tags get recalled and associated with ongoing perception. This can be thought of as a bottom-up effect in terms of overall brain structure (Section 6).

Overall the key point is that what we perceive visually is not just a record of incoming photons. It is a contextual construction which uses that sensory information to modulate prior expectations of what we should be seeing, and for example the entire scene is relevant to the perceived colour of any part of it ([117]: 149). The simple reductionist view of how vision works is simply wrong ([117]: 120–121, 219–233): top-down effects occur functionally [112]. Also vision has been shaped by evolution to enhance survival adaptively in response to the current situation ([117]: 135–142, [61]), and that is what determines its physical basis and the predictive nature of how it works. Past experiences and expectations play a crucial role in determining what we perceive now, as indicated in Fig. 2.

The underlying neural mechanisms are discussed inter alia in ([9,91,10,117]: 225–229), and [84] (“Prior expectations bias sensory representations in the visual cortex”). Gray gives evidence ([64]: 289–292) that wholes can affect the perception of the parts because of unconscious inference involving top-down control within the brain. Note that quite a bit of image processing takes place firstly in the layers of cells close to the retina [64], and secondly in the thalamus.

thalamus before the signals reach the visual cortex [4]. Top down effects are mediated by many more neurons projecting downwards to the thalamus from the cortex than vice versa.

The associated top down processing is discussed in [57,56,126,55,148]. In evolutionary terms, the structure of our visual system is what it is because it has developed to be that way through selective evolution that adapts it to the environment at macro and micro levels; for example squid eyes have protein gradients that enable them to see with adequate resolution in the context of their life underwater [28]. This is just the usual process of top-down causation during evolutionary selection [24,61,45].

Similar issues arise in speech perception, where our subjective experience depends not only on sensory information from the environment but also on our prior knowledge or expectations [128], and in reading, where the same is true [63]. The Visual Word Form Area (VWFA) is likely a neural substrate for the interaction of the top-down processing of symbolic meanings with the analysis of bottom-up visual properties of sensory inputs [131].

3. Learning, memory, the predictive mind, and planning

Next I consider the structure of Table 3 again, but this time applied to the issues of prediction and planning, based on stored memories that have been accumulated by learning processes at the macro level that are based in brain plasticity at the micro level. This allows the key feature of scenario planning, where we consider possible actions and their outcomes offline – that is we do not actually carry out the actions, we model them or simulate them in our minds.

What algorithm should be used in this case? As explained by Frith ([53]: 166) the brain uses guesses about the world to predict what will happen next as we act upon the world. The errors in our prediction then enable us to refine our guesses until we have a good model of what is out there in the world. This is a form of adaptive selection, a key kind of top-down causation [43,44], because it adapts the brain to the environment: alter the environment, and a different set of synaptic connections in the brain ensue.

In more formal psychological terms this has process been characterised by John Anderson as ACT* theory [5,6], standing for Adaptive Control of Thought, leading to “production systems”, that is algorithms to carry out a task, based in actor frameworks, theories, and models ([5]: 5–44). In computational terms it is largely agreed that the brain predicts the future on the basis of past experience together with current data by using Bayes’ Theorem. Andy Clark gives compelling support for this view in [31], with abstract

“Brains, it has recently been argued, are essentially prediction machines. They are bundles of cells that support perception and action by constantly attempting to match incoming sensory inputs with top-down expectations or predictions. This is achieved using a hierarchical generative model that aims to minimize prediction error within a bidirectional cascade of cortical processing. Such accounts offer a unifying model of perception and action, illuminate the functional role of attention, and may neatly capture the special contribution of cortical processing to adaptive success. This target article critically examines this “hierarchical prediction machine” approach, concluding that it offers the best clue yet to the shape of a unified science of mind and action.”

How these Bayesian principles are implemented at the neuronal level is discussed in detail by Bogacz [17] based on Friston’s work on a “Free Energy Principle” [52]; this is discussed also in [45]. The result at the psychological level is the basic processes of learning as demonstrated by psychological experiments ([64]: 93–135).

This all happens at an unconscious level all the time, in particular in the case of perception as discussed in the previous section: the brain is in essence a predictive machine both as regards perception and action [69,53,117]. However a crucial feature is that we can strengthen predictions by using reasoning ([64]: 351–395) based in language and symbolism ([64]: 397–433), and even more by using the scientific method based in mathematical representations.

These logical processes are made possible by the neural network structure of the brain and its representational properties ([101]: 193–237, [29]), where explicit thoughts about alternative possible future actions occur and are weighed up against each other in the light of their predicted possible outcomes. To understand the causal pattern one must include the use of cognitive concepts in neuroscience [48] otherwise one will be missing a key aspect of causation in operation. Explicit goal choices and evaluations of how to achieve them determine the options examined, and choices made between those options then causally effect what happens in the world, for example in terms of molecules being incorporated in a cake that is baked in an oven. Again the top-down feature of selective attention is a key issue in determining what happens [54], as are influences from above on memory [20].

4. Action planning, motivation, motor control, and action

Action planning and execution is yet another example where Marr’s three levels (Table 1) come into play. This time the goal is to move some body part (a limb, hand, finger, tongue, etc.) in a desired way to attain some goal (e.g. making a cake or giving a speech). Having adopted an action plan arising out of associated scenario planning, the algorithm is to use feedback control processes: start an action, see what happens as a result of your actions, and modify them as needed so as to correct errors and attain the desired goal. This homeostatic process is one of the key forms of top down causation [44]: the outcome is determined by the goal (e.g. grasp a glass in your hand) rather than the details of the mechanisms that attain that goal (which specific muscles get enacted in what order by what microprocesses, or which electrons flow in which biomolecular assembly).

As usual when top-down action happens, multiple realisability occurs as regards ways of achieving the goal, which is the driver of what happens. Several elements are key:

- Emotions underlie the motivation to take action ([64]: 185–229, [110,35,47]). This is a major aspect of what is going on that is bottom-up in terms of macro brain structures (sub-cortical areas influencing the cortex, see Fig. 3), and to a large extent this decides what actually happens. At the psychological level, rationality does indeed modulate emotions and their outcomes, but often with limited success. At the lower levels, underlying what happens is a neural substrate of (the precision or confidence in) prediction and reward [123,99] associated with neurotransmitters such as dopamine [47].
- The central nervous system internally simulates the dynamic behaviour of the motor system in planning, control, and learning [142,144]. Thus the brain internally predicts what will happen before action is initiated, and then corrects outcomes in the light of ongoing perception of what is occurring, which leads to learning [145]. This is a process of active inference [1].
- Any planned actions are themselves hierarchically structured and carried out in a serial order that reflects that logical hierarchy; The output of higher-level modules is a set of (top-down) prior probabilities of the subordinate modules, which act to prioritize lower-level module selection [144]. For example one may plan to bake a cake (Level 1) which involves getting a recipe, buying ingredients, preparing them, and cooking (Level 2), each one of which involves a selection process between alternatives. Buying ingredients involves travel to the store, selecting from the shelves, and paying (Level 3). And so on. Thus [44] there is a horizontal (logical) modular hierarchy at each level of the vertical (implementation) hierarchy. Top-down realisation takes place in this logical hierarchy as well, associated with implementation timing: thus one chooses to bake the cake before selecting the recipe, the latter taking place in order to realise the former; and in fact this kind of hierarchical top-down processing takes place in all cognitive domains [73].
- Attention is key to considered action [37]. However automation takes place so that learned actions become internalised and subconscious processes supervise most of what happens. The body learns to attain many of its goals in an automatized way, with the conscious brain only intervening where necessary because that process is not working correctly [64]. Thus the action algorithm includes such processes of automatization.

Associated top-down neural mechanisms are discussed in [90,81]. Overall this leads to a complex integrated system of planning and action [143] where the outcome is greater than the sum of the parts [14]. Wolpert et al. [144] state

“Recent empirical studies have implicated the use of the motor system during action observation, imitation and social interaction. In this paper, we explore the computational parallels between the processes that occur in motor control and in action observation, imitation, social interaction and theory of mind. In particular, we examine the extent to which motor commands acting on the body can be equated with communicative signals acting on other people and suggest that computational solutions for motor control may have been extended to the domain of social interaction.”

Through these processes, thoughts (in the mind) are causally effective in the real world. Action in the world is based in conscious plans: reason can have a causal grip on the brain ([101]: 193–237). This is possible because the brain can function in a symbolic way through the nature of its neural network structures ([101]: 147–192, [29]) allowing

logical processes of planning and off-line exploration of alternative possible scenarios. Park and Friston [111] make an interesting comment on how this works:

“How rich functionality emerges from the invariant structural architecture of the brain remains a major mystery in neuroscience. Recent applications of network theory and theoretical neuroscience to large-scale brain networks have started to dissolve this mystery. Network analyses suggest that hierarchical modular brain networks are particularly suited to facilitate local (segregated) neuronal operations and the global integration of segregated functions. Although functional networks are constrained by structural connections, context-sensitive integration during cognition tasks necessarily entails a divergence between structural and functional networks. This degenerate (many-to-one) function-structure mapping is crucial for understanding the nature of brain networks.”

Thus mental causation [147,121] is possible because of the multiple realisability that characterizes top down causation in the brain, leading to top down causation from thoughts to details of microstructure in the real world, such as the nature and location of atoms incorporated in the structure of an aircraft [44]. This is demonstrably a causal relation: change the concept of what you want to create, and a different constellation of atoms results.

5. The situated brain

A crucial final feature is top-down effects from the physical, ecological, and social environment into brain macro- and micro-levels of structure, allowing us to adapt to these contexts due to brain plasticity at both macro and micro levels.

The top-down effect from society into individual brains has been understood at the sociological and psychological levels for a long time, see for example Berger and Luckmann [15], Merlin Donald’s writing on the myth of the isolated mind [39], and Longres [92] on the causal impact on individuals of features such as social roles. It is also apparent in Robin Dunbar’s work on the social brain [40,41], giving solid evidence that evolutionary forces have shaped the brain to be what it is because of the survival benefits of social interactions. Above all, something like that must account for the existence of language [42]. Indeed culture transformed human evolution [119]. In psychological terms culture leads to the development of specific patterns of thought and language ([64]: 397–433) and individual social development ([64]: 435–473), guided by social influences on behaviour ([64]: 511–547). All of this is top-down causation from society to the individual.

At the micro level, Kiebel et al. write [83] “we suggest that cortical anatomy recapitulates the temporal hierarchy that is inherent in the dynamics of environmental states. Many aspects of brain function can be understood in terms of a hierarchy of temporal scales at which representations of the environment evolve”. Pursuing this leads to the burgeoning area of social neuroscience [22,23,13]. Famous examples are more hippocampal neurons in adult mice living in an enriched environment [80] and the effects of their training on the brains of London taxi drivers [93]. Such effects take place by social regulation of gene expression in the brain [32,33].

Of course one of the most obvious examples of such top-down causation is the fact that this paper is written and read in English. That is a result of social conditions causing detailed changes in the microstructure of cortical connections in the brains of the writer and reader.

6. The holistic view

Overall, the complex hierarchical structure of the brain [122,51,79] enables a large variety of consciousness and unconscious psychological processes [64], broadly interacting in the way summarised in Fig. 3 (from [110]), and enabled by physiological processes at lower levels as summarised in Fig. 1 (from [105]). Note that there is no claim here of a single physical sub-structure that embodies a highest level: rather there are ever changing constellations of oscillatory neural nets in the neocortex that are the physical basis for that highest level to emerge through the narrative unity of our perception [101].

The primary emotional systems play a crucial role in shaping what happens at the cognitive level [47], but equally cognitive processes are able to modulate these effects to some degree in a top-down way [110], for example the basomedial amygdala mediates top-down control of anxiety and fear [2]. Because this happens to an embodied mind [30,31] situated in a social context [39], one must bridge neuroscience, psychology and sociology to obtain an adequate

holistic view of human behaviour [68,38], including the top-down effects from society to individuals. As discussed above, a combination of bottom up and top down processes occurs in all aspects of brain functioning.

The way these top-down processes work out is exemplified by Kandell's discussion of a new framework for psychiatry, summarised in five principles as follows [76]:

Principle 1. *All mental processes, even the most complex psychological processes, derive from operations of the brain.... As a corollary, behavioral disorders that characterize psychiatric illness are disturbances of brain function, even in those cases where the causes of the disturbances are clearly environmental in origin.*

Principle 2. *Genes and their protein products are important determinants of the pattern of interconnections between neurons in the brain and the details of their functioning. Genes, and specifically combinations of genes, therefore exert a significant control over behavior... As a corollary, one component contributing to the development of major mental illnesses is genetic.*

Principle 3. *Altered genes do not, by themselves, explain all of the variance of a given major mental illness. ... behaviour and social factors exert actions on the brain by feeding back upon it to modify the expression of genes and thus the function of nerve cells. Learning produces alterations in gene expression. Thus all of "nurture" is ultimately expressed as "nature."*

Principle 4. *Alterations in gene expression induced by learning give rise to changes in patterns of neuronal connections. These changes not only contribute to the biological basis of individuality but presumably are responsible for initiating and maintaining abnormalities of behavior that are induced by social contingencies.*

Principle 5. *Insofar as psychotherapy or counseling is effective and produces long-term changes in behavior, it presumably does so through learning, by producing changes in gene expression that alter the strength of synaptic connections and structural changes that alter the anatomical pattern of interconnections between nerve cells of the brain.*

Thus top-down effects such as are represented in Fig. 1 act from the psychological level to the level of genes and thereby alter physiological outcomes mediated by proteins [114,45] The consequence is that a purely reductionist approach to dealing with mental illness is likely to run into difficulties. As stated by Solms [129],

"This paper reflects on the place of psychoanalytical thinking in a scientific context in which mental illness is increasingly being reduced to physiological and chemical factors. A small series of neurological patients with severe emotional disturbances is presented, in order to demonstrate that emotional symptoms can be neither described nor explained in physical terms. Even in cases where an organic aetiology is indisputable, physiological factors can only be invoked to explain somatic symptoms and the physiological correlates of mental symptoms. The mental symptoms themselves can only be understood psychologically."

7. Conclusion

The top-down mechanisms discussed in this paper show a non-reductive approach to how the brain functions makes sense, and indeed is obligatory in order to get an adequate causal understanding of how the brain functions. It is not the case that everything that occurs can be understood in a purely bottom-up way.

One needs to consider an integrated whole of causal factors, relating the brain to context, taking behaviour into account as well as neuroscience ([117]: 219–233, [86,110]). That is, one must take into account the top-down effects, encapsulated in Table 3 and Fig. 3, as well as the bottom up ones, if one wants to understand the brain in a fruitful way. This is stated in another way by Frégnac [50]:

"The critical point remains that causal-mechanistic explanations are qualitatively different from understanding how a combination of component modules performing the computations at a lower level produces emergent behavior at a higher level. The first difficulty arises because higher-level concepts are needed to understand the neural

implementation level. So, even when causality is demonstrated, it makes sense only when all levels are considered together simultaneously: . . . A second difficulty comes from Marr's "multiple realizability" argument, which states that the same function can be achieved through any number of different substrates. The impossibility of mapping behavior or function in a unequivocal way on the parametric state of the synaptic or conductance ensemble (defining observed dynamics of the neural net under study) was reproduced in simulation models of Aplysia and vertebrate cerebellum. This conundrum reveals unexpected complexity whichever way the hierarchy is read, from the computation or macro level to the substrate or micro level, or the reverse."

Actually (see Section 1.2) this is effectively just a statement that you need to look at the top-down causal processes at work in order to understand brain function and the mechanisms used to implement it. You won't be able to do it by bottom reductionist up analysis alone [95,80,50]. That is the key message of this paper.

Competing interests

The author has no competing interests.

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