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Conscious thought as simulation of behaviour and perception

Germund Hesslow

A 'simulation' theory of cognitive function can be based on three assumptions about brain function. First, behaviour can be simulated by activating motor structures, as during an overt action but suppressing its execution. Second, perception can be simulated by internal activation of sensory cortex, as during normal perception of external stimuli. Third, both overt and covert actions can elicit perceptual simulation of their normal consequences. A large body of evidence supports these assumptions. It is argued that the simulation approach can explain the relations between motor, sensory and cognitive functions and the appearance of an inner world.

Germund Hesslow
Dept of Physiological Sciences, University of Lund, BMC F10, Tornavägen 10, SE-22184, Lund, Sweden.
e-mail: Germund.Hesslow@mphy.lu.se

It might be said that cognitive science rests upon the assumption that human behaviour cannot be understood by taking only perceptual and motor processes into account and that distinct *cognitive* mechanisms are required to explain behaviour. Yet, developments in several fields during the last couple of decades suggest that cognitive and sensorimotor mechanisms are intimately connected. Among these are emerging ideas about embodied cognition [1,2] and findings that imagery relies heavily on sensory mechanisms and that certain kinds of problem solving involves motor structures.

The view to be defended here, is that this somewhat paradoxical situation can be resolved by what we might call the 'simulation hypothesis', essentially a combination of some ideas originally formulated by British empiricist philosophers in the 18th century [3] and their associationist descendants [4]. This hypothesis states that thinking consists of simulated interaction with the environment, and rests on the following three core assumptions:

(1) Simulation of actions: we can activate motor structures of the brain in a way that resembles activity during a normal action but does not cause any overt movement.

(2) Simulation of perception: imagining perceiving something is essentially the same as actually perceiving it, only the perceptual activity is generated by the brain itself rather than by external stimuli.

(3) Anticipation: there exist associative mechanisms that enable both behavioural and perceptual activity to elicit other perceptual activity in the sensory areas of the brain. Most importantly, a simulated action can elicit perceptual activity that resembles the activity *that would have occurred* if the action had actually been performed.

Simulation of behaviour

In his remarkably insightful book, *The Senses and the Intellect* from 1868, Alexander Bain suggested that thinking is essentially a covert or 'weak' form behaviour that does not activate the body and is therefore invisible to an external observer [4]. 'Thinking', he suggested, 'is restrained speaking or acting' (p. 340). This idea, which was central to behaviourism [5,6], was thought to have been disproved when it was shown that subjects paralysed by curare were still able to think [7]. It may have been prematurely rejected, however and a slightly modified version of it has lived on.

Behaviour is generated in a hierarchical fashion in the frontal lobes. Activity in sensory cortex is signalled via both intra- and sub-cortical pathways to the anterior parts of the frontal lobe. The main signal flow is then posteriorly through supplementary and premotor cortex to the primary motor cortex. Single muscle contractions are controlled by neurons in the primary motor cortex. More complex movements, such as gripping an object or saying a word, which require temporally organized activation of several muscles, are elicited by higher-level command signals in more anterior neurons. In the prefrontal cortex only the most global aspects of behaviour are controlled. At all levels, the frontal cortex interacts

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with the basal ganglia and the cerebellum, which contribute to shaping the final movement commands.

The idea that behaviour can be simulated means that the activity in the motor structures, which prepare and initiate an action, can occur while its execution by the primary motor cortex output is suppressed. There is now an impressive body of evidence to support this assumption (for reviews, see [8,9,10]).

Behavioural experiments have demonstrated a number of striking parallels between simulated and actual movements. The time it takes to simulate a simple motor task corresponds closely to the time it takes to perform the same task in reality. Decety *et al.* had subjects walk blindfolded to familiar places, indicating with a stopwatch when they started and when they thought that they had reached the goal. When they later imagined walking to the same places, there was a close correspondence between the time a particular subject used for the imagined and the actual walk [11].

The most impressive evidence for the simulation of behaviour assumption comes from studies using imaging techniques. Ingvar and Philipsson [12] showed that when subjects were instructed either to simulate or physically perform hand movements, activity increased in the pre-motor parts of the frontal lobes, whereas only the overt movements activated the primary motor cortex. Later studies have reported similar findings [13]. Although there are some subtle differences between imagined and executed movements, many later studies using PET and fMRI confirmed that there is activation of premotor and supplementary motor areas during movement simulation [14–16].

There is some recent evidence that the primary motor cortex is also activated during simulation of movement [16,17]. However, as no overt movement actually results in these cases, and as most studies fail to find activation, the activity of the primary motor cortex is most probably weaker.

Simulation of perception

The idea that we can simulate perception by activating the sensory areas of the brain so as to mimic the activity normally initiated by the sense organs was hinted at by Hume [3] and explicitly formulated by several writers during the 19th century [4,18], but the evidence for it is fairly recent [10,19,20].

Many investigators have compared the effects of concrete manipulations of physical objects with the corresponding 'mental' manipulations. In Shepard and Metzler's 'mental rotation task' (Fig. 1a), for instance, the time subjects took to find the solution proved to be closely correlated with the degree of rotation, as if the subjects were actually looking at rotating objects and had to wait for them to rotate to orientations at which they could be compared [21].

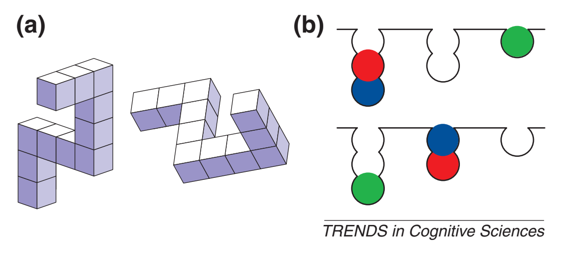

Fig. 1. (a) Mental rotation. Subjects are asked to determine if two members of a pair of objects are identical or mirror images. It is usually assumed that we solve the task by 'mentally' rotating one of the objects until they can be 'viewed' from the same perspective. (b) The 'Tower of London' task. There are three pouches, which can hold one, two and three balls respectively. The task is to move one ball at a time between the pouches in the lower panel in a minimum number of moves, so that the resulting pattern matches that of the upper panel. The task can be done physically or 'mentally'.

This and other similar experiments have been interpreted as evidence that imagery uses the same mechanisms as the visual system. Some investigators have gone much further and claimed that 'images' are like pictures in the head, that they have 'depictive' or 'pictorial' properties [20]. This controversial issue need not concern us here (see [22] for discussion). The simulation hypothesis does not rely on any assumptions about the nature of imagery or perception except that activity in sensory cortex can be elicited internally.

Another source of evidence is cortical blindness. Although the symptoms of damage to the visual cortex are quite variable, many patients lose their ability to form visual images [19]. A further striking example is a report on patients with 'unilateral neglect syndrome' (an inability to notice and respond to stimuli in one half of the visual field after damage to the contralateral parietal cortex) [23]. Such patients were asked to imagine that they were standing on one side of a familiar square and describe what they could remember. They could describe buildings only on the right side of the square, relative to the imagined vantage point. When asked to imagine standing at the opposite side of the square, they could describe the buildings that were now in the right visual field, but which they had been unable to describe the first time [23].

The most compelling support for the simulation of perception assumption comes from contemporary functional imaging techniques. Imagining a visual stimulus or performing a task that requires visualization is accompanied by increased activity in the primary visual cortex [24–26]. The same seems to be true for specialized secondary visual areas. A region of the occipito-temporal cortex called the fusiform face area is activated both when we see faces [27] and also when we imagine them [28]. Lesions that include this area impair both face recognition [29] and the ability to imagine faces [30].

Anticipation

There is evidence both from animal behaviour and human imaging studies, that perceptual simulation can be elicited by other perceptual activity [31,32],

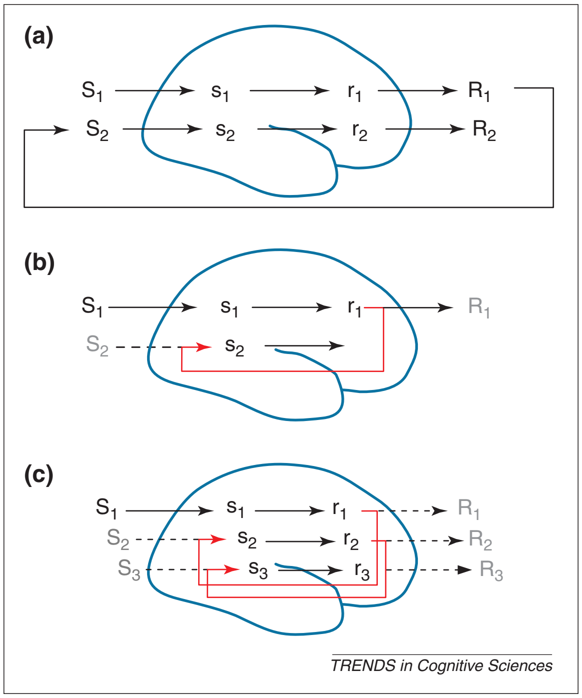

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Fig. 2. Internal simulation. (a) A situation (stimulus combination) S_1 elicits activity s_1 in sensory cortex, which leads to a response preparation r_1 and to an overt response R_1. This changes the situation into S_2, which causes new perceptual activity, and so on. (b) A predictable relation between a response and the consequent stimuli enables associations to be formed (indicated in red) such that response preparations will directly generate perceptual activity. (c) If the internally generated perceptual activity can elicit a response preparation, it should be possible to simulate long sequences of responses and sensory consequences.

but here we will only consider the possibility that perceptual simulation can be elicited from the frontal lobes by preparation for actions, or anticipation.

What we perceive is quite often determined by our own behaviour: visual input is changed when we move our head or eyes; tactile stimulation is generated by manipulating objects in the hands. The sensory consequences of behaviour are to a large extent predictable (Fig. 2a). The simulation hypothesis postulates the existence of an associative mechanism that enables the preparatory stages of an action to elicit sensory activity that resembles the activity normally caused by the completed overt behaviour (Fig. 2b). A plausible neural substrate for such a mechanism is the extensive fibre projection from the frontal lobe to all parts of sensory cortex. Very little is known about the function of these pathways, but there is physiological evidence from monkeys that neurons in polysensory cortex can be modulated by movement [33].

Anticipation does not necessarily involve the cerebral cortex. In classical conditioning of motor responses, the association is made between the conditioned stimulus and output neurons in the cerebellum [34,35]. Fear conditioning occurs in the amygdala, although conditioning to more complex stimuli probably requires cortical mechanisms [36]. However, an anticipation mechanism of the sort suggested above has obvious advantages. In particular it would enable the organism to interrupt activity that threatens to have dangerous consequences in situations where classical conditioning alone would be insufficient.

It is an interesting possibility that subcortical conditioning mechanisms could contribute to suppressing completion of a response 'in preparation'. Indeed, it has been suggested that the cerebellum participates in such suppression [16]. The cerebellum receives rich input from the visual cortex and simulated vision could function as a conditioned stimulus. If an initiated response is anticipated to have negative consequences, the cerebellum could generate a conditioned output signal to suppress execution of the response (cf. discussion in Ref. [37]).

An example of interruption of initiated responses might be the behaviour of rats in Tolman's classical T-maze experiments (see Box 1). In this situation, rats might perform responses that have never been differentially reinforced because they anticipate the response that leads to the aversive stimulus, and then suppress completion of the response. A selectionist account of purposive behaviour could still be right, but it is simulated responses rather than executed ones that are selected.

Simulating chains of behaviour

Once the mechanism of anticipation is in place, perceptual activity generated by a simulated action can serve as a stimulus for a new response, and so on (Fig. 2c), thus enabling long chains of simulated responses and perceptions. By such simulated interaction with the environment, an organism could evaluate not only single responses, but also whole courses of action, before putting them to physical, potentially dangerous, tests. Obviously, even if no overt movements and no sensory consequences occur, a large part of what goes on inside the organism will resemble the events arising during actual interaction with the environment.

It is tempting at this point to assume that there must be some part of the brain or some autonomous agent or 'self' that 'performs' the simulation by 'using' various structures, but that is expressly not what is being suggested here. The anticipation mechanism will ensure that most actions are accompanied by probable perceptual consequences, so that during normal behaviour, we will always, 'in our thoughts', be a few steps ahead of the actual events. A simulation can thus be triggered by the same stimuli that elicit overt behaviour. Neither do we need to posit an independent agent that 'evaluates' the simulation. The (simulated) sensory events will elicit previously learned emotional consequences, which can guide future behaviour either by reinforcing or punishing simulated actions (which may transfer to overt actions) or by serving as discriminative stimuli. (This important issue is outside the scope of this paper. For relevant discussions see for example, Refs [38,39].)

Box 1. Goal-directed behaviour and revaluation

According to Thorndike's 'Law of Effect', seemingly goal-directed behaviour is a function of the consequences of previous similar behaviour [a,b]. Thus, goal-directedness is really an illusion and can be reduced to a causal selection mechanism. However, animals sometimes perform responses that seem obviously goal-directed, yet have never been reinforced, as in the classic experiment of Tolman and Gleitman (Fig. I) [c]. Why do rats perform responses that have never been differentially reinforced? A simple explanation in this case is that when a rat reaches the choice point in the T-maze, it will sometimes *initiate* the response that leads to the aversive stimulus, but before the response is executed, it elicits the usual sensory consequence (the sight of the dark goal box), which has become aversive through conditioning. This would elicit conditioned anxiety, which suppresses completion of the initiated behaviour.

A similar logic applies to the 'revaluation' phenomenon. In a typical experiment, rats were trained to perform two different responses (pressing a lever, and pulling a chain) for two different reinforcers. One reinforcer was then paired repetitively with an aversive substance (lithium chloride). When the rats were again given the opportunity to respond, they avoided the response that had been followed by the now 'devalued' reinforcer although this response had never been punished [d,e].

Some authors have taken the revaluation phenomenon as indicative of a serious limitation of classical learning theory, and as evidence of causal 'beliefs' and true 'goal representations' in rats [f]. A simpler explanation is that the rats anticipate the consequences of a particular response by simulating it.

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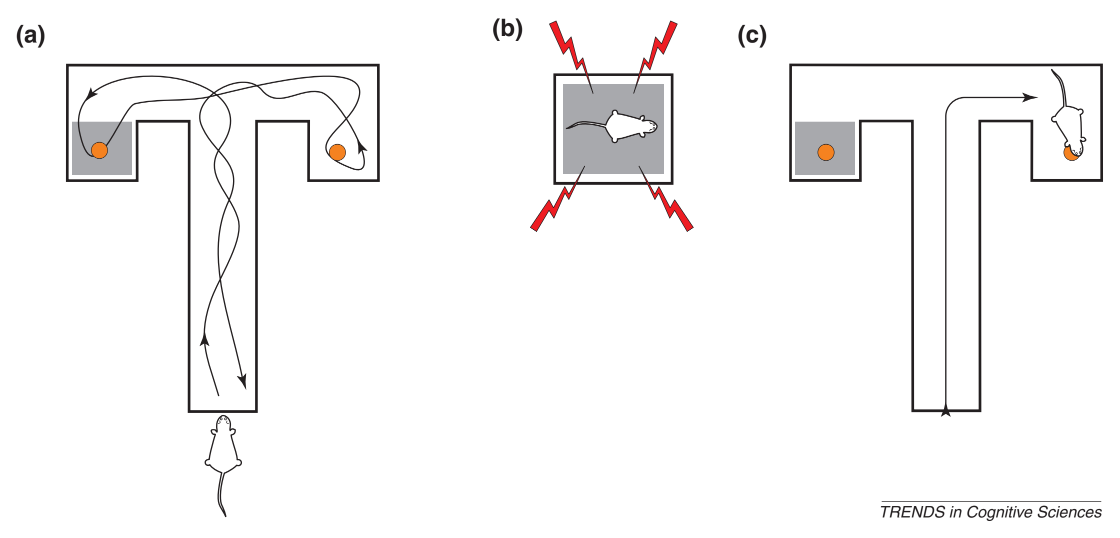

Fig. I. Tolman and Gleitman let rats freely explore a T-maze with a darkened goal box in the left arm and a light goal box to the right (a). Both boxes contained food. The rats were then placed in a dark chamber, similar to the left goal box, and subjected to electrical foot shocks (b). When later placed in the T-maze, the rats went directly to the right goal box, although left and right turns had been equally reinforced (c). It looked as if they had access to a 'map' of the maze and 'inferred' that an unpleasant experience awaited them in the left goal box.

Simulating chains of behaviour is a plausible interpretation of the problem-solving process in tasks like the 'Tower of London' (Fig. 1) [40]. The subject can test a certain move by simulating moving one ball, thereby internally generating a perception of the new configuration, which can function as a stimulus for the next move, and so on until a good or bad result is eventually achieved. Consistent with this suggestion, in imaging experiments subjects working on the Tower of London task show activation of premotor areas, including the supplementary motor area, and sensory areas (in particular the parietal and occipital cortices) [41,42].

A similar interpretation can be given of mental rotation. Subjects trying to solve the Shepard and Metzler task might simulate rotating the figures, thereby activating premotor areas of the frontal lobes and, as a consequence, sensory cortex. This has indeed been found: EEG recordings have revealed activation of premotor and parietal cortical areas [43]. fMRI studies have similarly found activation of the supplementary motor area as well as of the parietal cortex during mental rotation [44,45]. (Under some circumstances, the sensory simulation seems to be elicited by other sensory input rather than by simulated movement [46].)

Simulation of behavioural chains could underlie many other types of cognitive processes; for example, playing chess or assembling a piece of furniture. If the

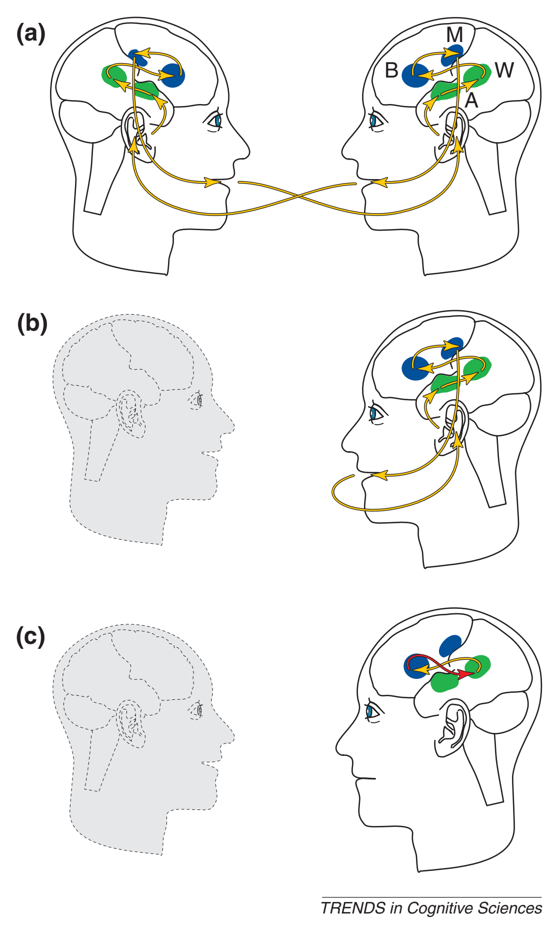

Fig. 3. Internal simulation of conversation. (a) We can respond to a question without being conscious of our behaviour. The verbal signal enters the primary auditory cortex (A) and then Wernicke's area (W). This will elicit formation of a reply in Broca's area (B) and the primary motor cortex (M). (b) We can also listen and respond to our own talk using the same brain regions. (c) If the preparation of the verbal response can be fed directly (red arrow) into auditory cortex or Wernicke's area, we can also speak silently to ourselves using essentially the same mechanisms.

preparation of a verbal response can generate activity in the auditory cortex or in Wernicke's area, it should be possible to 'hear' it before it results in overt speech and we should be able to speak to ourselves internally (Fig. 3). We can respond to a question without being conscious of our behaviour until a few hundred milliseconds later [47]. Thus, a process consisting of unconscious components might give rise to an inner conversation and to what might be called 'verbal thinking' [48].

Further advantages of the simulation hypothesis

In addition to the empirical evidence described above, I would like to mention four attractive features of the simulation hypothesis.

Role of the cerebellum and basal ganglia in cognitive function

The simulation hypothesis makes sense of the accumulating data showing that subcortical 'motor' structures, such as the cerebellum and the basal ganglia, appear to be involved in cognitive tasks.

The cerebellum is activated during imagined movements [16,49,50], in the Tower of London task [41] and during mental rotation [51]. Cerebellar lesions seem to cause various forms of cognitive impairment [52]. This should not be surprising. The cerebellum receives input from both frontal and sensory cortex and one would expect the simulation of both movement and perception to send signals to the cerebellum. This is highlighted by adaptation to laterally displacing prisms, which is now believed to depend on the cerebellum [53]. Such adaptation can occur when subjects merely imagine making pointing errors [54], suggesting that visual simulation can also send the appropriate error signals to the cerebellum.

The basal ganglia, particularly the striatum, are also activated during various cognitive tasks, such as the Tower of London [41,42], and performance in this task is impaired or altered in patients with Parkinson's disease [55,56]. Patients with Parkinson's disease and lesions of the basal ganglia also have other cognitive symptoms [57,58].

No extravagant ontological assumptions

The simulation hypothesis requires no assumptions about the existence of 'images', 'representations' or other mental entities. Simulation is conceptually firmly tied to basic behavioural and neural processes. That simple associations between actions and their sensory consequences are sufficient for internal simulation is demonstrated by recent robot simulations. Jirenhed and Ziemke have shown that a robot can successfully navigate in a simple environment using only predicted stimuli as input [59,60].

No evolutionary leaps

Although there are some obvious quantitative differences, the general construction of the human brain is quite similar to that of other, cognitively simpler, mammals, such as rats and cows, and it has not evolved any radically novel circuits for dealing with higher cognitive functions. From an evolutionary point of view, therefore, cognitive functions are likely to be based on more fundamental functions of the brain that evolved to enable organisms to move about, find food and reproduce. It is a strength of the simulation hypothesis that it can account for cognitive functions in terms of mechanisms shared by all mammals.

The inner world and consciousness

Perhaps the most exciting aspect of internal simulation is that it suggests a mechanism for generating the inner world that we associate with consciousness. There are many problems of consciousness, but one of them certainly is the existence of an inner world of experience that does not immediately depend on external input. How does this inner world arise? The simulation hypothesis provides a simple and straightforward answer.

Acknowledgements
I am grateful to several people for discussions on the topic of this paper, among them Mitchell Glickstein, Dan-Anders Jirenhed and Tom Ziemke. The work was supported by The Swedish Medical Research Council (09899).

Because simulation of behaviour and perception will be accompanied by internally generated sensory input resembling perceptions of the external world, it will inevitably be accompanied by the experience of an inner world [48].

Conclusion

The specific evidence for the first two assumptions of the simulation hypothesis, simulation of action and simulation of perception, is quite strong. The third assumption is less well supported by specific evidence but it is highly plausible. The most compelling argument in favour of the simulation hypothesis overall is the fact that it explains and makes sense of a wide range of phenomena and that it does so without relying on extravagant assumptions about underlying brain mechanisms.

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