It is commonly thought that conscious perception of a visual stimulus is mediated by the arrival in the inferotemporal cortex of a wave of activation carried by feedback connections from the visual cortical areas. A recent report of experiments using transcranial magnetic stimulation (TMS) challenges this view and shows instead that activation of the lowest cortical levels by feedback connections is necessary for conscious visual perception. This suggests that the lowest cortical stages act as ‘active blackboards’ for integrating the results of computations carried out in the different cortical areas of the visual system.

Visual perception is usually explained in the context of the feedforward model of visual processing. This model starts from the anatomical hierarchy of cortical areas, with areas V1 and V2 at the lowest levels and the inferotemporal and frontal cortex at the highest stages. Selectivity of a neuron at a given stage is assumed to result from the organized convergence of feedforward inputs from neurons located at lower stages. Because of this connectivity rule, neurons at low levels of the hierarchy have small and relatively simple receptive fields whereas neurons at the highest stages have large and very specialized receptive fields. That activity of neurons at the highest stages of the hierarchy is important for conscious vision is suggested by the results of imaging studies in humans and recordings in monkeys with bistable visual stimuli. Although this model explains a large number of observations in visual perception, it fails to account for the very dense network of feedback connections that connect cortical areas in the reverse direction. A recent report by Pascual-Leone and Walsh using transcranial magnetic stimulation (TMS) suggests instead that activation of feedback connections to the lowest stages of the hierarchy might be essential for conscious vision.

Feedback connections to V1 are necessary for conscious vision

It had been previously shown that a TMS pulse applied in the region of area V5/MT in humans could generate the impression of a moving set of light speckles. Such moving colorless phosphenes contrast with the static and colored illusory impressions generated by TMS stimulation of area V1. Pascual-Leone and Walsh used a dual-pulse TMS paradigm to study the role of V1 in the elaboration of the conscious illusion. The perception of a moving phosphene generated by stimulation around V5/MT (Ref. 4). To this end, they applied a subthreshold pulse to V5/MT and a subthreshold pulse to the region of occipital cortex corresponding to area V1/V2. They were able to study the timing of the interactions between these two cortical regions by varying the interpulse interval and asking their subjects to report the illusion they perceived (moving phosphene, static phosphene, or no phosphene). Contrary to what they expected, the perception of a moving phosphene was severely disrupted by a subthreshold stimulation of V1 applied to V1/V2 some 5–40 ms after the suprathreshold stimulus around V5/MT, and no effect was observed when stimulation was applied to V1 before the V5/MT pulse.

These results are difficult to reconcile with a purely feedforward model in which the perception of a moving phosphene (or percept) is supposed to be generated by the neural activity triggered by TMS (or feedback connections) in V5/MT and the connected higher-order areas. According to the model, this activity should be disrupted by the wave of activity generated by the pulse in V1 when it is applied before that in V5/MT, but not after. One can think of two ways in which a subthreshold TMS pulse applied to V1 after the V5 pulse could affect the quality of the induced illusion:

(1) Stimulation of neurons in V1 by the TMS pulse generates a wave of activity that is very rapidly sent upstream to a higher-order cortical area where it disrupts the transfer of the messages generated by the pulse in V5/MT and transmitted by slow conduction axons (Fig. 1a). This possibility is rather unlikely because it is known that areas around V5/MT have very short latencies and fast conducting axons.

(2) Another, simpler, possibility is that the TMS pulse in V1 disrupts the transmission of information from V5 through feedback connections and the generation of a proper spatiotemporal pattern of activity in V1 that, through interaction with other areas, normally leads to the conscious percept of a moving phosphene (Fig. 1b).

Earlier results from Pascual-Leone and Walsh’s group add credence to the second interpretation. In a recent paper, Cowey and Walsh studied the effect of a TMS pulse in the region of V5/MT in patient ‘GY’, the most famous case of a patient with a V1 lesion who shows, among other features, conscious residual vision of moving stimuli. Although moving phosphenes could be elicited in GY by stimulation of V5/MT in the cortical hemisphere with intact V1, the authors were unable to generate the conscious percept of moving phosphenes by stimulating the hemisphere with a lesioned V1, even when they targeted the cortical region that had been shown by brain imaging to be activated during perception of moving stimuli. Again, this finding is at odds with the prediction of the feedforward model that activity in V5/MT generated by the pulse, together with the wave of activity transmitted to higher stages of the hierarchy, is sufficient to generate the percept of a moving phosphene. Maybe the reason GY cannot perceive a moving phosphene after stimulation of his lesioned hemisphere is that the corresponding region of V1 is not there to process information sent through feedback connections from V5/MT. Thus, it could be the lack of feedback of V5/MT signals into V1 that is the cause of the inability of GY to perceive moving phosphenes. Similarly, it could be the interference with feedback signals from V5/MT by the TMS pulse applied to V1 that destroyed the percept of moving phosphenes in the normal subjects studied by Pascual-Leone and Walsh.

Timing of interactions across visual areas

The importance thus given to feedback connections for conscious vision is reminiscent of the arguments presented by Lamme and Roelfsema, who propose that conscious vision is subserved by a wave of...
takes some 10–20 ms to generate activity in a neuronal population5,8 and that feedback connections are very rapidly conducting13, the optimal inter-pulse delay reported by Pascual-Leone and Walsh is just what would be expected if the pulse in V1 disrupted the wave of feedback activation generated by the TMS pulse in V5/MT (Fig. 1b).

**Areas V1 and V2 act as active blackboards**

TMS, like electrical stimulation, is a highly artificial way of simultaneously activating large populations of neurons. The models illustrated in Fig. 1 merely correspond to artificial activation of two nodes of a vast network that subserves conscious vision. One should therefore understand how the mechanisms demonstrated by TMS experiments apply during the normal mode of visual function. In normal vision, at the completion of a saccade, neural activity starts first in area V1 and a small number of other cortical areas9–14. We demonstrated earlier that this early wave of activation is mainly driven by the magnocellular (M) cells of the lateral geniculate nucleus and reaches V1 some 20 ms earlier than activity relayed by the parvocellular (P) neurons15,16. This suggests that the first wave of M activity conveys a first-pass analysis of the visual scene and that the results of computation done in higher-order areas are rapidly retroinjected into lower-order areas in time for the arrival of the P wave of activity17. Combination of the early feedback activation and the feedforward input from parvocellular neurons may be essential for the proper processing of information by other cortical areas of the hierarchy. TMS activation of area V5/MT might thus be affecting this early wave of feedback activation.

Why is retroinjection through feedback connections necessary for conscious vision? I suggest that areas V1 and V2, instead of simply transmitting information, might act as ‘active blackboards’18 that integrate the results of computations performed in higher order areas, at least for the early stages of processing. This is an efficient way to solve the problem of computations that involve interactions between features that are not present in neighbouring neurons in any one cortical area (the so-called ‘binding problem’). Perception of a moving phosphene by TMS stimulation of V5/MT would therefore result from the activation of the ‘blackboards’ by an ordered spatio-temporal distribution of activity transferred to V1/V2 through feedback connections from area V5/MT.

**References**


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