Supplementary information S1

Box S1 | Strengths of the structural model

In 1991, Felleman and Van Essen proposed a hierarchical model of feedforward, lateral, and feedback connectivity between cortical regions based on visual cortex anatomy [1]. They classified each connection on the basis of termination site: feedforward connections were thought to terminate in mid layers (preferentially layer IV) of less differentiated visual regions (moving sequentially from primary visual cortex towards the front of the brain), whereas feedback connections were thought to predominantly avoid layer IV, terminating mostly in superficial layers of more differentiated visual regions (moving sequentially from the front of the brain towards primary visual cortex). Although the Felleman and Van Essen model is still widely used, the visual system is not an ideal prototype for building a general model of corticocortical communication because large swaths of cortex (e.g., frontal, temporal, and parietal association cortices) do not have a strict, linear posterior to anterior lamination gradient (cf. [2]). Even the visual system contains many violations of Felleman and Van Essen's hierarchy [3].

In contrast, Barbas and colleagues' structural model for corticocortical connections, which was developed analyzing patterns of connection within the prefrontal and temporal cortices of the macaque brain [4, 5], does not suffer from these problems. Importantly, the structural model not only predicts the flow of information between prefrontal and temporal cortices [6, 7] and between prefrontal and parietal areas of the macaque brain [8], but it also predicts patterns of connections in visual cortices of the cat [9].

The structural model better describes the flow of predictions and prediction errors across cortical areas that do not show a anterior–posterior lamination gradient in the macaque brain, which other models cannot account for [10]. Most hierarchical models of the cortex are predicated on some form a distance rule, where there is a linear relation between the distance between two areas and the percentage of cells that send projections to deep layers (if feedback connections) or to superficial layers (if feedforward connections) [11, p. 697]. For example, the distance rule model proposed by Kennedy and colleagues [12-14] was developed analyzing patterns of connection in visual areas of the monkey brain and works well for describing information flow in visual cortex because there is a relatively linear posterior to anterior laminar gradient: V1, the cortical area with the highest laminar differentiation, is located at the occipital pole and moving anteriorly visual cortex becomes increasingly less granular and more dysgranular. Therefore, in the occipital lobe, laminar differentiation and distance go in parallel. But laminar differentiation and distance do not go in parallel in the rest of the brain [15]. For example, in a recent paper on the distance rule model, Markov et al. excluded the prefrontal cortex from their analyses because the data did not fit their model. In a footnote to Table 6 in their paper, they stated "The prefrontal areas were excluded from the source and target list due to their tendency to overrun the distance and hierarchy rules" (pg. 243) [14]. The distance rule model may not be equally applicable to the entire cerebral cortex, while the structural model, by contrast, has successfully predicted patterns of connections independently of distances in frontal, temporal parietal and occipital cortices [6-9].

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